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# HANDBOOK OF ZOOLOGY

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

## ANNELIDA

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

## BASAL GROUPS AND PLEISTOANNELIDA, SEDENTARIA I

VOLUME 1

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**Handbook of Zoology**
Annelida

Volume 1:
Annelida Basal Groups and Pleistoannelida, Sedentaria I

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# Handbook of Zoology

Founded by Willy Kükenthal
continued by M. Beier, M. S. Fischer, J.-G. Helmcke, D. Starck, H. Wermuth
Editor-in-chief Andreas Schmidt-Rhaesa

## Annelida

Edited by Günter Purschke, Markus Böggemann
and Wilfried Westheide

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# Preface

Annelida, the segmented worms, comprise one of the most important taxa of invertebrates. The majority of annelid species occur in the marine environment, but they can be found also in fresh water and terrestrial realms. Especially the marine forms, also known as polychaetes, are one of the most widespread, abundant, and diverse elements of the world benthic fauna. Here, they are present from the upper intertidal down to the deep sea and constitute important members of the respective food chains. In contrast, the mainly terrestrial forms or clitellate oligochaetes are structurally more uniform but nevertheless comparatively speciose and important members in terrestrial decomposer communities. Surprisingly enough, one group of these oligochaetes is closely related to parasitic or carnivorous forms, the leeches.

Although at large comprising somewhat only 21,000 described species, annelids show a remarkable diversity comparable, for instance, with that observed in crustaceans. This diversity could be achieved only by the plasticity of their bauplan constituting prostomium, followed by a number of primarily identical modules, the segments, 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 of the smallest adult metazoans known belong to this group with body dimensions of less than 0.2 µm – the dwarf male of *Dinophilus* – as well as species exceeding body lengths of more than 3 m, such as *Eunice aphroditois*. The number of segments varies accordingly from less than ten to several hundreds. The marine forms often show broadcast spawning, and primarily, their life cycle comprises a planktonic larva, the trochophore, and a benthic adult. However, there are lots of deviations from this pattern, which inter alia are correlated with life style and body size.

The Annelid volume of the first edition of the *Handbook of Zoology* appeared in the years between 1928 and 1934, edited by W. Kükenthal and T. Krumbach. Especially the anatomical part still serves as a valuable resource of knowledge. However, since then, our knowledge has increased broadly. Although several reviews on annelids have been published, they usually cover only special topics in this group of invertebrates. So around the year 2010, the idea was born that a new edition of this very successful work would be urgently needed. Even more than in former times, today, such a task could not be achieved by a single person or just by a few authorities, and so we began looking for authors who could contribute to such a big effort. Very soon, we had to learn that for many annelid groups, specialists did not exist in the scientific zoological community or were not available for various reasons. Therefore, it took much longer than originally planned to compile the manuscripts, and in spite of our efforts, there will remain a few gaps of missing chapters. Since all authors have lots of other duties and writing of handbook chapters is rather time-consuming, it took some time to compile the manuscripts from our authors. It was a great advantage that each chapter ready for publication was published electronically in Zoology Online so that the chapters were available for the scientific community quite soon after acceptance. All contributions were peer reviewed and revised prior to publication. For these reasons, and very sadly, the important taxon Clitellata could not be included in the *Handbook of Zoology*. We still hope that it will be possible to supplement this sometime in the future.

This book is the first out of four volumes in the *Handbook of Zoology* series treating the morphology, anatomy, reproduction, development, ecology, phylogeny, and systematics of polychaetes. Polychaetes are seen here as those annelids that do not possess a clitellum. As written above, they comprise one of the most important groups of invertebrates in the marine food web, where they can be found in almost every habitat, often in high abundances. Generally, polychaetes are dominant members of the epi- and endobenthos, but there are also a few holopelagic species. However, a few species managed to colonize even freshwater and terrestrial realms. Moreover, polychaetes may occur in comparatively extreme environments from hydrothermal vents at the ocean floor spreading centers to the terrestrial ground water.

Recent phylogenetic analyses have confirmed that polychaetes constitute nothing else but a paraphyletic assemblage of the more or less plesiomorphic Annelida. Besides a so-called basal radiation, the majority of Annelida, now termed Pleistoannelida, fall into two large monophyletic taxa, Errantia and Sedentaria. In a highly derived position, the latter also comprise Clitellata, the earthworms and leeches. In addition, some taxa that in the past were regarded to represent separate phyla turned out to be nothing else but true Annelida, although being morphologically highly derived especially with respect to one so-called key character, segmentation. These taxa are Sipuncula, Myzostoma, Pogonophora, and Echiura, which are now placed in different positions in the phylogenetic tree of Annelida. This fact impressively demonstrates the adaptive capacity and potential of the annelid bauplan.

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This first volume covers members of the so-called basal radiation and the first part of Sedentaria. The chapters are mostly organized treating the families; their arrangement follows the most recent phylogenetic hypotheses. This first volume is supplemented by chapters on the history of annelid research, their fossil record, and an introduction to the phylogeny of annelids and their position in the tree of life. The second volume will be devoted to the remaining Sedentaria, with the exception of Clitellata, and the third volume will treat the Errantia.

All authors that have contributed to the *Handbook of Zoology* have done an excellent job, and we want to thank them sincerely. We also thank the various reviewers of the sometimes voluminous chapters for their helpful suggestions for improvements, helping to keep the scientific standard as high as possible. Last but not the least, the help of the lectors and employees of our publisher DeGruyter is gratefully acknowledged for their endless help during the publishing process.

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# Part 1: **Introduction**

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Geoffrey B. Read

# 1 A History of Annelida Research

## 1.1 Introduction

> Now turn to the annelids! What do they lack when compared with the most splendid inhabitants of earth or air? Yet they shun the light, they withdraw themselves from our view, but with no design to attract; and the naturalist alone knows where to seek the strange wonders, which are hidden within the recesses of the rock and beneath the sandy beds of the ocean. (Armand de Quatrefages 1857)

> The Annelids, as a class, are animals of very obscure habits, living principally under stones, in mud, or, as the common earth worm and its congeners, in garden and other soil. Their forms and appearances are, generally speaking, not very attractive, except to the enthusiastic naturalist, who is determined on investigating the various forms of life. (Edward Parfitt 1867)

Annelids have indeed been of interest to many enthusiastic investigators over hundreds of years, despite their usual retiring nature as suggested by Quatrefages and Parfitt, because annelids are an integral and diverse part of many aquatic and terrestrial environments. They can be plain in shape, but many are intricately structured, and we can endorse Parfitt's further comment that terebellid polychaetes "when seen alive in a glass of sea water...are some of the most elegant creatures inhabiting the great deep." Today, more than at any previous time, larger numbers of researchers are believed to be studying some aspect of annelid biology, with "annelid" mentioned in the title of over 220 research articles published in 2017.

A historical review of a more inclusive Annelida, containing former phyla Echiura, Sipuncula, Pogonophora, and Vestimentifera, as established by phylogenetic analysis of molecular and morphological data, has enough scope to be worthy of a book. This is a first attempt at the topic in article length and only selectively covers some of the history of interest to annelid workers. General histories of annelid research include Quatrefages (1866b: 154–173), Ashworth (1912: 1–25), and Fauchald and Rouse (1997: 73–76 and appendices). Later, for polychaetes, there are succinct summaries of the topic by Hutchings and Glasby (2000: 3,7) and Rouse and Pleijel (2001: 1), with both works also including group-specific histories. The history of myzostome worm research is separately covered by Grygier (2000). Next, for sipunculans and echiurans, Stephen and Edmonds (1972) have some history information, as does Cutler (1994) for sipunculans. Ivanov (1963: 3–6) has a historical review for the former phylum Pogonophora (now Siboglinidae), with Rouse (2001) covering the history since Ivanov's monograph, and for oligochaetes, there are contributions by Vejdovsky (1884: 12–14), Reynolds and Cook (1976: 1–4), Brinkhurst (1999), and Rota (2011). Also, for biogeographic history, Stephenson's (1930) oligochaete monograph (Chapter 18) covers some of the early tendency to invoke land bridges preplate tectonics to explain "palaeogeographical problems" with terrestrial worms. There is less analysis of research history available for the leeches, but see Moquin-Tandon (1846: 7–17).

This chapter is focused on a general history of studies on the taxonomy, classification, and biology of Annelida, particularly in relation to technological change. There is an emphasis toward taxonomy, early history, and the traditional polychaete groups. Time and space did not permit inclusion of more world and regionally significant monographies, of major early species-level biology studies, and more on the history of traditional non-polychaetes and clitellates especially, but also the echiurans and sipunculans. Elsewhere in the handbook, in the other general chapters, there are in-depth reviews of annelid phylogeny, and fossil record, as well as chapters by specialists on each taxon group, with more on morphology, reproduction, development, biogeography, phylogeny, plus taxonomic histories. The history of research on fossil annelids is not covered here, as this topic is dealt with in a separate chapter on annelid fossils (see Parry, Eriksson, and Vinther).

The science and the understanding of Annelida began with names created to label and communicate about what was in the environment. Ever since Aristotle, the use of taxonomy for recording and extending knowledge has been important, and it still is. In the 2017 calendar year, there were 155 new species of polychaetes published, and currently, 21,126 species have been described, of which 56% or 11,758 names are valid (Read and Fauchald 2018), with in one estimate, over 6,000 further polychaetes remain undescribed, and a possible upper range of more than twice that number of undescribed oligochaetes may exist (Appeltans *et al.* 2012), based on a likelihood of many cryptic species in that group (e.g., Taheri *et al.* 2018).

## 1.2 In the beginning – annelids and humans

> One does not see these worms all year round, but only on the 2nd, 3rd, and 4th night after a full moon, which takes place

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> when the sun is in Pisces, in February and March; one should look for them at that time after the sun has set by the light of torches... (Rumphius 1705, Beekman (1999) translation)

> ...they are on every bush and tree, from which they frequently drop on the head and neck of the passer-by, while they always creep up his legs; nay, they can even spring to reach their victim. (Haeckel 1883, on land-leeches)

For thousands of years, each generation of humans must have been aware of the variety of annelids in their environment. Annelid worms are easily visible to the unaided eye, unlike many invertebrates. In warmer, wetter places, unwelcome blood-seeking leeches would have intruded on passers-by and would have been as much a nuisance to early humans as they were to Haeckel in Sri Lanka, whereas in more benign encounters, worms would have been seen whenever hunger or human curiosity led to fossicking for hidden life on the shore, in forest plant-litter, and in diggings. Annelids are welcome food for many animals, but skilled early human gatherers might have preferred tastier, more inviting items to consume, except when starving at times of famine, so it is hard to know what extent of folk knowledge about annelid ecology, habits, and uses was linked to local names for them and passed on to the next generation. There were likely earlier uses in folk medicine preceding those recorded in CE 50–70 by Greek physician Pedanius Dioscorides (*fide* Ashworth 1912). Earthworms, as easily collected, obvious, and harmless, continued to be used as medicinal ingredients through to the 1700s in Europe (Rota 2011) and into the twentieth century in China, Japan, and Burma (Stephenson 1930: Chapter 17). Collection for fish bait was probably common in many prehistoric cultures and is still popular and widely commercialized today (Watson *et al*. 2017). New Zealand postcontact Maori still both ate earthworms and used them as bait (Benham 1904, Miller 1952), with one bioluminescent species said to be used as a lure (Springett *et al*. 1998). Blakemore (2009) reviews work done on the likely translocation of earthworms as humans migrated in the neolithic, carrying soil with their crop plants, possibly important in relation to island or trans-oceanic colonization, and states that 120 (of about 6000) earthworm species have become widely distributed in association with humans.

Consumption of great quantities of marine annelids, spawning ripe and packed with nutritious gametes, occurred in the western Pacific islands and Indonesia, where there is a tradition of collecting and eating worms named "Palolo" (also "Wawo"; local names vary), which are mass-swarming reproductive morphs, mostly of Eunicidae, but also Nereididae. In other places, this harvesting also involved a degree of predicting the times when the Palolo/Wawo swarms will appear based on past observations (Rumphius 1705, as translated in Beekman and Rumpf 1999, Stair 1897, Burrows 1955; Herdrich and Armstrong 2008). Rumphius also gives recipes for cooking Wawo. Echiurans (*Urechis* spp.) are now eaten in Japan and adjacent countries, but whether this is a traditional food rather than for gourmet adventures is uncertain. Swarming Japanese nereidid worms may also have been eaten in the past (so-called Japanese palolo).

In general, annelids, apart from leeches and amphinomid marine fireworms, are harmless, indeed beneficial to human interests (e.g., soil-conditioning by earthworms). Leeches also had a supposed useful role in medicine, with vast numbers once harvested, but it is doubtful if blood-letting through application of hungry leeches was often beneficial, although the practice continued for at least 2000 years (Brookes 1763: 295, Johnson 1816), and still does; leeches have a useful minor role in medical practice today for increasing blood flow and in pharmacology as a source of bioactive compounds (Siddall *et al*. 2007). Today, marine annelids as a commercial product are used for aquaculture food, for waste processing, as well as for fish bait, while freshwater annelids are also used to process sewage sludge (*Lumbriculus* and other genera) and grown as aquarium fish food (*Tubifex*). *Eisenia* "tiger" earthworms are present almost everywhere humans have settlements and are used to process organic waste, both industrially and domestically (vermicomposting). As mentioned, *Hirudo* leeches are cultured for biomedical research. In the recent past, there was a market for earthworms, lugworms, nereidids, and serpulids for educational dissection and as robust animals for respiration and fertilization experiments (Moore 2012).

## 1.3 The written record

> From the time of Pliny onwards for more than a thousand years little real advance was made in regard to the knowledge of worms. (Ashworth 1912)

> These works are still occasionally consulted, though they afford little useful information, and might without any loss to science be consigned to oblivion. (MacGillivray 1834)

The written record of annelid observation begins in the Mediterranean with Aristotle (384–322 BCE[1]) and Pliny (CE

**1** Calendar-year epoch abbreviations BCE "before common era" and CE "common era" are used here as neutral terms for indicating the year count of before and following CE year 1 of historic convenience, with BCE placed *after* the date and CE placed *before* the date.

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23–79) (Tab. 1.1). Aristotle reported his own marine discoveries, often very accurately from what we know today, and is much the more reliable of the two. In contrast, Pliny's biota information includes a mixture of secondhand fables, and he was less scientific and more credulous. Pliny's *Historia Naturalis* is a wide-ranging encyclopedia of all knowledge, which is mainly why it was so influential for over 1,500 years and is still analyzed today – this is not so much because part of it concerned "natural history" as we use the term now. However, as eventually published in typeset print for the first time (Pliny 1469), it is said to be the first "printed" natural history book. It may not be widely known that there were no biota illustrations in the original scrolls, nor in the many later medieval copies and derivative extracts, nor in the printed complete editions of Pliny in the fifteenth century, although these were "illuminated" (with elaborate color paintings for enlarged first letters of chapters). This lack did not deter Cuvier from suggesting in 1827 identifications for the *Historia Naturalis* animals (comments repeated as footnotes in Bostock and Riley 1855: vol. 2, 117, etc.).

Aristotle has the earliest recorded observation of Mediterranean Sea sea-scolopendra (sea 'centipedes') as transcribed in the following.

> The so-called "sea-scolopendra," after swallowing the hook, turns itself inside out [proboscis everts?] until it ejects it, and then it again turns itself outside in. The sea-scolopendra...will come to a savoury bait; the creature does not bite with its teeth, but stings by contact with its entire body... (Aristotle ~335 BCE, in English translation by Thompson 1910: 621a)

That account fits an amphinomid fireworm. It is interesting to compare the subsequent Pliny version of the observation, in which the event has become more cataclysmic for the worm but is clearly derivative from Aristotle.

> The scolopendra...if it chances to swallow a hook, will vomit forth all its intestines, until it has disengaged itself, after which it will suck them in again. (Pliny CE ~78, in English translation by Bostock and Riley 1855: vol. 2 Chapter 67, p. 453)

Carrion-feeding amphinomids are known to swim to bait and to swallow baited hooks (Glasby and Bailey-Brock 2001). According to those authors "this bait-taking behaviour appears not to have been previously documented...," but it seems likely Aristotle did that over 2000 years earlier.

Ashworth (1912) has an excellent review of many of the early works mentioning annelids and of how successive authors built on from their predecessors or simply repeated previous content (a common failing according to historians of this period of natural history). The authors and names are summarized here (Tab. 1.1). These were convenient Latin descriptive names for referring to various kinds of worms, but sometimes, we can guess what species they might have been. Rondelet is the most reliable of these authors.

The higher classification was still in flux before Linnaeus (and after), and a lot of small biota were "insects" (e.g., annelids as *insectis marinus* in Gessner). Ashworth points out that, following Aldrovandus' (1602) book on "insects" ("classifying" by *aquatica/terrestria* and by *pedata/apoda* so that terrestrial *lumbricus* was far divorced from aquatic *lumbricus*), for a period, several writers, oddly from our evolutionary viewpoint now, split annelids between a very-inclusive "insects" group (which included some marine worms) and a more terrestrial *vermes* group, which included parasitic worms, leeches, and earthworms. However, it should be obvious that these strange early "classifications" are for tracking groupings that are strictly practical (aquatic/land, legs/no legs, etc.) rather than being intended as relationship groupings. Later, Linnaeus (1758) had the second group in his *Vermes Intestina*, with *Nereis* in *Vermes Mollusca*, with *Scolopendra marina* now a synonym in *Nereis*, and with *Serpula* in *Vermes Testacea* (shelled organisms, including today's molluscs). This was still puzzling to Shaw by 1802, who got partly in line with today's usage with the comment: "The genus *Serpula* is inhabited by a very different race of animals from the rest of the testaceous tribe, and which seem to bear some analogy to the Amphitritae and Nereides among the Mollusca, and to the Scolopendrae among Insects." ("naturalist's miscellany", Shaw and Nodder 1789–1813, vol. 14 of 1802: 177)

## 1.4 Linnaeus and the first annelid genera – the dawn of available names

Although some ancient names are still in use, the original descriptions and usages of all names prior to the 10th edition of Linnaeus, a work assigned the date of 1 January 1758, are excluded from nomenclatorial priority (ICZN 1999). It is important to realize that Linnaeus adopted previous names or newly created his names in relation to name usages by others, cited by him in short synonymies, and for animals he had not seen. The second Strickland Code ended the priority of all names earlier than Linnaeus, including the ancient ones. The authors (Strickland 1878) caustically commented "The nomenclature of [John]

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**Tab. 1.1:** Some early works and name usages on annelids, up to the 10th edition of Linnaeus, adapted and extended from Ashworth (1912).

| Author | Date | Taxa names | Title | Figures/of worms | Country/area/occupation |
|---|---|---|---|---|---|
| Aristotle (Aristoteles) | ~335 BCE | *scolopendra marina* | *Historia Animalium* | No/no | Greece/Athens/teacher |
| Pliny the Elder (Gaius Plinius Secundus) | CE 78 | *scolopendrae, hirudo, lumbricus, sanguisuga* (leech) | *Historia Naturalis* | No/no | Italy/Naples/soldier-scholar |
| Claudius Aelianus (Aelian) | ~220 | *scolopendrae* | *De Natura Animalium* | No/no | Italy/Rome/teacher |
| Isidore (Isodorus) of Seville[1] | ~600 | *sanguisuga, lumbricus* (=a parasitic worm) | *Etymologiae Book XII De Animalibus* | No/no | Spain/Seville/bishop |
| Jacob van Maerlant | ~1266 | *sanguisuga, vermis* (=earthworm) | *Der Naturen Bloeme* (in Dutch rhyme, not Latin) | Yes/yes | Netherlands/Utrecht or Flanders/scholar-poet |
| Pierre Belon (Petrii Belonii) | 1553 | *lumbricus marinus* (=first lugworm), *eruca marina* (=indet. marine "caterpillar") | *De Aquatilibus* | Yes/no | France/Paris/physician |
| Guillaume Rondelet (Rondeletius) | 1555 | *scolopendrae marinae, hirudo, vermis macrorinchoteros, v. microrinchoteros* (=sipunculids), *penicillo marino* (=marine "paint-brush" = first sabellid), *physsalo* (=aphroditiform), *vermibus in tubulis* (=serpulids) | *Libri de Piscibus Marinis…* | Yes/yes (Rondelet worm figures much copied) | France/Montpellier/ physician-teacher |
| Conrad Gessner[2] (Conradi Gesneri) | 1558 | *Hirudo/sanguisuga*, *eruca marina* (=Rondelet's aphroditiform. Figures copies other Rondelet marine annelids) | *Historiae Animalium* (also as *Icones Animalium*) | Yes/yes | Switzerland/Zurich/ physician-teacher |
| Adriaen Coenen | 1578 | (Figures copy Rondelet) *scolopendra marina*, *lumbricus marinus, vermis in tubulis, vermis* spp, *eruca marina, hirudo marina* | *Visboeck* (in Dutch) | Yes/yes | the Netherlands/ Scheveningen/ fisherman-merchant |
| Ulysses Aldrovandi/o[3] (Ulisse Aldrovandus) | 1602 | *lumbricus terrestris, l. marinus, scolopendra marina, vermes in tubulis* (serpulids), *hirudo paludosa, h. marina, vermis* spp (figures after Rondelet) | *De Animalibus Insectis libri septem* | Yes/yes | Italy/Bologne/ teacher-naturalist |
| Thomas Willis | 1672 | *lumbricus terrestris* anatomy | *De Anima Brutorum* | No/no | England/Oxford and London/ physician-anatomist |
| Francesco Redi | 1684 | *lumbricus terrestris* (as not a helminth), *scolopendra marina* (nereidid), *hystrix marina* (marine "porcupine" = Aphrodita) | *De Animalculis Vivis…* | Yes/yes | Italy/Florence/physician-biologist |
| John Ray[4] (Joanne Raio) | 1710 | *lumbricus terrestris*, *hirudo*, lugs, *scolopendra marina* | *Historia Insectorum* | No/no | England/Essex/parson-naturalist |
| Frederik Ruysch (Fredericii Ruischii) | 1710, 1725 | *eruca marina* (marine "caterpillar" =Aphrodita) | *Thesaurus Animalium primus…* | Yes/no | the Netherlands/Amsterdam/ physician-botanist-collector |
| Hans Sloane | 1725 | *teredo or scolopendra maxima* (perhaps *Amphinome rostrata*) | *A voyage to the islands… Jamaica* | Yes/yes | Britain/London/physician-naturalist |
| Albertus Seba | 1734 v1 1758 v3 | *eruca marina* (=Aphrodita), *millepeda marina* (amphinomid), *penicillum marinum* (here a serpulid, not sabellid) | *Locupletissimi Rerum Naturalium Thesauri…* | Yes/yes | Netherlands/Amsterdam/ pharmacist-collector |
| Carl Linnaeus | 1735 | *Lumbricus, Hirudo, Scolopendra marina* | *Systema Naturae* (1st) | No/no | Sweden and the Netherlands/ Leiden/biologist-teacher |

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**Tab. 1.1:** (continued)

| Author | Date | Taxa names | Title | Figures/of worms | Country/area/occupation |
|---|---|---|---|---|---|
| Carl Linnaeus | 1748 | *Lumbricus, Hirudo, Amphitrite, Nereis, Aphrodita* | *Systema Naturae* (6th) | No/no | Sweden/Stockholm/ biologist-teacher |
| Carl Linnaeus | 1758 | *Lumbricus terrestris, L. marinus* (lugworm), *Hirudo, Aphrodita*, *Nereis, Serpula* (total >40 species) | *Systema Naturae* (10th) | No/no | Sweden/Stockholm/ biologist-teacher |

These early titles are well known, mostly encyclopedic, and not included in the references list unless cited in the text. Early biota names in Latin are not capitalized to avoid confusion with post-1735 Linnaean Latin binominals.

[1] The *Etymologiae* of Isidore (c. 560–636), scholar and archbishop of Seville, is a compendium that Isidore gleaned from other sources and was much copied and later printed in many editions, and the text was used in medieval bestiaries. However, annelids barely register; under a subheading of "*De Vermibus,*" Isidore briefly characterizes a *sanguisuga* as a leech, but the *lumbricus* mentioned seems to be intestinal, not a terrestrial annelid. *Lumbricus* was simply the Latin for either an intestinal worm or earthworm; likewise, *sanguisuga* was a leech.

[2] The *Historiae Animalium* of Gessner (1516–1565) is a vast compendium of over 3,500 folio pages in four volumes, with editions in Latin and in German, and a pioneer in zoology publishing for the copious illustrations, also printed separately as *Icones Animalium* (1560) with marine annelids grouped in *insectis marinis,* and with the whole work produced in color in just a few copies (Kusukawa 2010). Gessner freely acknowledged the sources he copied from, notably citing Rondelet for marine annelids – an admirable practice but perhaps also intended to add authority.

[3] The *De Animalibus Insectis* of Aldrovandi (1522–1605) is another compendium, notable for an early example of a bifurcating "classification" diagram at the beginning, which includes his worms. The diagram appears intended as a key for identification rather than for showing hierarchical relationships, but there is no caption. Aldrovandi met Rondelet when both were in Rome and was then inspired by his example to take up natural history. In his other works, there are splendid copperplates, but the in-text worm figures in this work appear to be mostly adaptations from Rondelet, and amusingly, Aldrovandi's artist has added little faces with eyes to Rondelet's realistic sipunculans.

[4] Parson-naturalist John Ray (1628–1705) has a preliminary layout following the worm arrangement of Aldrovandi so that his earthworms were in "Apoda" but "lugs" (text Latin, but a few words are written in English) = lugworms(?) were in "Polypoda aquatica." Again, the layout is for practical identification rather than for indication of relatedness. His name was commemorated some 60 years later in the founding of The Ray Society in 1844 by George Johnston (1797–1855). Johnston was a marine naturalist who published (posthumously) the significant British Museum book (Johnston 1865) *A Catalogue of the British Non-Parasitical Worms*. A later John Ray connection with annelids is that the Society subsequently published McIntosh's British Annelids monographs.

Ray [1627–1705] is chiefly derived from that of Gesner [1516–565] and Aldrovandus [1522–1605], and from these authors we might proceed backward to...Pliny, and Aristotle, till our zoological studies would be frittered away amid the refinements of classical learning." However, this is an exaggeration; in the case of most early annelid names, there is not much of a problem, as the Latin words applied were in everyday use (*eruca*, *hirudo*, *lumbricus*, *scolopendra*, *vermis*), may even have been used in Greek earlier *(skolopendra*), and may be simply descriptive (*penicillus*, *sanguisuga*, *lumbricus marinus*, *scolopendra marina*). Greek *skolopendra* was the name for multipeds, land or marine, but Greek *skolekos* was a worm, with the Latinized combining-form "scoleco" later giving us a variety of still-used genus names, notably *Scolecolepides* and variant names in Spionidae, and the higher rank names Scoleciformia in Benham (1896) and Scolecida in Rouse and Fauchald (1997). Also, fossilized scolecodonts, which are annelid jaw elements, especially of Eunicida, are the most common form in which annelids occur in the fossil record (see fossils chapter).

Linnaeus combined the two early Latin leech names for his *Hirudo sanguisuga* (now *Haemopsis*). It is more difficult to resolve the new names created by contemporaries of Linnaeus just prior to 1758. No one has compiled them (except perhaps McIntosh (q.v.) as dispersed in his monograph synonymies), but Knight-Jones and Perkins (1998) show how, based on the good figure in Ellis (1755: plate 34), the *corallina tubularia melitensis* of Ellis became named *Serpula penicillus* Linnaeus, 1758 and now corresponds to the well-known *Sabella spallanzanii* (Gmelin 1791). The striking figure of a *penicillo marino* printed much earlier in Rondelet (1555: 111) is probably this species also (Fig. 1.1 A, B, and see later for history of illustrations).

The Linnaeus 10th edition (1758), as the start of nomenclature, established polychaete genera *Aphrodita*, *Nereis*, and *Serpula* (which included names later moved into *Sabella* and into phylum Mollusca [vermetids

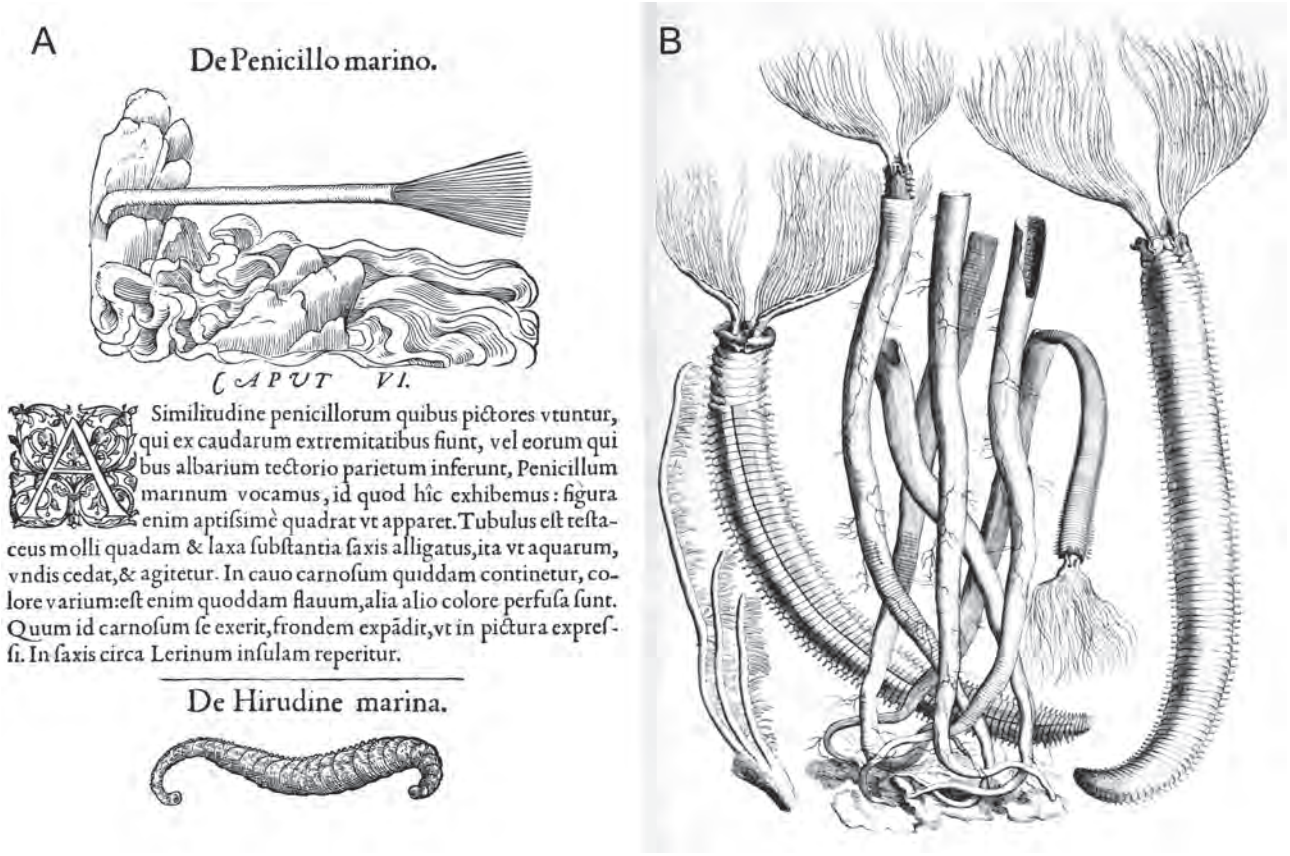


**Fig. 1.1:** Early representations of *Sabella spallanzanii* from the Mediterranean Sea in Rondelet (1555) and Ellis (1755). A, Rondelet penicillo marino figure and description (with a marine leech below), collected from Lérins Islands near Cannes (immersed tubes can be remarkably straight as in the Rondelet miniature). B, Ellis plate 34, corallina tubularia melitensis from Malta (=Melita) (Ellis's specimens were not alive when examined; the description is clearly of *S. spallanzanii*). Scale: an adult *S. spallanzanii* is more than 300 mm in body length. Originals at https://biodiversitylibrary.org/page/41733271 and https://biodiversitylibrary.org/page/10676353

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and pholads]), oligochaete genus *Lumbricus*, and leech genus *Hirudo*. Later, in the 12th edition (1767), *Sabella*, *Terebella*, and *Sipunculus* were added. No new annelid genera appeared in the 13th edition in 1791, but *Amphitrite* Müller, 1771 appears again there, after a long gap following a dubious listing in the Linnaeus 6th edition (1748). The *Systema naturae* appears not to have been popularized in English until Turton (Linné and Turton 1806) translated the 13th edition (edition inferred from Turton's inclusion of Gmelin on the title page), but by then, it had long been an influential work among scientists. The *Systema naturae* had no illustrations, but (as in the *Sabella* case) sometimes, illustrations can be found in the works Linnaeus cited.

As mentioned, ancient *scolopendra* was long also used for centipede-like marine annelids as well as for multiped land arthropods, starting from before Aristotle, and mostly, those illustrated seem to have been large amphinomids. The grey *Teredo* (a mistaken name usage) or *Scolopendra maxima* worm found with ship-worm-bored driftwood by Sloane (1725: v. 2 plate 234) might have been an *Amphinome rostrata* (Pallas, 1766). Likewise, the Indonesian marine "millipede" "*millepeda marina*, *amboinensis*" of Seba (1734) was suggested to have been a *Hermodice*. Seba's plate (Fig. 1.2) is of an amphinomid, identity uncertain. The Linnaeus *Systema* first edition (1735) still included a dubious *S. marina*, but ultimately, the genus *Scolopendra* was lost to the Arthropoda: Myriapoda: Chilopoda, which are indeed the centipedes, and genus *Nereis* soon replaced it for a while as a parking lot for a diversity of errant and sedentary marine worms (e.g., *Nereis norvegica*, Linnaeus, 1767, a *Eunice*).

The year after the 10th *Systema* was published, the Royal Society *Transactions* printed an article by Jean André Peyssonnel (1759), as "Observations upon the Sea Scolopendre or Sea Millepes," in which Peyssonnel described the external features and the action of the pharynx of what Ashworth placed as a nereidiform

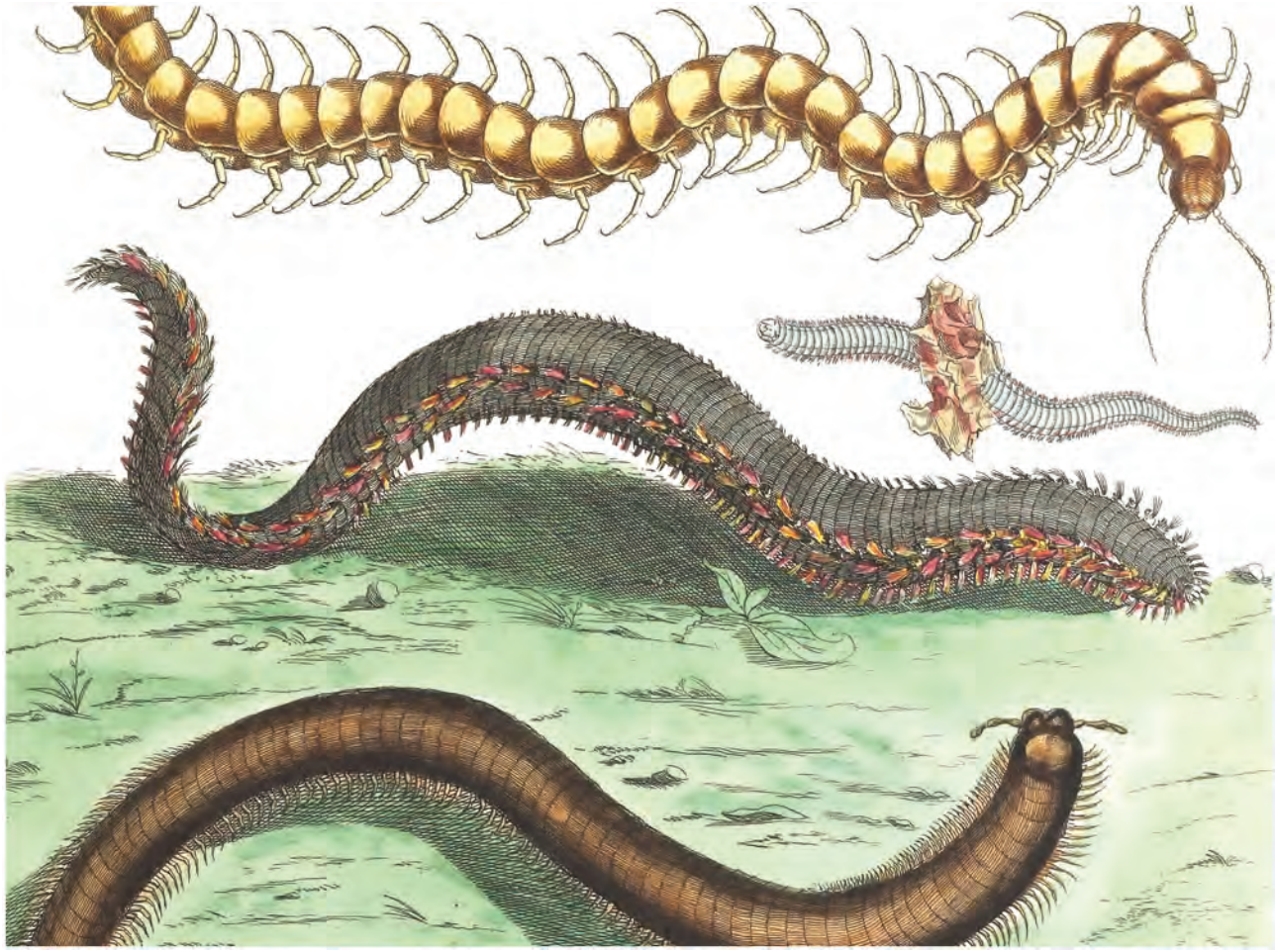

**Fig. 1.2:** Albertus Seba (1734) unidentifiable amphinomid (as millepeda marina) from Amboina, figure from plate 81, sandwiched between two terrestrial multipedes. No scale. Original at https://biodiversitylibrary.org/page/41047664

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worm, but Thompson (1910: 621a) doubted it was a *Nereis*. The description, especially of the prickles penetrating Peyssonnel's fingers, indicates this scolopendre (probably from Guadeloupe), although an elongate "nereidiform" worm was again (as in Aristotle) likely to be a large amphinomid like a *Eurythoe*, *Hermodice*, or *Amphinome*. He wrote: "it was like fire upon the part. It was in vain that I rubbed and washed the part; and tho' the prickles were broken, yet the parts that stuck in the flesh, produced their effect, and caused the pain I felt for some hours."

Finally, it is worth mentioning because of some surrounding taxonomic confusion that Slabber (1781), in a strange late usage, applied the name *S. marina* to two very different forms of marine worms, looking nothing like the *Scolopendra* concept. The first was to a *Polydora*-like spionid that he stated to be closer to *Nereis*, also by Linnaeus, than to *Scolopendra* (Slabber 1781: 25–29, plate VII, Figs. 1–2), and the second was to an indeterminable autolytine syllid (Slabber 1781: 44–46, plate X, Figs. 3–5). These could not be either the same species or an amphinomid-like *Scolopendra*.

## 1.5 Discoveries and major changes in understanding in Annelida

Interesting changes in the perception of annelid taxa at various levels, began early in the nineteenth century at the top level with the name annelid itself. Jean-Baptiste Lamarck (1802), in his annual major speech at the Paris museum, addressed the assembled *citoyens* of the French Republic to introduce and define "Annelides" (no é accent initially) as the French name of an additional new main "classe" of the animal kingdom, slotting between molluscs and crustaceans and separate from another "vers" group. Mammals were the top group in Lamarck's table, with the groups following in his table supposedly showing a "degradation" of specialized organs. His further representation of groups within the Annelides did not solidify until Lamarck (1818: 286), where he separated Annelides antennées, Annelides sédentaires, and Annelides apodes (echiurans and leeches) within his classe Annelides.

As an alternative to Annelides, Blainville (1816) introduced the French Sétipodes in a formal classification layout, later morphing it to Chétopodes in his *Dictionnaire* entries, and eventually, it was Latinized as Chaetopoda. Fischer von Waldheim (1808) appears to be the first to use "Annulata" for the group when, in a classification summary, he used the informal French Annélides (with é accent) matched with formal Annulata, a name he attributes to Cuvier. Later, Örsted (1842), then notably Grube (1850), used and kept using Annulata as the formal name for Annélides, a practice followed subsequently by a few, notably Kinberg and Malmgren. Grube (1850) also introduced Polychaeta and Oligochaeta for the first time, while finally, Hatschek (1893) Latinized Annélides as class Annelida, which included as subclasses Archiannelida (named in Hatschek 1878 as Archiannelides), Chaetopoda, Hirudinea, and Echiurida, with associated groups Sipunculacea and Chaetognatha.

Phylum as a formal taxonomic rank name was not a term familiar to Lamarck, Cuvier, Blainville, and their contemporaries in the early nineteenth century, at least not as a top-rank label, but previous reviews may not make this clear. Phylum (from Greek *phylon*, a tribe) was the term that gradually became universally accepted following the introduction and use of it by Haeckel (1866) for each main branch of the genealogical tree (Lankester 1890). Before that, the concept was understood, but a phylum-level category could have various early names such as type, branch (embranchment), subkingdom, and class (Lamarck used classe).

Cuvier (1817 (vol. 2): 508) introduced a new concept of a group above the phylum-level annelids of today when he named *Les Animaux Articulés* as his *Troisième grande divivision du Règne animal*. He included in it the annelids, crustaceans, arachnids, and insects, purely on the common structural feature of segmentation. This was the first suggestion that an Articulata grouping (mostly arthropods) should also include annelids as their sister group, and the idea proved to be enduring, although long debated since. While cladistic analysis was dependent on morphological data, an argument could still be made into the late 1990s for the Articulata concept to have an annelidan component (Rouse and Fauchald 1995, 1997, and see the "Phylogeny of Annelida" chapter). With the aid of compelling molecular data, beginning with the first evidence for a split between major clades becoming known as the Ecdysozoa and Lophotrophozoa (Aguinaldo *et al*. 1997), plus better data on embryonic cleavage, we now know that Articulata *sensu* Cuvier is not a natural lineage and that the arthropoda are an Ecdysozoa group, while annelids are in Lophotrophozoa along with the unsegmented molluscs, etc. (e.g., Bourlat *et al*. 2008).

It is not necessary here to further work through all the many progressive changes and substitutions in names for the subgroups of annelids and allies since Lamarck, or over the 260 years since the 10th edition of Linnaeus (for some of these, see Fauchald and Rouse 1997, particularly Appendices A and B, and the "Phylogeny of Annelida"

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chapter), nor to create a chain of synonyms and variant spellings of names of higher ranks, but there are some other significant ones to look at briefly. By the second edition of *Traité de Zoologie* (Claus and Moquin-Tandon 1884), the standard classification of annelids was starting to emerge in a form we would recognize today. In that treatise, Vermes (still included platyhelminths, nemerteans, and nematodes) had a class Annelides, with subclasses of Hirudinei [sic] and Chaetopoda, the latter with orders of Oligochaeta and Polychaeta, the latter with suborders Sedentaria and Errantia. Myzostomes, as single genus *Myzostoma*, were questionably an adjunct to Polychaeta, and a further class of Vermes was the Gephyrei [sic] (or Sipunculacea), including *Echiura*, *Sipunculus*, *Phoronis*, and *Priapulus*.

Vermes continued to be used for a grouping of miscellaneous "minor" worm-like "phyla" plus Annelida, and even as late as the 1930s, "Vermes Polymera" was the annelids category in the Kükenthal and Krumbach edited *Handbuch der Zoologie*. Remarkably, Vermes was still used by *Zoological Record* into the 1970s as a convenient shorthand title for an all worm-like groups part-issue, with or without a group named Annelida inside it, although the first volume in 1864 had used only Annelida. In 1900, the *Zoological Record* Vermes even included Hemichordata, and in 1924 and earlier, it included the Gephyrea, a concept dealt with next.

Gephyrea was proposed by Quatrefages (1847: 340), from Greek *Gephyra*, meaning a bridge, for a supposed link to holothurian echinoderms, as a sister class to his concept of class Annelida (part of his "Vers" mixture), and just for some hard-to-place worm-like genera of general sac-like form. Later, these genera were believed, except for *Sternaspis*, which was added to the Sedentaria in Annelida, to each belong in the separate phyla of Echiura, Sipuncula, and Priapulida, with the first two remaining in Spiralia and the priapulids becoming much more distant as one of the Ecdysozoa groups. Quatrefages' creation of Gephyrea appears not to be overtly influenced by Rolando's (1822) earlier belief that his new *Bonellia viridis* (Fig. 1.3), now in Echiura, was a new type of echinoderm, but he does comment that it probably belongs in his Gephyrea. Quatrefages (1866b: v.2 563) elaborated on the grouping, and the name was present in titles of taxonomic works up to the 1930s and beyond (Wesenberg-Lund 1934), perhaps in later times just for convenience, and even used later as a phylum (Monro 1931). Although Stephen and Edmonds (1972) state that the name "has no standing in zoological nomenclature" (they meant not valid), they and others also continued to find it appropriate to treat at least sipunculans and echiurans together. Currently, molecular analyses place sipunculans as a basal group within annelids and place the echiurans within the Sedentaria annelids (Andrade *et al*. 2015).

Hatschek (1878) created Archiannelides for *Polygordius*/Polygordiidae, also Archichaetopodes for *Saccocirrus*/Saccocirridae. Then, Hatschek (1893) had Polygordiidae and *Dinophilus*/Dinophilidae in Archiannelida with a new name of Protochaeta (soon forgotten) as the group for Saccocirridae. Further genera for which families were created were found, all meiofaunal and microscopic and not seemingly related, but "archiannelids" remained a convenient holding place for them, so much so that Archiannelida became presented as a class firmly outside Polychaeta to the generations of students who used the editions of Dales (1963, 2nd Ed. 1967) as a university text, despite skepticism (Hermans 1969) or disregard (Pettibone 1982), and despite the perceptive comments of Goodrich (1901) that the Haplodrili (a name of Lankester's for archiannelids) were specialized taxa rather than ancestral. However, an archiannelid group is polyphyletic and not taken seriously for some time due to a lack of support from molecular analyses, with Andrade *et al*. (2015) placing *Polygordius* and two other meiofaunal genera among representatives from the major errant families, and especially with regard to the analysis of Struck *et al*. (2015), which placed representatives of Polygordiidae, Saccocirridae, and three other meiofaunal families as a sister group to errant groups Eunicida and Phyllodocida, split from Nerillidae and three other meiofaunal families grouped

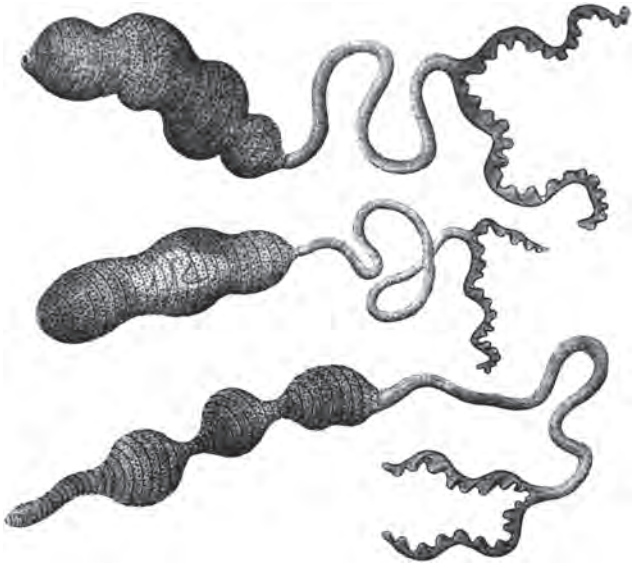

**Fig. 1.3:** The first Bonelliidae echiuran species, *Bonellia viridis* Rolando, which Rolando (1822) thought was a new type of echinoderm. No scale. Original at https://biodiversitylibrary.org/page/7654161

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with Sedentaria Orbiniidae. Struck *et al* (2015) concluded, "inhabiting the interstitial realm and possessing a simple body organization are not ancestral traits of Annelida. The 'Archiannelida' concept has to be rejected…."

The enigmatic and interesting disc-like myzostomes, obligate parasites and commensals of echinoderms, especially crinoids, have been slotted variously within and outside the annelids, and were placed in the helminths when a *Myzostoma* was first found (by Leuckart 1827, but see World Register of Marine Species [WoRMS] for the validity of early names). The biodiversity within the myzostomes is proving to be considerable (>150 species, eight families, *fide* Grygier 2000; Summers and Rouse 2014), so they are not the usual minor group that specialist parasitic annelids tend to be, with some possible taxonomic rank inflation creeping into classifications. Although a molecularly supported platyhelminth link has earlier been put forward (Eeckhaut *et al*. 2000, and others), most annelid specialists have long been comfortable with morphological and other data that myzostomes are annelids, probably a sister group to Errantia (e.g., Summers and Rouse 2014, Weigert *et al*. 2014, but see also Wang and Xie 2014), despite molecular analysis problems with myzostome long-branch attraction to outgroups.

An article title of nearly 20 years ago included the assertion that "Pogonophora is not a phylum" (Boore and Brown 2000). How did we get to have the pogonophorans ("beard-bearer" worms) anyway? They were discovered late, overlooked as being a form of animal life. Researchers on deepwater benthos may sheepishly relate to the possibly apocryphal story, told by the translator in the preface to Ivanov's monograph, that on an Antarctic voyage of *Discovery II* in the 1920s, masses of thread-like fibrous material from abyssal depths were repeatedly simply shoveled back overboard, not recognized as living. The first such extraordinarily slender siboglinid found, *Siboglinum weberi*, collected on its genus namesake vessel, the *Siboga* (derived by Caullery as *Sibog* – plus *linum* "thread"); had no gut, no chaetae, a single tentacle; and was thought to have a dorsal nervecord (Caullery 1914, 1944). In a very brief outline of the further history, more similar forms were discovered, and eventually, there were about 100 species that Ivanov (1960, translated 1963) included in Pogonophora, which he declared to be an independent deuterostome phylum, dismissing Hartman's (1954) polychaete-relative placement, and the earlier detection of posterior chaetal platelets by Caullery (1944). However, a protostome-placement faction developed, which led on to the placement of pogonophorans as annelids or annelid allies (van der Land and Nørrevang 1977). Later, Jones (1985) escalated the vent- and seep-associated Vestimentifera group (first named by Webb 1969) of pogonophorans with much larger body size (*Riftia*, *Lamellibrachia*, etc.) to their own phylum. However, molecular evidence began to support an annelid placement, and Rouse and Fauchald (1997), using morphology, concluded that both groups belonged with the Sabellida annelids at family level. Finally, Rouse (2001) suggested that "all taxa within Siboglinidae that are not genera or species are redundant…." This simple reduction to Siboglinidae of the detailed hierarchies of phyla Pogonophora and Vestimentifera by Rouse (2001, q.v. for a more detailed historic account), and Rouse and Fauchald earlier, based on morphological cladistics, not molecular work, and its acceptance by almost all other scientists interested in the topic, must qualify as one of the most emphatic deflations of superfluous higher taxonomic ranks in the history of biology.

When our knowledge of the variety of animal forms was still poor, a hitherto-unknown major alteration between life stages, a "metamorphosis," could lead to some surplus genera names being created, which subsequently might be useful as the general name for the life stage. This has occurred in annelids, just as it has in other phyla. The best-known is the heteronereid, a gravid member of Nereididae, modified for swimming, after *Heteronereis* Örsted, 1843, erected for two Greenland nereidids. Ehlers (1868) and Malmgren (1869) soon sunk the genus into *Nereis*, but a heteronereis (Fig. 1.4) became the name of the morphology (e.g., review of Clark 1961), although the less family-specific "epitoke" is the term used more today. Similarly, in the Autolytinae syllids, the genera names *Polybostrichus* Örsted, 1843 and *Sacconereis* Müller, 1853 became the technical names, respectively, for the fast-swimming male stolons with their enlarged trailing head appendages and the egg-sac carrying female stolons.

For small planktonic forms, it is understandable that some get named before they were first realized to be only larvae and then later matched to adults. For annelids, *Mitraria* Müller, 1851, figured in Müller (1854), and *Rostraria* Häcker, 1898 are unusual planktonic larval forms in Oweniidae and Amphinomidae, respectively, with the names continuing to be used today for plankton with similar morphologies, although their affinities are now known. Häcker (1898) also came up with the name *Chaetosphaera*, but that was clearly for a spionid larva. The *Mitraria* name of Müller is from the Greek for headdress, presumably because of the miter-shaped head and apparent lack of body (Fig. 1.5). The *Rostraria* name is

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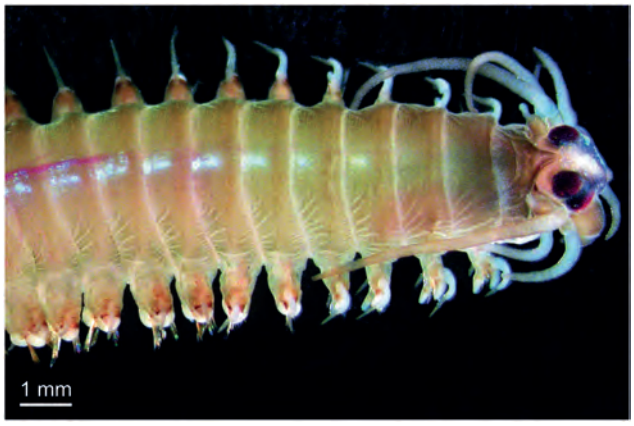


**Fig. 1.4:** Heteronereis-morphology anterior body of a New Zealand *Platynereis australis* live female, first described as *Heteronereis australis* Schmarda, 1861 (©G.B. Read).

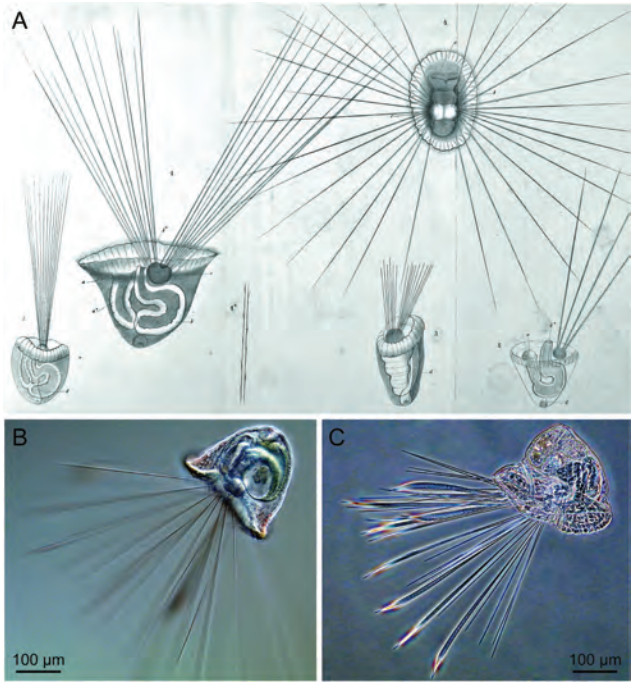


**Fig. 1.5:** *Mitraria planktonic* larvae that do not resemble the Oweniidae adult. A, *Mitraria* larvae first published figures in Müller (1854, plate 5), original at https://biodiversitylibrary.org/page/14341920; B and C, differential interference contrast and phase-contrast *Mitraria* larva photomicrographs, probably of a *Myriochele* species, Bay of Santander Spain (©R. Martin-Ledo).

analogously formed but does not refer to the main identifying rostraria-larva character of a pair of thick ciliated head tentacles of disproportionate size, particularly noticeable in young larvae. The history of the eventual matching of *Mitraria* to Oweniidae and *Rostraria* to Amphinomidae is given by Wilson (1932) and Bhaud (1972), respectively.

## 1.6 Use of journals – the path from natural history to model organisms

Preparing and publishing a book in the eighteenth century was a major commitment, and for its readers with a serious interest in natural history, the investment in a useful set of supporting works was also considerable, as books remained expensive during the period of relatively unmechanized printing (Allen 1993). The new avenues for both publication of annelid discoveries and for learning about them were the scientific society and subscriber journals devoted to all sciences or exclusively to various biological sciences, not first appearing until 1665 in France and England with *Philosophical Transactions* (of the Royal Society of London, volume 1, subtitled "giving some account of the present undertakings, studies, and labours of the ingenious in many considerable parts of the world"). The *Transactions*' first definite polychaete seems to be an aphroditid found in a codfish stomach (Molyneux 1695), but in that 1665 first volume, there is a dubious description of "shining worms in oysters" (Anon 1665), reprinting in paraphrase a letter published elsewhere (in the then new French publication *Journal des Sçavans*). Authentication of content was at first up to the editor's judgment, while peer review by Society members was introduced only decades later in 1752 (Spier 2002).

Probably the most important nineteenth and twentieth century English-language journal for annelid biology was the *Annals and Magazine of Natural History* (1841–1967), which was the survivor from a pack of hopeful competitors (Allen 1996), beginning in 1828 under an earlier name and continuing today as *Journal of Natural History*. In such journals, the early natural science reports on annelids, whether morphological, experimental, or taxonomic, were relatively short, unstructured, discursive, and sometimes verbose, but rarely uninteresting. Early titles often indicated the observational content ("An account of...," "Observations on...," "Remarks on...," or simply "On the...," which is still a favorite today). The *Annals* also usefully printed translations of significant work from other countries for its subscribers. Thus, Quatrefages' then new annelid classification in *Annales des Sciences Naturelle* was reprinted in English (Quatrefages 1866a).

The tireless William McIntosh (or as M'Intosh) (1838–1931), in an early career article in the *Annals* (McIntosh 1868), writing on the boring of *Leucodore ciliata* (now *Polydora*), has an example of the loose style. McIntosh is usually very polite, but as a 30-year-old includes sly jabs at fellow scientists ("the want of scientific accuracy in the figures...

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renders identification difficult"). A look at McIntosh's style of nearly 20 years onward in the *Challenger Report* (McIntosh 1885) shows no improvement in conciseness, but as an expedition report, it is effectively a book. By how much would an editor of today reduce its nearly 1,000 pages (including plates)? Over time, the book has remained the ultimate publication for science prestige compared to journal articles, the latter always regarded as having a somewhat fleeting impact, but few individuals of earlier periods or today have the resources to publish a specialist book of limited potential readership. The enormous *Challenger* publications were presumably government subsidized, and McIntosh's Ray Society monographs (e.g., McIntosh 1923) were supported by society subscribers. The other obvious avenue was to be backed by a for-profit publisher for a work with many illustrations intended for the general public (see later sections), but that (then and now) is an unlikely path in the case of annelids.

Annelid researchers seem to have been in no hurry to adopt the present required arrangement for science journal articles of an introduction, methods, results, and discussion (known as IMRaD), although helpful use of some headings including a "methods" appeared in annelid experimental articles as early as the 1900s (e.g., Allen 1904, Hargitt 1906). Indeed, strict IMRaD first became widespread in science only in the 1950s and was not a formal standard until 1972 (Day 1989). The first annelid experimental article might be Bonnet (1742) on worm regeneration, and the first article with "experiment" in the title is Vaney and Conte (1898), who reported work on the regeneration of *Sabella spallanzanii*. The first journal article predominantly on the ecology of annelids is hard to determine, given that ecology is often a multiphylum community study, but was likely well before the word Ökologie itself was first used by Haeckel (1866). Darwin's (1840) early examination of earthworm formation of vegetable "mould" (soil-like castings) is ecology. Much later, his further research formed his last book (Darwin 1881), and he described how mosaic floors of ruined Roman Britain buildings had been buried under layers of earthworm castings at Silchester. However, the first article on a named polychaete with ecology in the title (i.e., autecological) is Flattely (1916) on *Cirratulus tentaculata* (now *Cirriformia*).

At the other end of the timeline for journals, indicative of new research avenues and the application of increasing technological power, the development of adequate computer power and software code was required first for Hennigian cladistic analysis to replace the creation of subjective taxa groupings by intuition and experience, at first with morphological character data (e.g., Fauchald 1992, Rouse and Fauchald 1997), then with molecular data. The specialist journals *Molecular Biology and Evolution* and *Molecular Phylogenetics and Evolution* began in 1983 and 1992, respectively, with the first annelid sequence data of the latter journal presented by Dick and Buss (1994), and in the former journal, annelid, vestimentiferan, pogonophoran, sipunculan, echiuran (then all separate) nuclear 18S rRNA sequences were used for phylogeny by Winnepenninckx *et al*. (1995). Siddall and Burreson (1998), Dahlgren *et al*. (2000), and others subsequently used mitochondrial cytochrome oxidase I (CO I or CO1) for higher annelid phylogeny, with Apakupakul *et al*. (1999) also using nuclear 18S rDNA data. The first polychaete-group annelids "barcoded" may have been the *Escarpia* Siboglinidae species studied by Kojima *et al*. (2002). Barcoding in molecular biology is obtaining CO I DNA sequences as used for species delimitation (reviewed in Taylor and Harris 2012), even before CO I was chosen as a standard convenient surrogate for any animal whole genome in 2003.

The first annelid mitochondrial genome was completed for *Lumbricus terrestris* L. by Boore and Brown (1995) and for *Platynereis dumerilii* (Audouin & Milne Edwards, 1833) by Boore (2001). Eventually, randomly sequenced clones of mRNA transcripts became a way to assemble large datasets of annelid species for phylogenetic analyses, beginning with Struck *et al*. (2011), which included 29 annelid species (see also Weigert *et al*. 2014, Weigert and Bleidorn 2016). By 2015, so-called next-generation sequencing techniques more readily enabled the first mitochondrial genome of a syllid to be sequenced (Aguado *et al*. 2015), which was of the remarkable branching annelid *Ramisyllis multicaudata* Glasby, Schroeder & Aguado, 2012. A transcriptome (set of all RNA molecules) has recently been completed for the echiuran *Urechis unicinctus* (von Drasche, 1880) by Park *et al*. (2018). Elucidation of a whole draft genome have been completed (Simakov *et al*. 2013) for model organisms *Helobdella robusta* Shankland, Bissen & Weisblat, 1992 (but see identity comments later) and *Capitella teleta* Blake, Grassle & Eckelbarger, 2009, both annelids with comparatively small genomes. Furthermore, whole genomes for other annelid species must surely be imminent.

So far, at least four annelid species have become regarded as so-called model organisms maintained in laboratory culture, mostly for examining developmental and evolutionary biology (evo-devo) with advanced techniques, including gene expression mapping. These are *P. dumerilii*, *C. teleta*, *Hirudo medicinalis* L., and *H. robusta*. A setback for the reliability and reproducibility of data from research on cultured *Helobdella robusta* occurred when it was discovered to be two species at the original type locality, and a further possible model species

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was named from a different culture (Kutschera *et al*. 2013). Kutschera and Weisblat (2015) have discussed how to move on to take advantage of the biological and genetic complexity now evident within the group of similar *Helobdella*. Similarly, past biomedical research results on *H. medicinalis* are compromised as the usual commercial supply was found to be of another leech, *Hirudo verbana* Carena, 1820 (Siddall *et al*. 2007). The same danger for the unwary laboratory biologist from the presence of cryptic species exists for the other two model taxa (*C. teleta* is a member of the *Capitella capitata* complex), suggesting that cultures should be molecularly verified. Prospective additional model-organism species have been discussed by Weigert and Bleidorn (2016).

As a last comment on journals, a specialist journal for annelid science has not yet been established (noting *Polychaete Research* ISSN 0961-320X had two issues around 1995–1998, with a brief presence online), although the idea has been talked about at meetings. At times, certain journals (e.g., *Proceedings of the Biological Society of Washington*) have been more favored with frequent annelid taxonomy submissions, and currently, the sheer volume of articles flowing from *Zootaxa*, with its daily online publication, makes it a favored journal for publishing new worm taxa, although most articles in it are not open access.

## 1.7 The expeditions, explorers, and travelers

How did early naturalists/scientists get to collect worms outside the countries of Europe? It was by vessel, as not just the only way to travel across oceans but also the easiest way to live while travelling and to transport back the volume and weight of samples collected, even if the locations visited were connected by land. Ships were still favored for personal travel for traveling the world, rather than by aircraft, right up until the 1960s, and of course are still used for major scientific voyages today, especially for the higher polar latitudes, still to dredge, trawl, and net as in the nineteenth century, but also to map and explore the deep-sea bottom with high-technology multibeam sonar and unmanned remotely operated underwater vehicles (ROVs) and landers. Early voyages did not always go smoothly, either for the ship or the crew, with shipwreck, illness, and possible death quite likely, nor did the collected material always survive. Naturalists allowed on board, especially on navy ships, likely had other primary duties, such as ship's surgeon (e.g., Quoy and Gaimard, as discussed later).

Some of the prominent scientific exploration ships that were used on voyages resulting in annelid works published in the expeditions' own monographs were *Eugenie* (1851–1853; Kinberg as monograph author and onboard naturalist), *Challenger* (1873–1876; monographs by McIntosh, Selenka, von Graff), *Ingolf* (1895–1896; Ditlevsen, Wesenberg-Lund), *Belgica* (1897–1899; Fauvel), *Valdivia* (1898–1899, Ehlers, Michaelsen), *Siboga* (1899–1900; Caullery, Horst, Mesnil, Pettibone, Sluiter, Southward), *Discovery I* (1901–1904; Ehlers, Lanchester, Stummer-Traunfels), *Discovery I* and *II* (*I*, 1924–1931, and *II*, 1929–1951; Harris, Monro, Stephen, Tebble), *Terra Nova* (1910–1913; Benham, Boulenger, Harding), and *Galathea* 2nd expedition (1950–1952; Kirkegaard, plus brief reports by Hutchings and Holthe). See Hartman (1951), Read and Fauchald (2018), or WoRMS for monograph author references. There were many other lesser-known expedition vessels and particularly many Antarctic expedition voyages named for the sponsoring nation rather than the support vessel. There is even a vessel, the *Michael Sars*, named after an annelid biologist, with a 1910 North Sea expedition (polychaetes by Støp-Bowitz).

The ships that did not produce, but should have or could have produced, annelid work include the first *Endeavour* voyage (1768–1771) of Cook, the *Erebus & Terror* voyage (1839–1843) of James Clark Ross, and possibly the *Beagle* voyage (1831–1836) of Fitzroy with Darwin. In all of those, part of the material was lost or neglected when back in England. The Joseph Banks team on board the famous first *Endeavour* expedition to the "South Seas", commanded by James Cook, evidently paid much lesser attention to marine invertebrates outside of crabs and molluscs, overwhelmed as they were with new discoveries of vertebrates and plants. Additionally, a unified publication of the zoology of the voyage never happened (Whitehead 1969, Carter *et al*. 1981). A first passage around New Zealand was a significant part of the voyage, but disappointingly, no polychaetes are known, although at least a collection of serpulid tubes was likely (Glasby and Read 1998).

Charles Darwin was a gentleman naturalist on the *Beagle*; there was also a ship's physician-naturalist, but Darwin has the subsequent fame for obvious reasons. It is notable that Darwin makes almost no mention of annelids in his zoology notes (Keynes 2000). The surviving labeled annelid material, at least that known about at Oxford, is only four jars (Chancellor *et al*. 1988).

Jean Quoy and Joseph Gaimard have their names forever linked as the surgeon-naturalist collectors on voyages through the Pacific, on both Freycinet's *Uranie* (1817–1820) and d'Urville's *Astrolabe* (1826–29). On the first voyage, *Uranie* was wrecked early in 1820 with loss

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of some collections, but the crew survived and reached home by buying a replacement, the *Physicienne*, which is why there are two ships in the title of the expedition results (Freycinet *et al*. 1824). While they published almost no annelid work themselves (one species in Tomopteridae), their annelid material was received into the Paris museum, and they are thus recorded as joint collectors for about 40 taxa just in Quatrefages' (1866b) *Histoire naturelle* alone.

Baird's (1865, 1869) subsequent description of a few worms from the James Clark Ross *Erebus* and *Terror* Southern Seas Expedition has created one enduring mystery. Where is elusive Narcon Island? Baird named a subantarctic serpulid *Serpula narconensis* Baird, 1865, later found to be widespread and reef-forming, and he named a not-yet-seen-again eunicid *Eunice narconi* Baird, 1869. This island is embedded in the literature and in the London Natural History Museum specimen catalogues, yet no support for it can be found in the voyage narrative or anywhere, and the most favored explanation is that it was created by Baird's misreadings of a cursive script "Marion Island" on a label (Helmut Zibrowius and GBR unpublished).

Later, as shipping routes established, it was not always necessary to be on a dedicated expedition ship. Notable scientist/collectors who collected annelids worldwide by "hitchhiking" on passenger ships or government-operated vessels include the Austrian Ludwig Schmarda in mid-nineteenth century and the German Hugo Schauinsland and Dane Theodor Mortensen in late nineteenth to early twentieth century, all visitors to the still remote and relatively unknown New Zealand main islands. Schmarda was the pioneer and annelid taxonomist of the three. He travelled around the world (1853–1857), collected intertidally, and wrote a book about it (Schmarda 1861a, typeset in difficult-to-read cursive German). On the way homeward, Schmarda lost his luggage to thieves while crossing the Panama Isthmus, with the loss of a large part of his documents and specimens from his work in New Zealand and Australia (Schmarda 1859), but at least some of his New Zealand type specimens made it back to the Naturhistorisches Museum in Vienna (Glasby and Read 1998). Schmarda contributed 21 annelid names for New Zealand and 223 mostly for the southern hemisphere, including 17 oligochaetes and 3 leeches (Schmarda 1861b). Although he had color plates and some in-text figures in his monograph books, these were inadequately detailed and descriptions were brief; consequently, annelid workers view Schmarda's work with some ambivalence.

Schauinsland and his wife travelled (1896–1897) through Pacific Coast North America, Australia, Ceylon, and Egypt, and to some remote places in the Pacific, and later did more trips. He spent time on Laysan in the Hawaiian chain and the Chatham Islands off New Zealand, with his diaries and letters home later written up as an around-the-world travel book (Dünzelmann *et al*. 1999). Mortensen, an echinoid expert, travelled remarkably widely and produced a prodigious output on his speciality. His trip to Japan, the Philippines, Australia, New Zealand, Hawaii, California, and Panama was in 1914–1916, with many researchers later publishing on his collections as part of the series "Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16." In New Zealand, Mortensen managed to get himself onto government scientific vessels, and in summer 1914–1915, he travelled to the subantarctic Auckland and Campbell Islands. Schauinsland and Mortensen collected a variety of marine taxa; their polychaetes were written up by European-based Ehlers and Augener, respectively, who both made major contributions to knowledge of polychaetes in New Zealand (Glasby and Read 1998). Michaelsen (1899) wrote up Schauinsland's oligochaetes.

## 1.8 Tracking specimens – museums, nomenclature, and taxonomy

> Our unrivalled store of scientific wealth, [...] available for the instruction and amusement of the people... (Jeffreys 1863: 237)

> There appears to be an optimum period during which the observations from a biological expedition have to be completed... The stores of museums, laboratories and universities all over the world are cluttered with collections which are "going to be worked up." (Wheeler 1984, Endeavour collections)

> Where I found it I do not remember. (Hans Sloane 1725: v. 2 p. 194)

Until institutional museums were founded, naturalist's hard-won specimens were in personal "cabinets of curiosities" and were traded between wealthy private collectors. This did not bode well for long-term preservation, for continuity, or for tracking provenance, even though collections from foreign lands had real monetary value, notably the one founding the British Museum (physician-naturalist Hans Sloane's priceless lifetime acquisitions), acquired in 1753 by the state for a nominal £20,000 (de Beer 1953). The Paris museum began in 1718 as Jardin du Roi, reorganized in 1793 during the revolution as Muséum national d'Histoire naturelle, and the British Museum, London, began in 1759, a year after the 10th edition of *Systema Naturae*. Even after museums were well established, specimens

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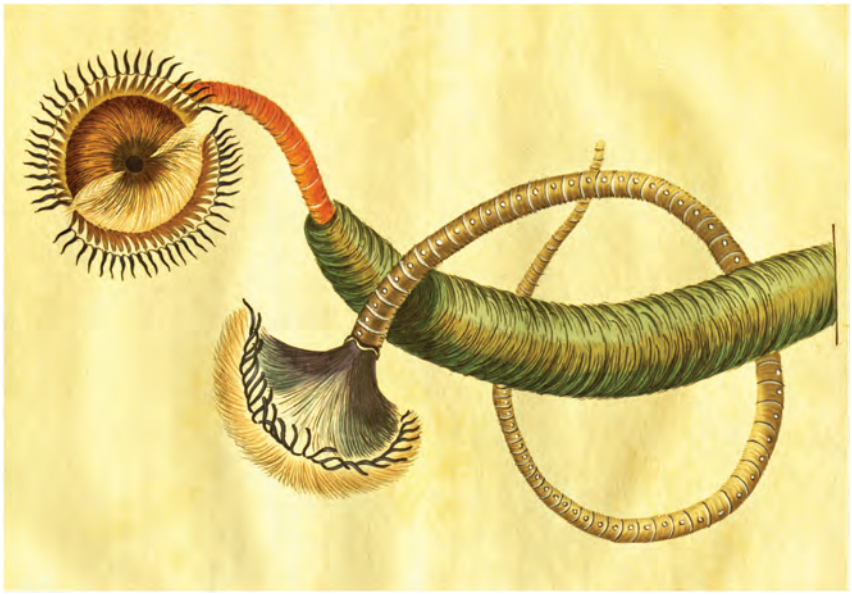

**Fig. 1.6:** *Amphitrite infundibulum* Montagu, 1808 (now *Myxicola*), painted by Liza Dorville. No scale. Original at https://biodiversitylibrary.org/page/757878

could be lost through neglect or mischance (Sloane's zoological specimens in the British Museum later rotted or were ruined by vermin). It is an imperfect world. Although Joseph Banks and the participants in the first James Cook "South Seas" voyage of 1768–1771 have been admired and celebrated ever since, much of the material they gathered ultimately decayed unlooked at or lost provenance as it was dispersed (Whitehead 1969), with, for example, Linnaeus eventually receiving "Cookian" first-voyage molluscs via one or more intermediaries (Dance 1967). In another example in the next century, the hard-won dredged samples from the James Clark Ross, *Erebus* and *Terror* Southern Seas Expedition (1839–1843), in a bad state, were discovered by Hooker in Ross's back garden after Ross died in 1862 (Rainbow 2005).

Part of the collection of Devon naturalist George Montagu did make it to the British Museum, purchased for the then substantial sum of £1,100 according to Oliver *et al*. (2017: 363), but by 1863, it was almost annihilated. "Nearly the whole of his priceless collection of British shells [...] has unluckily been lost to science; and [for] the few specimens that are still preserved [no care was taken] in the course of rearrangement to retain the names affixed by the donor to his types" (Jeffreys 1863: 237). It seems that some of Montagu's polychaetes in spirits (i.e., diluted alcohol) did rather better as the important Montagu specimens of *Amphitrite volutacornis* (type species of *Bispira*), *Aphrodita clava* (type species of *Lepidonotus*), and *Amphitrite infundibulum* (Fig. 1.6) (the probable type of *Myxicola*) are all in The Natural History Museum, London. However, usually, alcohol-stored specimens are more vulnerable to permanent destruction through evaporation of the liquid. As assessed in 2008, the London Museum contained about 288,000 specimen lots of annelids, the vast majority of which would be in spirits, and 4,500 annelid types (Rainbow 2008). Maintaining good condition in such a large collection is not a trivial task. Preservation in spirits, rather than dry, was done from the mid-seventeenth century. Wet preservation is essential for annelids, and polychaete worker George Johnston is said to be one of the two early nineteenth century naturalists to adopt spirit-filled corked glass tubes for keeping individual specimens, when glass became cheaper (Allen 1976).

The specimens from Linnaeus's collection were purchased privately in 1784 and transferred to London and eventually to the Linnean Society (Dance 1967). Linnaeus named 65 annelids (WoRMS data) that remain valid species, including at least eight species now in other phyla. Types of four *Serpula* species (actually molluscs) survive, but it is uncertain what else. Dance (1967) lists 17 Linnaean annelids, all *Serpula* or *Sabella*, that are *not* in the Linnean Society collection. There is some possibility that the Museum Adolphi Friderici collection within the Swedish Museum of Natural History also has some annelids examined by Linnaeus. Types have also got destroyed through mischance, such as the wartime damage to European museums, but occasionally, rediscoveries are made. Types of some significant Langerhans species from Madeira, at least those on slides, were rediscovered at Naturhistorisches Museum Wien by the late Phyllis Knight-Jones in 1994, along with Langerhans' inventory of manuscript names (personal communication).

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Another problem with collections was lack of documentation. Early labeling was inadequate for proper tracking and, coupled with mistaken matching by post hoc curatorial guessing of provenances for specimens, is fraught with danger of error. We can laugh at the stark honesty of the Hans Sloane "I do not remember" quote earlier, but the historic literature shows that loss of memory by the collector might not be the real problem, as keen describers looking through specimens with minimal-associated information did not let that get in the way of creating a new name, perhaps with a bad description. There is the heretical idea of whether we would be better off without some of these early names and the confusion of unwinding exactly what they named. Glasby and Read (1998) commented on the problems regarding polychaetes extracted from New Zealand by early collectors.

The type specimen concept in zoological taxonomy is of quite recent origin, or at least the formal rules surrounding it are, so we must accept that an early annelid taxonomist cannot be castigated for lack of type material for his/her names. A type species concept for a genus was introduced by the Strickland code (1878), the product of a committee including Charles Darwin. The type specimen concept was present in the "*Règles internationales*...," the first truly international code (Blanchard *et al*. 1905), but only in an appendix as a recommendation. However, in the first edition true ICZN code (1961), the importance of holotype specimens is very clear and entrenched. Type specimens are highly significant today, yet the type collections of translocated native life from colonized countries as held in major natural history museums are alienated from the country of origin where they are now most needed for active research (the biotic equivalents of the "Elgin" marbles). New techniques of displaying images of type specimens are likely to help to some extent, but annelids are very difficult to identify just from whole-body photographs.

Contemporaries Edouard Claparède and Armand de Quatrefages in the nineteenth century had different approaches to types, or at least to the use of preserved specimens. The two, both excellent annelid biologists, were in open conflict after publication of a preliminary outline of Quatrefages' *Histoire Naturelle des Anneles* and Claparède's (1866) adverse comments on many mistaken classifications in it. Their different work practices were an additional matter, and Claparède (1868) wrote (in translation),

> "Why did M. de Quatrefages, who so admirably knows the annelids, let himself be led to describe so many genera and species according to individuals preserved in alcohol at the Paris Museum? He knows, better than anyone, that this kind of work is profoundly useless, that annelids can only be studied at the seaside, using live individuals. Describe, as he does, so many alcohol varieties [variétés alcooliques], is to embarrass the science of a *caput mortuum* [useless residue] which will take long years to get rid of."

The disapproving terminology "variétés alcooliques" appears to be unique to Claparède. Fauchald (1989) has commented that "Claparède, true to his principle, deposited no specimens in any museum [gbr – maybe some reached museums], making many of his new taxa difficult to define accurately" and "The most important aspect of Claparède's work was that he demonstrated that a remarkable amount of information could be gained by looking at live organisms." No one would disagree with Claparède and Fauchald on that, but it is not always possible, and the Paris Museum specimens came from many distant locations and are still available (Solís-Weiss *et al*. 2004).

## 1.9 Cataloguers

An enduring problem for annelid researchers in the nineteenth and twentieth centuries, especially those in more remote places, was how to learn of new research and new species and then how to get hold of the publications in timely fashion. This was a once fundamental limitation on keeping up with contemporary research activity if you were not at one of the upper-echelon of universities and museums and were as yet without a network of personal contacts with your peers who would send you their papers. It is a problem now vanished with the universality of access to the Internet. There is now free access to older literature scans via the Biological Heritage Library Consortium (BHL), a major advance scarcely believable to those who, not many decades ago, once waited weeks for journal loans and spent hours making blurry copies at primitive photocopy machines. Once there was no possibility for most biologists to see the quite rare and expensive Ray Society monographs of McIntosh (eight monographs between 1874 and 1923), but now, they are all online except the last (McIntosh 1923), because it was published past the BHL public-domain cutoff date of pre-1923. We also learn of new work via casual publicity pushed out to the world on open social media networks (e.g., Twitter, starting from 2006) and via free e-mail journal publisher alerts and special-interest mailing lists (e.g., "Annelida" run by one Geoff Read from 1995 to present) and can learn of forthcoming research via conferences for taxa groups, with the first international polychaete conference held in 1983.

One of the venerable commercial print alerting services for annelids is *Zoological Record* (yearly issues, began 1864, developing complex subject analysis), important as

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an authority for tracking name changes and publication dates. It included abstracts and subjective commentary on major works only up to 1906 (Bridson 1968). The related, much more frequent, *Biological Abstracts* began in 1926 for all life sciences, and both are now accessed mainly online in integrated form. In Germany, other nineteenth century journals ran literature-recording/commentating sections for periods, with the extracted or paraphrased content sometimes mistaken for a new publication by the unwary. These were *Archiv für Naturgeschichte* 1835–1923, *Zoologischer Anzeiger* (later *Bibliographia Zoologica*) 1878–1934, and *Zoologischer Jahresbericht* 1879–1913.

Early cataloguers of zoological species and genera names include Sherborn with *Index Animalium* (Sherborn 1902–1933) and Neave with *Nomenclator Zoologicus* (Neave 1939–1945, genera only), both now as online databases, and Hartman (1951) has a list of other bibliographic sources. William McIntosh could be considered among the cataloguers as an earlier compiler of comprehensive polychaete synonymies. His coverage in the monographs on British annelids (e.g., McIntosh 1923) is exhaustive, including pre-Linnaean names, and was later used by Hartman (1959, 1965) for her catalogues. His knowledge of the literature of his time and the historic polychaete literature is impressive given his many non-annelid commitments and duties.

We know nothing of how McIntosh recorded information but to compile their seminal works (Hartman 1959, 1965; Fauchald 1977) Olga Hartman (1900–1974) and Kristian Fauchald (1935–2015) used index cards, a standard precomputer technique, which developed from the practice of Linnaeus and others to keep organized paper slips in a "file," a term derived from the woven thread (Latin *filum*) first used to bundle loose papers (Charmantier and Müller-Wille 2014). Sherborn reportedly created over a million slips/cards (Shindler 2016). For a time, Hartman aimed only to cover the Western Hemisphere polychaetes fully (Hartman 1951: vi). Hartman's sources checked for names are not fully known, although undoubtedly were extensive – she lists some in Hartman (1951: v, 284), including *Zoological Records* and museum catalogues. She does not mention Sherborn, but she does mention Neave's *Nomenclator Zoologicus*. Hartman took all her index cards with her on her travels to museums, a somewhat risky practice as at least once, at the outbreak of WWII when travelling alone, she was separated from them in Europe for a period, and there were no duplicates. A contemporary letter in 1939 from Waldo Schmitt, Invertebrate Curator at the Smithsonian, indicates his concern at this situation (unpublished letters held at Smithsonian National Museum of Natural History and Natural History Museum of Los Angeles County (LACM)). At a later stage of preparation of the Catalogue (Hartman 1959, 1965), the index cards were transcribed from cards onto larger loose sheets typed and hand annotated and filed in a series of binders (Leslie Harris personal communication). These binders of annotated sheets are still held at LACM, but the content is from a later time; the index cards and sheets of 1959–1965 can no longer be found.

Overall, Hartman's cataloguing work rightly should be regarded with awe. The World Catalogue (Hartman 1959, 1965) was an amazing achievement and remarkably accurate given its ad hoc construction from original handwriting. A particularly useful feature today when much of the old literature can quickly be found online is that she included page numbers for original descriptions coupled to an item number in the 1951 bibliography. WoRMS editors are still using these page numbers and are including them in species records. However, Hartman's World Catalogue has several idiosyncrasies that are sometimes misunderstood because people have such faith in her work. For instance, she included at least 42 pre- and post-Linnaean names from McIntosh's synonymies in the form "*aus bus* X in McIntosh," which, if taken literally, seems to be saying McIntosh had published and made them valid, when all she meant was a personal shorthand to record a name attributed to X and harvested by her while she was reading McIntosh. One example is the unavailable William Leach museum label name "*Alveolaria arenosa*." There is no such genus. There are numerous similar examples relating to authors besides McIntosh. Another oddity was her practice as a convenient shorthand to cite the name then thought to be the valid senior synonym name to a type species of a genus as the "genotype" rather than the actual logical type species by date. The entry for *Dorvillea* is an example. Researchers have occasionally incorrectly interpreted this as if she had wrongly newly Code-designated an ineligible name as a type species.

Hartman's sources or rationale for her innumerable synonymies are very likely to be the prior literature (Hartman 1959: 1), but while she may have recorded them originally, she did not cite these sources, probably due to space limitations. In retrospect, from our point of view, this was a mistake, and they would have been so useful now. Researchers often assume Hartman miraculously made these synonymies de novo out of her head and cite her as the first recombiner or synonymizer. Sometimes, this will be true, but it is likely to be most usually untrue. The Hartman catalogue has also been influential in determining by subsequent designation which candidate original species was type species of a genus. Hartman consistently

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used page order priority, which seems reasonable and was part of the code applicable to her time, known as the *Règles* (Blanchard *et al*. 1905); page priority was possible then if no other factor applied.

Fauchald (1977) produced what became known as the "pink book", an invaluable set of polychaete genera keys and listings. He later transferred Hartman's catalogue data to his personal computer database, also adding new literature. He worked on it alone, including during his evenings, for many years, keeping it private, but finally donating it in 2007, together with linked sources, to what became the WoRMS database (Horton *et al*. 2017; Vandepitte *et al*. 2018). The WoRMS database coverage of Annelida continues today, contributed to by several editors via direct editing online (Read and Fauchald 2018). Earlier, a database continuation of Hartman's (1951) bibliography had been made available for public download (Ward and Fauchald 1997, assisted by GBR).

Oligochaeta were catalogued by Michaelsen (1900), with a then worldwide species total of 1,200, and subsequently in *Nomenclatura Oligochaetologica* (Reynolds and Cook (1976, with printed supplements in 1981, 1989, 1993), and now online as *N. O. – Editio Secunda* (Reynolds and Wetzel 2013–2018), and also with its data being added to WoRMS. Brinkhurst and Jamieson (1971) had earlier catalogued the aquatic oligochaetes. Other divisions of the current Annelida have also been presented in various monographic books, notably Stephen and Edmonds (1972) for Echiura and Sipuncula and Ivanov (1963) for Pogonophora (=siboglinids), and the online WoRMS catalogue is in the process of extending from a predominantly marine annelid content to also covering freshwater and terrestrial annelids.

## 1.10 Prolific species describers

Gesa Hartmann-Schröder is the (first-author) taxonomist with the most polychaete species still valid. From 1758 to 2016, 835 individuals were first authors, with Hartmann-Schröder (517 species), Olga Hartman (473), and Adolf-Eduard Grube (472) the top three most prolific first authors, and along with another 22 prolific authors, these individuals have provided descriptions of almost 5,250 species, or nearly 46% of total polychaete species (unpublished WoRMS data analysis by Joko Pamungkas). Hartmann-Schröder was active from 1956 to 1998 (last article finalized by another author) and had mostly worked alone. Hartman was active from 1936 to 1971 and did have collaborators later in her career. Grube was active from 1840 (17 still-valid names) to 1881 and almost invariably worked alone. He would take top honors for the most very short descriptions, so his unusual productivity may be a consequence of brevity both of examination and description, a tactic probably not endearing him to his peers and certainly not to later taxonomists.

In the decade 2007 to 2017, the most prolific authors or co-authors with more than 50 polychaete species were Hutchings (99), Nogueira (94), San Martin (81), Salazar-Vallejo (77), Blake (75), Rouse (53), and Carrerette (52) (data from Read and Fauchald 2018). These authors mostly worked collaboratively, with Hutchings solo for just 3 species and Nogueira for 2, whereas Salazar-Vallejo and Blake were the most prolific solo authors at 47 and 45 species, respectively.

## 1.11 Illustration and early photography

Annelid art has evolved somewhat patchily over the centuries, until now when we regard quality illustration as an essential adjunct to annelid research and to communication with the public. Drawings of animals had first appeared thousands of years ago, first as cave art, then in early Egyptian culture as decoration and story-telling on walls, household objects, and papyrus scrolls. Wall art is more durable than papyrus, and we know that by c.1600 BCE, the first marine organisms (swimming fish) had been depicted by Mycenaeans on Cretan walls. Also, we know that food-item marine invertebrates have been skillfully recorded for over 2000 years because mosaics created at Pompeii c.100 BCE showed realistic octopuses and lobsters (Dance 1989). However, it is not surprising that we can only speculate on the first depiction, if ever to be discovered, of the less edible, less obvious annelids. Perhaps, an Egyptian artist might have included common sights such as a bird with an earthworm or ragworm in its beak, or fishermen using worms for bait.

Papyrus scrolls with illustrations have been found in tombs of Old Kingdom Egypt, 3000 BCE, and the library of Alexandria held 700,000 scrolls, many of which would have been illustrated (Weitzmann 1971). Aristotle and Pliny were not illustrated, but it was quite possible to include small figures on scrolls in Pliny's time, except that Pliny did not approve of the practice and comments disparagingly about the colored figures in certain Greek herbals (Pliny book 25, Chapter 4). The biota illustrations that might have accompanied text on scrolls of papyrus or parchment before CE 300 are largely unknown now. Around that time, codices (singular codex), which were bound, handwritten, hand-illustrated books, and easier to handle, were taking over from scrolls.

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**Fig. 1.7:** Miniature painted scenes in Van Maerlant (~1266, copy of ~1350) of a leech (sanguisuga) and of land worms (vermis), where the artist has rendered them like fat eels with faces. A, river leech leaving bloody cuts on a human foot. (B) Two earthworms (in translation "With these [earth]worms it is that one fools the fish hook and the fish"). Original work at https://www.kb.nl/en/themes/middle-ages/der-naturen-bloeme-jacob-van-maerlant

Bestiaries were a feature of codex manuscripts of the European medieval period (about CE 400 to 1500). They were didactic religious works in Latin with moral tales based around an illustrated animal, realistic or imagined, mainly vertebrates, sometimes interacting with people, and including the unicorn and phoenix. Various worm-like biota might be mentioned briefly in the text, including leeches correctly described by Isidore as "*vermis aquatilis*, *dicta quod sanguinem sugit*" (water worm that drinks blood). The Flemish religious poet Jacob van Maerlant (~1230 to ~1291) produced the first bestiary around 1266, that was in Dutch (rather than Latin) and in rhyme, but it was a derivative codex condensed from contemporary works in Latin. The art is crudely drawn, but he has lively miniature watercolor scenes of a leech (*sanguisuga*) in action and of land worms (*vermis*) waving their bodies (Fig. 1.7 A, B, from van Maerlant ~1350, original lost, copy dates from ~1350).

Around 1578 to 1585, Adriaen Coenen, who lived in the Dutch fishing port of Scheveningen, produced the unique handcrafted, handwritten *Visboeck* (fish book) and *Walvisboeck* (whale book), both including his marine animal watercolors, which he exhibited to the public for a fee. The presentation is rather naïve and scrapbook-like, but there were recognizable named annelids (Tab. 1.1), including a *vermis*, which appears to be a sipunculan; an *eruca* aphroditiform; and a *hirudo marina* marine leech (Coenen 1578). The works were not circulated as copies at the time, but both survive and are an insight into the nonscholarly knowledge of marine annelids of the time, even if some figures are replicated from a copy of Rondelet (1555) printed earlier, as they appear to be.

When considering early printing-press illustrated books, a relevant example would be *Das Buch der Natur* (*Book of Nature*), a late medieval manuscript credited to the German scholar-priest Konrad von Megenberg (1309–1374), but not first print published until 1475. It also has some plates of purely fanciful life forms in the style of the time, but there is one plate, interesting because it is a farming-related, semi-ecological mixture of animals showing bees at bee hives, a large snail, butterflies, flies, grasshoppers, and lastly indeed what seem to be earthworms exposed from a digging into the soil (Megenberg 1475: in online pdf, p. 245]). Dance (1989) claims that it is the "first illustrated book which attempted to inform its readers about animals," and this included worms.

Rondelet's *Libri de piscibus marinis* is an impressive achievement both for the text and woodcut figures (Rondelet 1555). The cluster of serpulids clearly shows their stalked opercula. Gesner's *Icones animalium* serpulid figure of 1558 is a mirror-image direct copy and credited to Rondelet.

In the seventeenth century, pioneer conchologist Martin Lister (1639–1712) produced the first illustrated books for the public on molluscs, and shells books have been popular ever since, but not worm books! It seems that an annelid-only illustrated popular book has yet to make it into print, perhaps because of worms lacking the reliable eye-appeal of shells, not being enduring structural objects, and lacking the same ease of classification. Nevertheless, excellent marine annelid color images have appeared in monographs and more recently as photographs in field-guide sections and in more technical works such as Rouse and Pleijel's *Polychaetes* (2001).

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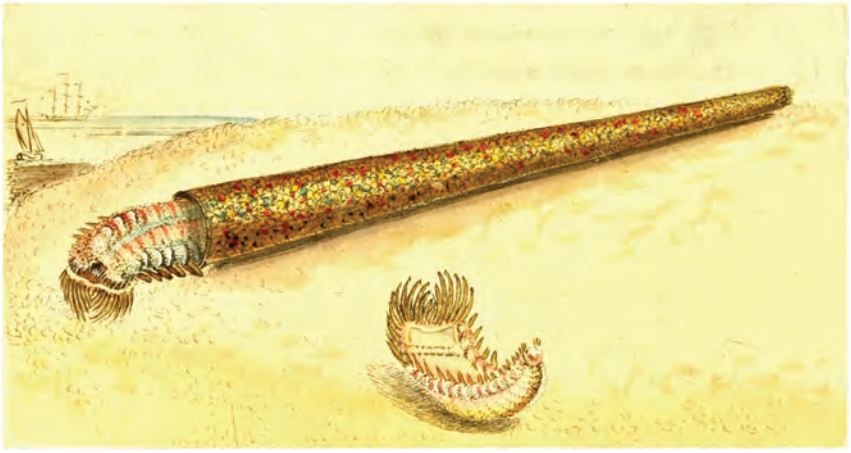

**Fig. 1.8:** Sowerby's (1806, plate 51) colored pectinariid and its cone tube, as *Nereis pectinata*, watercolor, with ship in distance. Original at https://biodiversitylibrary.org/page/28913891

The natural history collector Seba's 1734 *Locupletissimi rerum naturalium thesauri* is noteworthy for the increased quality of the printed art, with the originals contributed by 12 artists. According to Holthuis (1969), "Seba's text [in both Latin and French] is very poor and non-binomial, [but the good] plates make Seba's work one of the more important of its time, also for purposes of zoological nomenclature, as Linnaeus and many subsequent authors based new species upon figures from Seba's work." Seba's annelids are not new forms or many, but he has a natural-looking presumed amphinomid (Fig. 1.2) among arthropod *scolopendra*, perhaps the first color *Aphrodita*, and his *penicillum marina* appears to be a serpulid bare of its tube.

A major illustrated popular work of the 1790s, George Shaw's "The Naturalists' miscellany" (Shaw and Nodder 1789–1813), contains dual Latin/English text by Shaw introducing over 1,000 hand-colored plates from the global fauna, haphazardly ordered, and drawn by the Nodder family. This commercial venture is notable for introducing numerous new species names, including for echidna and platypus. As it was issued as a monthly part-work of a few plates each, sold for one shilling and sixpence, and to be bound later as volumes were completed, there was much dating uncertainty in taxonomy later (Dickinson *et al*. 2006). How did the annelids rate among the vibrant exotic birds and strange quadrupeds? Their appearances could not have enthused the English public for the group – a leech plate, some uninteresting serpulid tubes, an *Amphitrite* (here a limp-looking Mediterranean sabellid), and a more life-like amphinomid as *Terebella rostrata* from Indian seas, perhaps *A. rostrata* (Pallas, 1766).

Around the same time as Shaw's series, James Sowerby (1806: plate 51) published a splendid hand-colored figure of a realistic pectinariid and its cone tube as *Nereis pectinata* (Fig. 1.8). George Brettingham Sowerby II (1812–1884) illustrated later editions of Kingsley's *Glaucus*... (Kingsley 1873) with colorful marine biota scenes. There are *Sabella*, *Serpula*, and a "*Terebella*" (=*Lanice*), but most interesting is the "*Siphunculus Bernhardus* in shell of *Turritella*," an observation of a sipunculan using a shell in a hermit-crab-like manner – as they do. About three decades later, Ernst Haeckel (1904) published his "Kunstformen der Natur" (art forms of nature), a much-admired and influential work of 100 plates, including one for various Chaetopoda. Altogether, Haeckel's art is spectacular and stylish, with overriding themes of symmetry and organization. It should be successful for the metameric form of annelids, but those familiar with the live worms of his color plate 96 might think that his depictions look more like prototypes for plastic toys—not real, but we know approximately what they are supposed to be.

Those, other than authors, who did the technical plates of annelids are largely anonymous to readers, unless they check the exhaustive compendium of Nissen (1969). Due recognition is not helped by the usual practice of signing plates with initials only. Artist Pierre Lackerbauer in the mid-nineteenth century is one exception, as he signed his name in full and is known to have illustrated many taxa. In Moquin-Tandon and Lackerbauer (1866: 380, plate 21), he has a magnificent color plate of a multispecies group of worms on the sea bottom (Fig. 1.9). The worms, including a swimming nereidid epitoke, are in vivid natural pose, albeit somewhat diagrammatic in finer detail. His next plate is a convincing *S. spallanzanii* shown in situ (as "Sabelle unispirale" plate 22), drawn from a live aquarium specimen at Concarneau. Around the same time Quatrefages (1866b) had produced figures with superior anatomical detail (Fig. 1.10) and initialed his own monograph color plates (as ADe Q del.). It looks very much like Lackerbauer had used certain of those as models;

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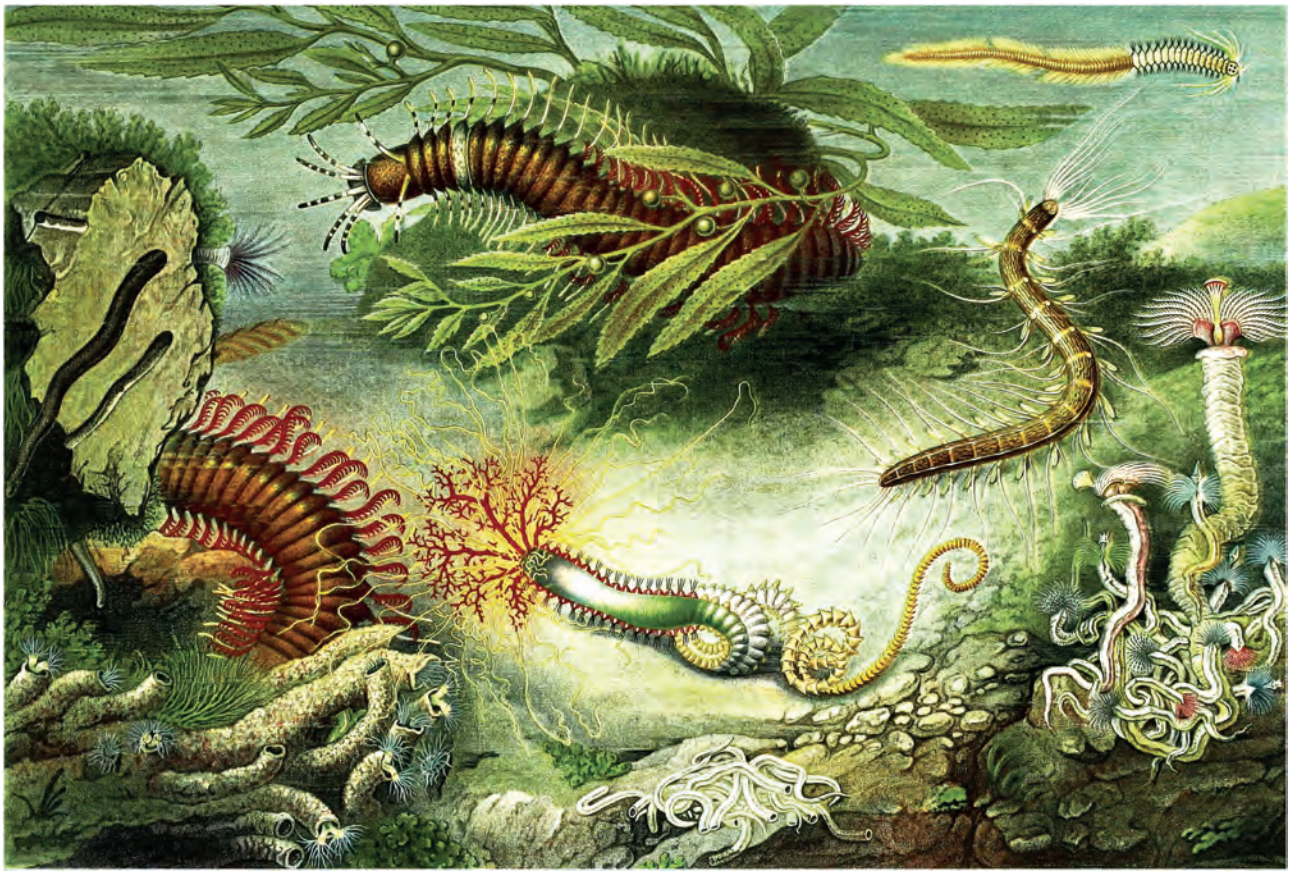

**Fig. 1.9:** Moquin-Tandon and Lackerbauer (1866 plate 21) plate by artist Pierre Lackerbauer of a multispecies group of worms on the sea bottom. Original at https://www.biodiversitylibrary.org/page/2073453

notably, the *Terebella* of his plate 21 matches plate 14 in Quatrefages.

Three family-associated and strictly amateur artists are Liza Dorville (1760s–1844), illustrating for her partner George Montagu; Catherine Johnston (1794–1871), artist for her husband George Johnston; and Roberta McIntosh (1842–1869), artist for her brother William McIntosh. William was also a skilled artist but was very proud of his young sister's work and arranged for exhibitions of her annelid paintings (Gunther 1977). Liza Dorville, who inspired genus *Dorvillea*, is said to have learned on the job, getting more skilled later (Cleevely 1978). Liza did a spectacular first illustration of what became *Myxicola infundibulum* (Fig. 1.6), although the worm tube she shows as free is in nature embedded in mud. Gosse (1853) wrote of Catherine: "The skilful pencil of Mrs. Johnston, employed in the delineation of the interesting forms that stand on the verge of animal life, has succeeded in presenting them to us with peculiar truth and beauty." He named *Johnstonella catharina* for her [sic for Catherine]. Roberta's most famous and popular worm painting is of a green sinuous *Alitta virens*, which has been widely reproduced in books (e.g., as an uncredited full-page plate in *Traité de Zoologie*, Avel *et al*, 1959) and once appeared on the front page of a leading journal of science. Sadly, Roberta died young. McIntosh dedicated the first *British Annelids* monograph of 1874 to her, and much later, Ada Hill Walker (1879–1955) did the figures for McIntosh. Unfortunately, little can be found on Ada and her connection to McIntosh, although her art features in nearly 60 plates of the monographs. She was inter alia a St. Andrews art teacher and painted local scenes. McIntosh (1923: xi), in the final *British Annelids*, noted that "for many years [she] has, with rare ability, drawn the annelids from life and represented the typical structures under the microscope."

A demonstration of the variation in skill of representation, and particularly the increase in detail possible as decades pass and printing quality improves, is given in Parapar and Hutchings (2015: figs. 2 and 3), who show the successively more realistic drawings of the no-longer "cosmopolitan" *Terebellides stroemii* Sars, 1835 published by authors, beginning with the very basic first attempt by Sars, with the suggestion that the recent ones might reveal more than one species.

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**Fig. 1.10:** Terebellidae painted by Quatrefages (1866b plate 19): main painting *Terebella edwardsii* Quatrefages, 1866 (now *Neoamphitrite*); at the bottom right, an unidentified terebellid; other objects visible are not terebellid related. No scale (scan by GBR from original).

Photography had become available after 1839, but at first, there were severe technical limitations on what live fauna could be illustrated from life, so early photographs were of rigidly dead taxa (Bridson 1989). Use in microscopy was found to be easier and is covered in the next section. In some non-microscope-based early appearances, Darwin (1881) presents earthworm cast piles as engravings taken from photographs. Half-tones, allowing integrated machine printing of photographs with text, did not come into regular use until the early 1880s (Bridson 1989). By the early twentieth century, Enders (1909) had photos of *Chaetopterus* bodies, tubes, and beach occurrences in *Journal of Morphology*, and Walcott (1911) presented numerous Burgess-shale Cambrian fossil photos, including of the *Canadia* polychaetes (plate 23) and other fossils then misinterpreted as annelids. Malaquin and Carin (1914, war-delayed to 1922) had body photographs of *Tomopteris*, and Caullery (1915) presented, in a use for demonstrating an unusual interaction, a photograph of a *Polycirrus* with two large copepod parasites attached on the body. Thus, publication of photographs for annelid research was becoming more commonplace, but it is likely that in journals, there were restrictions or special costs for authors including photographic figures in articles, as there still are today for some, whereas for photos in monographs and books, the cost was proportionately less.

## 1.12 Microscopy and photomicrography

> ...my microscope and lenses revealed an infinite world to my eyes, my pencils and brushes enabled me to secure rough illustrations of these treasures to be filled up at some future time with more care and exactitude... (Quatrefages 1857: vol. 1: 57)

> ...the figures of such minute objects highly magnified under a microscope; the eye which examines, and the pencil which delineates them, will occasionally vary... (Montagu 1803: 190)

What optical aids did annelid researchers have before the twentieth century? Also, might occasional misinterpretations occur with early poor optics, like the imaginary canals on Mars seen through a telescope by straining eyes? Specimen detail better-than naked-eye from use of low-power magnifying hand lenses and spectacles was available around CE 1300 before the early microscopes were developed from the early 1600s onward (Carpenter and Dallinger 1901). There were early low-power compound microscopes as used by Hooke of *Micrographia* fame, but at first, a much higher magnifying power could be achieved with just a single bead-like lens attached to a specimen-support that could be focused. By 1690, an improved microscope design with rack and pinion and a substage condenser had been created (Blackham 1882). By the early nineteenth century, microscope usage was widespread, but good instruments, each carefully handmade, were evidently expensive and still scarce until the 1840s, at least in Britain (Allen 1976, Cleevely 1978). Nevertheless, Devon naturalist Montagu became a keen microscopist, with its aid referred to many times in his writings of 1808 and before, especially in *Testacea Britannica* (Montagu 1803), which includes many polychaetes. He was occasionally unfairly criticized for seeing things that were not there (*fide* Cleevely 1978), but his comment quoted earlier appears in context to be a not-too-subtle jab at another worker.

By 1831, young Charles Darwin was well set up for microscopy as he had purchased a Bancks single-lens unenclosed microscope to take on the *Beagle* voyage (Keynes 2000). It was a remarkably versatile simple system, with a set of several lenses, and could be used for reflected light dissecting as well as transmitted light (Ford 2009). However, by the 1840s Quatrefages (1857: 5) was travelling with a more sophisticated compound Oberhäuser drum

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microscope which he thought was excellent. Correction of compound microscopes for chromatic aberration (multicolored edge artifacts) via achromatic lenses had first appeared around the later 1820s from a design by Lister (Blackham 1882). By the 1880s, Langerhans is known to have preserved his small polychaetes from Madeira on microscope slides, which still exist today (see "Tracking Specimens" section). Also, by the 1880s, researchers were producing excellent histological figures by using compound microscopes (e.g., Vejdovsky 1878 on *Tomopteris*, 1884 on Oligochaeta). Also, indicative of the increased public interest, there was a "Postal Microscopical Society" established in the 1870s (and still going) that circulated parcels of interesting slides. It had a short-lived journal which inter alia published an article on *Tubifex* (Hammond 1882).

Annelid researchers need good "dissecting" microscopes as well as compound microscopes. Several optical designs of twin-eyepiece microscopes with prisms splitting light from a single objective were tried from the mid-1800s, including that of Nachet, but twin-objective stereo-binocular dissecting microscopes, image not reversed (which is the popular Greenough system as still used today), were not manufactured until the 1890s, and the addition of a further common main objective and continuous zoom did not appear until the late 1950s (Wise 1950, Sander 1994, Chambers 2014). Viguier (1886: 350) used a Nachet microscope for studies on live *Alciope* and *Iospilus*. Pierantoni (1908: 125), searching samples for live *Protodrilus*, was an early adopter of the Zeiss Greenough microscope. Meyer's (1887) microscope technique is not explained, but he produced brilliant figures of dissected *S. spallanzanii* internal anatomy (Fig. 1.11).

The camera lucida, an optical drawing tool for artists, was invented by Wollaston, who published a design in 1806 (Usselman 2015). Naturalists and taxonomists, with their need for accurate illustration, soon tried out the instrument and have been keen users ever since. Quatrefages (1857: 59) took his on his travels but confessed that the mirror became ruined by a flood of seawater. There is no indication that he used it attached to his microscope, but Mörch (1863: 483) might have done so for his camera lucida operculum figures, and Allen (1904: 148) certainly did use one later to draw his microtomed and stained sections of *Poecilochaetus*. The microtome itself, an important histological tool for cutting serial tissue slices for microscopy, much finer than could be cut by hand, has an unclear history, but its development had begun in the late 1700s, and a century later, Allen (1904: 85) tells us his was made by Jung, evidently by then a standard design.

It has long been the custom for respected biologists to be photographed for a portrait sitting alongside their microscope, although sometimes it might be an obsolete ornament included to add ambience, so there was no guide to what technology was in use at the time. A nice example of this ambivalence is a 1928 photograph of an elderly Professor McIntosh, obviously posing for the camera, not using the antique monocular microscope alongside him but instead peering through a magnifying glass (Gunther 1977). In contrast, the Japanese polychaete worker Minoru Imajima (1930–2016), noted for his fine illustrations, is photographed with what are clearly his working microscopes (Sato-Okoshi 2017).

Photomicrography, demonstrated by Delves (1853) only 14 years after photography was possible, was an early successful application for reaching "beyond the limits of human vision" (Bridson 1989). Viguier (1886: 349) implies that photomicrography was common at the time he wrote. He took photomicrographs of alive, but likely anesthetized, pelagic polychaetes, but his figures are drawings from the photographs, and likewise, Whitelegge's (1890) *Polydora* larva drawings are "from a photomicrograph." Half-tone printing of "real" photographs (see previous section) was still recent technology, but by 1914, Malaquin and Carin (publication delayed until 1922) had prepared plates of multiple *Tomopteris* photomicrographs.

While ordinary light microscopy is still the basic tool for annelid biologists, scanning electron microscopy (SEM), with its great depth of field removing the ambiguity of interpreting narrow focal planes, is also particularly useful for annelid chaetal structure and body microornamentation, and its use has been commonplace since the 1970s. The first use for annelids has not been determined, but Holborow (1971) and Gustus and Cloney (1973) are early users for trochophores of *Harmothoe imbricata* and chaetae of *Nereis vexillosa*, respectively, and by 1984, the *Proceedings of the First International Polychaete Conference* has four articles using SEM images, mostly for chaetal structure. Like computers, SEM size has reduced, and now, instead of a large, dedicated room, desktop models can be of similar dimensions to an optical microscope. Specialist high-resolution SEM machines, usually equipped with field emission illuminating systems, are still large and expensive but allow observations of very delicate structures.

Whereas SEM techniques are primarily applied for clarifying taxonomical questions and enabling sophisticated species descriptions, transmission electron microscopy has greatly increased knowledge of ultrastructural annelid morphology and anatomy since the 1960s. The first structures to be studied in annelids were integument (epidermis and cuticle), chaetae, musculature, and sense organs, especially eyes (e.g., Eakin and Westfall 1964,

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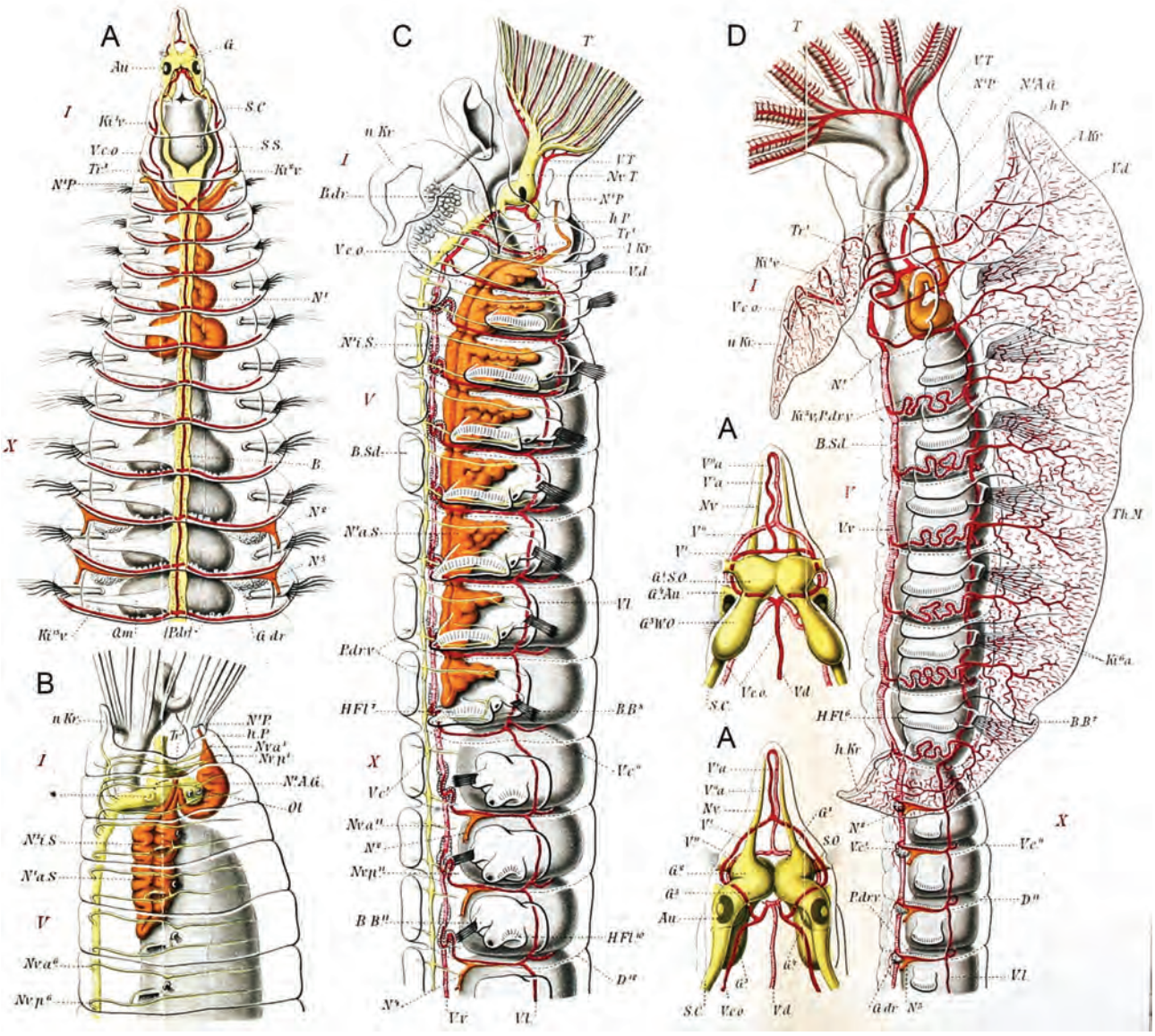


**Fig. 1.11:** Annelid internal anatomy reconstructed by Meyer (1887: plate 23) from serial sections with orange, red, and yellow as nephridial, circulatory, and nerve structures, respectively, no scale. Figures (plate right side) relabeled here. A, Cirratulid *Chaetozone setosa* (three figures); B, sabellid *Myxicola infundibulum*; C, sabellid *Sabella spallanzanii* (as *Spirographis*); D, serpulid *Protula tubularia* (as *Psygmobranchus protensus*). Original at https://biodiversitylibrary.org/page/47101780

Röhlich and Török 1964, Krasne & Lawrence, 1966). Bartolomaeus and Purschke (2005) and Purschke *et al.* (2014) have reviewed the many studies of annelid ultrastructure since published.

Phase contrast light microscopy for live transparent cells and semitransparent larvae has been available since the 1930s, but the halo around objects is a drawback, and differential interference contrast (or Nomarski) microscopy, available from the 1950s, may give superior detail, although both are useful (Fig. 1.5). Confocal laser scanning microscopy (CLSM), coupled with immunohistochemistry, can be used to investigate the structure and function of cell types within annelids. Worsaae and Rouse (2010) have an early use on males of *Osedax* bone-worms. Finally, while not strictly microscopy, microcomputed tomography (X-ray microtomography) is being adapted to study three-dimensional structures in annelids that are difficult to visualize by other techniques (Faulwetter *et al.* 2013). Although currently providing less resolution than conventional microscopes and CLSM, the main advantage of this method is that it is nondestructive, allowing investigation of internal structures even in valuable museum types.

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## 1.13 Encyclopedic works and their role

We expect encyclopedias and dictionaries to be distillations of information already published elsewhere, just like *Wikipedia*, today's all-encompassing online encyclopedia, with its "no original research" dictum. However, this was not the policy of early encyclopedists, notably those in France, for their works were good opportunities for advocacy of new ideas and even for presenting original taxonomy, with new classifications, and new species (sometimes deliberate, sometimes unintentional). In France, during the late eighteenth through to the first half of the nineteenth century, there was a drive to show new natural history knowledge to the public via ambitious publishing projects, involving the many eminent scholars associated with the Paris museum and using "collection du museum" specimens for the taxonomy. Today, there are many thousands of pages of French erudition accessible to us in sets of volumes via the BHL digitizations, but the long years of laborious production, the sheer quantity, the often-similar short versions of titles (variations on *Histoire* [or *Dictionnaire*] *Naturelle des*...), and the various editions do make for confusion over the relative timelines and over who were the authors/editors.

The most prominent mid-eighteenth century French true encyclopedia was probably the *Encyclopédie*, *ou dictionnaire raisonné des science*s, edited by Diderot and d'Alembert, but if they put in worm content, then it is hard to find. The pioneer for the field of natural history was their influential contemporary, Comte de Buffon (1707–1788), with an illustrated highly successful series titled *Histoire naturelle*, *générale et particulière avec la description du Cabinet du Roi* of 1749–1788. However, lesser known is that this series, and its later editions and translations, got no further than the vertebrates. Even so, Buffon's name was used in later titles, including invertebrates, notably the various editions of the so-called *Les Suites à Buffon*... (sequels to Buffon, also as *Novelles Suites à Buffon*), a series title inferred but usually missing on title pages. Table 1.2 is an outline of some of the major works published in Paris during several productive decades to 1850, in first-volume date order. The influential authors for annelid taxonomy are Lamarck (1744–1829), with his 1818 *Histoire naturelle*... and over 100 annelid names, and Savigny (1777–1851) in the 1822 *Description de l'Égypte* (36 annelid names, discussed later), whereas Cuvier (1769–1832), with his 1817 *Règne Animal*, although famous worldwide and much translated, was relatively weak on annelids. Quatrefages' (1810–1892) *Histoire Naturelle des Annele*s... of 1866 is more significant than any of the preceding works, and is included in the table as a natural late part of the *Suites à Buffon* series, but was published beyond the half century.

Savigny was one of the adventurous "savants" who travelled to Egypt to study its natural history while the Napoleonic army was there and at 21 years old was a junior biologist of the team. From 1802, he worked in Paris on the collections made, including preparing many plates, but his later career did not go well due to eye disease, and he finally became a near-blind recluse. The use of Savigny (1822) manuscript-derived information, adapted to be included in Lamarck (1818), is contentious regarding present-day "credit" or priority via authorship for names that may have been devised by Savigny but for which the associated species were described by Lamarck first, due to the delayed and spaced-out publication of *Description de l'Égypte* works (see background in Álvarez-Campos *et al*. 2015). Strictly, what is published in Lamarck is text written by Lamarck; species authorities are utilitarian, not hinging on modern notions of fair-play.

In contrast to the enthusiastic French biologist-encyclopedists, the authors of the English-language *Encyclopedia Britannica* first edition 1768–1771 contributed nothing significant on annelids (as Vermes), and even for the 11th edition (1910–1911), the Annelida entry was still very short. However, a somewhat anomalous early nineteenth century entry written by the British Museum's William Elford Leach (5th edition supplement, ~1816) included Vermes in "Annulosa" and had a classification with much information and even introduced new Polychaeta taxa with figures, including the well-known genera *Lepidonotus* and *Cistena* (decreed a synonym of *Pectinaria*). In the twentieth century, after production had moved to the United States, Olga Hartman wrote a long Polychaeta entry in the 14th edition *Britannica* of the 1960s. The main Annelida article, first written in the late 1940s, was by endocrinologist Grace Evelyn Pickford (1902–1986), who had done her doctoral thesis on African earthworms, and the Hirudinea section was by J. Percy Moore (1869–1965), better known for his Polychaeta work.

Also, various late nineteenth to early twentieth century book series, intended as overviews of all biota for an undergraduate to research level of understanding, summarized annelid information, sometimes in vast detail. William Benham (1896) in the *Cambridge Natural History* had his own version of a higher classification for Annelida, created suborder Spioniformia, and proposed a separate family Polydoridae for the *Polydora*-like genera. At around the same time (1900), his mentor Ray Lankester was series editor for an intended eight-volume *A Treatise on Zoology*' but an annelid volume did not appear. The

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**Tab. 1.2:** Overview of French encyclopedia-style works between 1750 and 1850 that are relevant to annelids.

| Main editor | Dates | Title and content description |
|---|---|---|
| Buffon, Comte de (Georges-Louis Leclerc) and later Lacépède, Étienne de | 1749–1788, 1788–1804 | *Histoire naturelle, générale et particulière avec la description du Cabinet du Roi*: 36 volumes + 8 under Lacépède; volumes by taxa group and within by informal categories (e.g., Oiseaux de proie. Des aigles) and species by French names (taxonomy as footnotes); discursive style; *vertebrates only*; many editions and translations followed. |
| Bomare, Valmont de | 1764 | *Dictionnaire raisonné universel d'histoire naturelle*: five volumes (ultimately 15 v. in the 4th edition of 1800); unbroken flow of encyclopedia-style entries; include Aphrodite, Nereide, etc.; no new annelid taxa; a first successful model for all subsequent dictionnaire. https://doi.org/10.5962/bhl.title.102034 |
| Panckoucke, Charles-Joseph (editor/publisher) | 1782–1832 (Vers 1789) | *Encyclopedie methodique, ou par ordre de matières*: 156 volumes; successor to the Diderot Encyclopédie; volumes by topic (otherwise, text alphabetical by genera), with 3 volumes for *Histoire Naturelle des Vers*, vol. 1, first part by Jean Guillaume Bruguière; at least eight new polychaeta names (tagged as nob. = our name), including *Amphinome*; content analyzed by Evenhuis (2003). https://doi.org/10.5962/bhl.title.8638 |
| Lamarck, Jean-Baptiste (author/publisher) | 1801 | *Systeme des Animaux sans vertebres, ou tableau general des classes…*: one-volume book; phyla chapters with annelids as "vers extérieurs" inside "vers"; at least six new annelid names. http://dx.doi.org/10.5962/bhl.title.14255 |
| Castel (series editor) Bosc, Louis Augustin Guillaume (vers author) | 1802 | *Histoire naturelles des vers, contenant leur description et leurs moeurs; avec figures dessinées d'après nature*: Imprint Chez Deterville (only on half-title page [may be missing] as in ~62 volume series *Histoire naturelle de Buffon*, or *suites à Buffon*); 3 small format volumes. Bosc also contributed crustacean and mollusca volumes; with 2nd edition 1828; 11 new annelid taxa including *Polydora*. https://doi.org/10.5962/bhl.title.64025 |
| Commission d'Egypte Savigny, Jules-Cesar (*Annelides* author) | 1809–1822 (Annelides 1822) | *Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française…*: 23 volumes; *Histoire Naturelle* vol. 1(3), a taxonomic monograph as *Système des annélides* (1822) by Savigny; 36 new annelid names. 2nd Panckoucke edition 1826; https://doi.org/10.5962/bhl.title.62506 |
| Lamarck, Jean-Baptiste (author) | 1815–1822 (Annelides 1818) | *Histoire naturelle des Animaux sans Vertèbres, présentant les caractéres généraux et particuliers…*: seven volumes, >4,100 pages; at least 107 new annelid names; with 2nd edition 1838. https://doi.org/10.5962/bhl.title.12712 |
| Cuvier, Baron (Georges Cuvier) (author, except Latreille vol. 3) | 1817 | *Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux…*: four volumes, 1,809 pages; nine new annelid names, including *Eunice*; 2nd edition 1829–1830. Multiple editions and translations followed. https://doi.org/10.5962/bhl.title.41460<br>*Iconographie du Règne Animal* is a separate work (1829–1844) of 448 new plates edited by Guérin-Méneville. |
| Saint-Vincent, Bory de | 1822–1831 | *Dictionnaire classique d'histoire naturelle*: 17 volumes; encyclopedia-style entries, with author initials; Annelides by Latrielle, *Nereis* by Audouin, etc.; two annelid color plates (using figures prepared for Savigny?); new names in molluscs, but not known for annelids. https://doi.org/10.5962/bhl.title.33901 |
| Levrault, F.G. (not Cuvier) | 1828–1845 | *Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature*: 61 volumes, encyclopedia-style entries, with author initials, vol. 57 includes *Vers* entry by Henri Marie de Blainville; about 26 new annelid taxa including *Capitella*, *Lumbrineris, Scolelepis*. https://doi.org/10.5962/bhl.title.42219 |
| Audouin, Jean Victoire and Milne Edwards, Henri | 1829 | *Précis d'Entomologie ou d'Histoire naturelle des animaux articulés. Première Division. Histoire naturelle des annélides, crustacés, arachnides et myriapodes…*: one volume; overview of families and species; seven annelid plates; no new taxa. https://doi.org/10.5962/bhl.title.1857 |
| Guérin-Méneville, Félix Édouard | 1833–1839 | *Dictionnaire pittoresque d'histoire naturelle et des phénomènes de la nature*: nine volumes; encyclopedia-style entries, with author initials; Annelides topic by Rousseau, with color plate, but other authors likely. Includes species-level annelid taxonomy. |
| Roret, Nicolas (editor, publisher de Quatrefages, Armand (author *Anneles*) | 1834–1890 | *Suites à Buffon formant avec les œuvres de cet auteur un cours complet d'histoire naturelle…*: 89 volumes under imprint *Librairie encyclopédique de Roret*; includes Quatrefages' two volume (1866) *Histoire Naturelle des Anneles…* (around 465 new annelid names); Vaillant (1889) authored a clitellates volume. |
| "Une Réunion de Disciples de Cuvier" (authors) | 1836–1849 | [Disciples edition of Cuvier, *Le Règne Animal…*] also known as "*Le règne animal illustré*" (short title used by Fauvel and Quatrefages): by Audouin, Blanchard, Deshayes, d'Orbigny, Doyère, Dugès, Duvernoy, Laurillard, Milne Edwards, Roulin et Valenciennes; 22 undated volumes (but see Cowan 1976 for collation), Les Annelides vol. 9; text nearly unchanged from Cuvier 1817, but volumes of plates by Milne Edwards and Quatrefages added nine new annelid names. https://doi.org/10.5962/bhl.title.39612 |
| d'Orbigny, Alcide… Dessalines | 1847–1849 | *Dictionnaire universel d'histoire naturelle*: (editor) 13 volumes, three atlases of plates; encyclopedia-style entries, with author initials; Annelides and Vers, etc., by Paul Gervais; one annelid color plate, one new annelid name. https://doi.org/10.5962/bhl.title.23115 |

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two-volume Parker and Haswell (1910) *A Text-Book of Zoology* was the next standard in English of its day. The authors used Gephyrea as a class in "Annulata" alongside class Chaetopoda for polychaetes and oligochaetes. Later, the *Traité de Zoologie* series third edition for annelids (Avel *et al*. 1959) was a stunning achievement, with over 1,100 pages of high-quality printing (Fauvel wrote the polychaete sections). For zoologists based in Germany, Austria, Switzerland, and the Netherlands, as well as the Scandinavian Countries, some *Handbuch der Zoologie* titles with different lead editors were published that included annelids, of which the 1930s Kükenthal and Krumbach edition has already been mentioned and is the most well known. The massive series *Das Tierreich*, initiated by *Deutschen Zoologischen Gesellschaft*, has a taxonomy scope only, and for annelids, only the Oligochaeta volume was published (Michaelsen 1900).

More recent single-volume works intended for student purchase were the multiple editions (8th in 2009) of *Invertebrate Zoology* by Robert D. Barnes (later with E. Ruppert), from which for decades many English-speaking university students worldwide had their first taste of annelid biology and diversity. The first edition (Barnes 1963) was reviewed by no less than Libbie Hyman, famed American author of the influential six-volume McGraw-Hill *The Invertebrates* series (published 1940–1967). Hyman never managed to do the seventh volume, intended to be annelids and echiurans, but in 1959, McGraw-Hill had published her volume 5, *Smaller Coelomate Groups*, which included the pogonophorans and sipunculans (Hyman 1959). Later, the Brusca and Brusca–initiated *Invertebrates* (1st edition 1990) became a rival to the Barnes work, and Greg Rouse has authored the 2016 3rd edition Annelida chapter, cautiously subtitled *The Segmented (and Some Unsegmented) Worms* (Rouse and Giribet 2016).

## 1.14 Educators and popularizers

> Worms [...] are out every mild night in the winter, as any person may be convinced that will take the pains to examine his grass-plots with a candle; are hermaphrodites and much addicted to venery, and consequently very prolific. (White 1789)

> "Oh! Papa," cried May, "I do think here is a sea-mouse lying on the shore. Bah! I don't much like to touch it." [...] "I do not think, papa," said Jack, "that it looks much like a worm." (Houghton 1870: 11)

> You are going down, perhaps, by railway, to pass your usual six weeks at some watering-place along the coast, and as you roll along think more than once, and that not over-cheerfully, of what you shall do when you get there... (Kingsley 1855, *Glaucus*..., opening sentence)

There have been many popularizers of nature. Gilbert White (1789), quoted from the classic and much reprinted *Natural History of Selbourne* collection of letters to friends, did not overlook reporting on the local earthworm reproductive activity of his rural setting. At the coast, Houghton's (1870) book of seaside walks used a similar literary device, and if his quotes seem too contrived today, nevertheless, his observation rings true. *Aphrodita* do strand just as he described, do not look like worms, and what follows in Houghton is a page or so of believable detailed information. This conversational or letter-to-a-friend style gradually lost its appeal in favor of a more scientific presentation according to Moore (2014), who reviews the many works of a seaside-visit self-improvement genre, published in the British Isles between the mid-nineteenth and early twentieth century. The best-known early exponents were Philip Gosse, author of *A Naturalist's Rambles*... and *The Aquarium*), and Charles Kingsley, friend of Darwin, author of *Glaucus or, the Wonders of the Shore* (for the annelids, see earlier section on illustration). Such works were knowledge reportage and might describe live behaviors and interactions that were not yet recorded or widely known elsewhere, particularly by taxonomists. Also, in Britain, for a time in the mid-nineteenth century, keeping marine aquaria became a national craze according to Allen (1976: 138–140), with a railway-travelling, more literate public having an appetite for learning about natural history for themselves, although consequently, the accessible coastal stretches "were largely stripped of their attractive inhabitants."

In the twentieth century, local seashore guides of various levels of understanding and readability that included annelids were common enough. At the upper technical end, the "Light's Manual" for Californian shores is a classic, first published 1941 for S.F. Light's summer field course for Berkeley students (attended by Olga Hartman in 1933), and now in the 4th edition (Carlton 2007) as a bulky tome of 1,000 pages, with six Annelida editors, but lacking worm photographs. More typical is Morton and Miller's (1968) local classic *The New Zealand Sea Shore*, structured by habitats, with a conversational style, but science based, using binominals not invented vernaculars, with sets of photographs and color plates, and presenting new information on New Zealand annelid occurrences. Another recent genre containing marine annelids are the diver-generated field guides with an array of miniature color photographs and minimal text, such as the *Reef Creature Identification* series (e.g., Humann 2010), with its identifications checked by experts.

Photograph-based community identification sites where scientists and citizens can interact for mutual benefit to reach "research-grade" identifications (e.g.,

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www.inaturalist.org) are a new tool and a source of useful distribution data for scientists. Also, a stunning feature of science outreach to the public today, with direct viewing replacing written reportage, are the live streamings worldwide of video from ROV deep-sea explorations from ships such as the *Nautilus*, *Falkor*, and *Okeanos Explorer* during voyages in 2016–2017 (reviewed in Bell *et al*. 2017, Raineault *et al*. 2018). Live streaming, with further social media transmission, has been very popular with the public and equally so with scientists, who can see for the first time such unusual annelids as swimming squid worms, live siboglinid colonies around vents and seeps, polynoids and alvinellids feeding millimeters away from dangerously hot hydrothermal fluid, methane-ice hesionids, and caterpillar-crawling *Hyalinoecia* quill worms.

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## 1.16 References

Aguado, M.T., Glasby, C.J., Schroeder, P.C., Weigert, A. & Bleidorn, C. (2015): The making of a branching annelid: an analysis of complete mitochondrial genome and ribosomal data of *Ramisyllis multicaudata*. *Scientific Reports (Nature)* 5.

Aguinaldo, A.M.A., Turbeville, J.M., Linford, L.S., Rivera, M.C., Garey, J.R., Raff, R.A. & Lake, L.A. (1997): Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* 387: 489–493.

Aldrovandi, U. (1602): *De animalibus insectis libri septem, cum singulorum iconibus ad viuum expressis*. Ioannem Baptistam Bellagambam, Bologna.

Allen, D.E. (1976): *The naturalist in Britain: a social history*. 1st Ed. Allen Lane, London.

Allen, D.E. (1993): Natural history in Britain in the eighteenth century. *Archives of Natural History* 20: 333–347.

Allen, D.E. (1996): The struggle for specialist journals: natural history in the British periodicals market in the first half of the nineteenth century. *Archives of Natural History* 23: 107–123.

Allen, E.J. (1904): The anatomy of *Poecilochaetus*, Claparede. *Quarterly Journal of Microscopical Science*, *London* (new series) 48: 79–151.

Álvarez-Campos, P., Gil, J. & San Martín, G. (2015): Unveiling the Rosetta Stone of syllids: redescription and neotype designation of *Syllis monilaris* Savigny in Lamarck, 1818, type species of type genus of family Syllidae Grube, 1850 (Annelida). *Zootaxa* 4040: 317–330.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Anon (1665): Observations about shining worms in oysters. *Philosophical Transactions* 1: 203–206.

Apakupakul, K., Siddall, M.E. & Burreson, E.M. (1999): Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. *Molecular Phylogenetics and Evolution* 12: 350–359.

Appeltans, W., Read, G.B., Appeltans, W., *et al*. (2012): The magnitude of global marine species diversity. *Current Biology* 22: P2189–2202.

Ashworth, J.H. (1912): *Catalogue of the Chaetopoda in the British Museum*. *A. Polychaeta: Part. 1. Arenicolidae*. British Museum, London.

Avel, M., de Beauchamp, P., Brien, P., Dawydoff, M. et al. (1959): Traité de Zoologie. Anatomie, Systématique, Biologique. Tome V(1). Annélides, Myzostomides, Sipunculiens, Echiuriens, Priapuliens, Endoproctes, Phoronidiens. Masson et Cie, Paris.

Baird, W. (1865): Description of several new species and varieties of tubicolous annelides (=Tribe Limivora of Grube), in the collection of the British Museum. *Zoological Journal of the Linnean Society*., 8, 10–22, pls1–2.

Baird, W. (1869): Remarks on several genera of annelides, belonging to the group Eunicea, with a notice of such species as are contained in the collection of the British Museum, and a description of some others hitherto undescribed. *Journal of the Linnean Society of London, Zoology*, 10, 341–361.

Barnes, R.D. (1963): *Invertebrate zoology*. Saunders, Philadelphia.

Bartolomaeus, T. & Purschke, G. (eds.) (2005): Morphology, Molecules, Evolution and Phylogeny in Polychaeta and related taxa. *Developments in Hydrobiology* 179, 1–387.

Beekman, E.M. [translator] & Rumpf, G.E. (1999): *The Ambonese Curiosity Cabinet*. Yale University Press, New Haven, CT; London.

de Beer, G.R.C. (1953): Sir Hans Sloane and the British Museum. *The British Museum Quarterly* 18: 2–4.

Bell, K.L.C., Flanders, J., Bowman, A. & Raineault, N.A. (2017): New frontiers in ocean exploration: The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2016 field season. *Oceanography* 30: 1–94.

Benham, W.B. (1896): Archiannelida, Polychaeta, Myzostomaria. In: Harmer, S.F. & Shipley, A.E. (Eds.) *The Cambridge Natural History*. Macmillan and Co. London: 241–334.

Benham, W.B. (1904): On some edible and other new species of earthworms from the North Island of New Zealand. *Proceedings of the Zoological Society of London* (year 1904): 220–263.

Bhaud, M. (1972): Identification des larves d'Amphinomidae (annélides polychètes) recueillies près de Nosy-Bé (Madagascar) et problèmes biologiques connexes. *Cahiers O.R.S.T.O.M. Série Oceanographie* 10: 203–216.

Blackham, G.E. (1882): President's address: the evolution of the modern microscope. *Proceedings of the American Society of Microscopists* 4: 25–47.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

de Blainville, H. (1816): Prodrome d'une nouvelle distribution du regne animal. *Bulletin des Sciences par la Société Philomatique de Paris* year 1816: 113–124.

Blakemore, R.J. (2009): Cosmopolitan earthworms – a global and historical perspective. In: Shain, D.H. (ed.) *Annelids in Modern Biology*. Wiley-Blackwell, Hoboken, New Jersey: 257–283.

Blanchard, R., Maehrenthal, F.v. & Stiles, C.W. (1905): *Règles internationales de la nomenclature zoologique adoptées par les congrès internationaux de zoologie: International rules of zoological nomenclature. Internationale regeln der zoologischen nomenklatur*. F.R. de Rudeval, Paris.

Bonnet, C. (1742): An abstract of some new observations upon insects: By M. Charles Bonnet of Geneva. Communicated in a letter to Sir Hans Sloane, Bart. Late president of the Royal Society & Translated from the French by P. H. Z. Esq; F. R. S. *Philosophical Transactions* 42: 458–488.

Boore, J.L. (2001): Complete mitochondrial genome sequence of the polychaete Annelid *Platynereis dumerilii* [letters to the editor]. *Molecular Biology and Evolution* 18: 1413–1416.

Boore, J.L. & Brown, W.M. (1995): Complete sequence of the mitochondrial DNA of the annelid worm *Lumbricus terrestris*. *Genetics* 141: 305–319.

Boore, J.L. & Brown, W.M. (2000): Mitochondrial genomes of *Galathealinum*, *Helobdella*, and *Platynereis*: sequence and gene arrangement comparisons indicate that Pogonophora is not a phylum and Annelida and Arthropoda are not sister taxa. *Molecular Biology and Evolution* 17: 87–106.

Bostock, J. & Riley, H.T. (1855): *The Natural History of Pliny [Annotated Translation of Historia Naturalis]*. Vol. 2. Henry G. Bohn, London.

Bourlat, S.J., Nielsen, C., Economou, A.D. & Telford, M.J. (2008): Testing the new animal phylogeny: A phylum level molecular analysis of the animal kingdom. *Molecular Phylogenetics and Evolution* 49: 23–31.

Bridson, G.D.R. (1968): The zoological record – a centenary appraisal. *Journal of the Society for the Bibliography of Natural History* 5: 23–34.

Bridson, G.D.R. (1989): From xylography to holography: five centuries of natural history illustration. *Archives of Natural History* 16: 121–141.

Brinkhurst, R.O. (1999): Retrospect and prospect: reflections on forty years of study of aquatic oligochaetes. *Hydrobiologia* 406: 9–19.

Brinkhurst, R.O. & Jamieson, B.G.M. (1971): *Aquatic Oligochaeta of the world*. Oliver and Boyd, Edinburgh.

Brookes, R. (1763): *A New and Accurate System of Natural History (vol. 4). The Natural History of Insects, With Their Properties and Uses in Medicine*. J. Newbery, London.

Burrows, W. (1955): Palolo. Notes on the periodic appearance of the annelid worm *Eunice viridis* (Gray) in the southwest Pacific Islands. *Journal of the Polynesian Society* 64: 137–154.

Carlton, J.T. (ed.) (2007): *The Light and Smith Manual. Intertidal Invertebrates from Central California to Oregon*. 4th edition (previously as Light's manual.) University of California Press, Berkeley.

Carpenter, W.B. & Dallinger, W.H. (1901): *The Microscope and Its Revelations*. 8th ed. J. & A. Churchill, London.

Carter, H.B., Judith, A.D., Humphries, C.J. & Alwyne, W. (1981): The Banksian natural history collections of the Endeavour voyage and their relevance to modern taxonomy. *Archives of Natural History* 1981 special issue. History in the service of systematics, 61–70.

Caullery, M. (1914): Sur les Siboglinidae, type nouveau d'invertebres receuillis par l'expedition du Siboga. *Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences* 158: 2014–2017.

Caullery, M. (1915): Sur les Térébelliens de la sous-famille Polycirridae [sic] Malmgr. 1. Délimitation des genres. 2. *Polycirrus arenivorus* n. sp. *Bulletin de la Société Zoologique de France* 40: 239–248.

Caullery, M. (1944): *Siboglinum* Caullery, 1914. Type nouveau d'invertebres, d'affinites a preciser. *Siboga-Expeditie, Leiden Monographie* 138 (monograph 25): 1–26.

Chambers, B. (2014): More zoom in stereo microscopy. *Quality Magazine*.

Chancellor, G., DiMauro, A., Ingle, R. & King, G. (1988): Charles Darwin's beagle collections in the Oxford University Museum. *Archives of Natural History* 15: 197–231.

Charmantier, I. & Müller-Wille, S. (2014): Carl Linnaeus's botanical paper slips (1767–1773). *Intellectual History Review* 24: 215–238.

Claparède, E. (1866): Remarks on Quatrefages' notes on the classification of the Annelids [translation]. *Annals and Magazine of Natural History* 17 (series 3): 100–107.

Claparède, E. (1868): *Les Annélides Chétopodes du Golfe de Naples*. Ramboz et Schuchardt, Genève.

Clark, R.B. (1961): The origin and formation of the heteronereis. *Biological Reviews* 36: 199–236.

Claus, C. & Moquin-Tandon, G. (1884): *Traité de zoologie*. 2nd ed. 2. éd. française, traduite de l'allemand sur la 4. éd., entièrement refondu et considérablement augm./par G. Moquin-Tandon. Ed. F. Savy, Paris.

Cleevely, R.J. (1978): Some background to the life and publications of Colonel George Montagu (1753–1815). *Journal of the Society for the Bibliography of Natural History* 8: 445–480.

Coenen, A. (1578): Visboeck (Fish book). In: *Medieval Manuscripts*. Koninklijke Bibliotheek, National Library of the Netherlands, Scheveningen, the Netherlands. p. 410 leaves. With watercolour drawings made by himself.

Cowan, C.F. (1976): On the disciples' edition of Cuvier's Règne Animal. *Journal of the Society for the Bibliography of Natural History* 8: 32–64.

Cutler, E.B. (1994): *The Sipuncula. Their Systematics, Biology, and Evolution*. 1st ed. Cornell University Press, Ithaca.

Cuvier, G. (1817): *Le règne animal distribé d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparee. Volume 2. Contenant les Reptiles, les Poissons, les Mollusques et les Annélides. [Les Annélides. p. 515–532].* Deterville, Paris.

Dahlgren, T.G., Lundberg, J., Pleijel, F. & Sundberg, P. (2000): Morphological and molecular evidence of the phylogeny of Nereidiform polychaetes (Annelida). *Journal of Zoological Systematics & Evolutionary Research* 38: 249–253.

Dales, R.P. (1963): *Annelids*. 1st ed. (2nd ed. 1967). Hutchinson University Library, London.

Dance, S.P. (1967): Report on the Linnaean shell collection. *Proceedings of the Linnean Society of London* 178: 1–24.

Dance, S.P. (1989): *The Art of Natural History*. 2nd ed. Bracken Books, London.

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Darwin, C. (1840 [read 1837]): On the formation of mould. *Transactions of the Geological Society* 5: 505–509.

Darwin, C. (1881): *The Formation of Vegetable Mould, through the Action of Worms: With Observations on their Habits*. J. Murray, London.

Day, R.A. (1989): The origins of the scientific paper: the IMRAD format. *American Medical Writers Association Journal* 4: 16–18.

Delves, J. (1853): On the application of photography to the presentation of microscopic objects. *Transactions of the Microscopical Society of London* 1: 57–58, plate VII.

Dick, M.H. & Buss, L.W. (1994): A PCR-based survey of homeobox genes in *Ctenodrilus serratus* (Annelida: Polychaeta). *Molecular Phylogenetics and Evolution* 3: 146–158.

Dickinson, E.C., Bruce, M.D. & Dowsett, R.J. (2006): Vivarium naturae or the naturalist's miscellany (1789–1813) by George Shaw: an assessment of the dating of the parts and volumes. *Archives of Natural History* 33: 322–343.

Dünzelmann, A.E., König, V. & Lüderwaldt, A. (1999): *Hugo H. Schauinsland. Unterwegs in Uebersee. Aus Reisetagebüchern und Dokumenten de früheren Direktors des Bremer Übersee-Museums*. Verlag Hauschild, Bremen.

Eakin, R.M. & Westfall, J.A. (1964): Further observations on the fine structure of some invertebrate eyes. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, 62, 310–332.

Eeckhaut, I., McHugh, D., Mardulyn, P., *et al.* (2000): Myzostomida: a link between trochozoans and flatworms? *Proceedings of the Royal Society London* 267: 1383–1392.

Ehlers, E. (1868): *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Wilhelm Engelmann, Leipzig.

Ellis, J. (1755): An essay toward a natural history of the corallines and other marine productions of the like kind commonly found on the coast of Great Britain and Ireland. To which is added the description of a large marine polype taken near the North Pole, by the whale fisheries, in the summer 1753. A. Millar in the Strand, London.

Enders, H.E. (1909): A study of the life-history and habits of *Chaetopterus variopedatus* Renier et Claparede. *Journal of Morphology* 20: 479–531.

Evenhuis, N.L. (2003): Dating and publication of the Encyclopédie Méthodique (1782–1832), with special reference to the parts of the Histoire Naturelle and details on the Histoire Naturelle des Insectes. *Zootaxa* 166: 1–48.

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

Fauchald, K. (1992): A review of the genus *Eunice* (Polychaeta: Eunicidae) based upon type material. *Smithsonian Contributions to Zoology*, 523, 1–422.

Fauchald, K. (1989): The second annual Riser lecture: Eclecticism and the study of polychaetes. *Proceedings of the Biological Society of Washington* 102: 742–752.

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

Faulwetter, S., Vasileiadou, A., Kouratoras, M., Dailianis, T. & Arvanitidis, C. (2013): Micro-computed tomography: introducing new dimensions to taxonomy. *ZooKeys* 263: 1–45.

Fischer von Waldheim, G. (1808): *Tableaux synoptiques de zoognosie: publiés à l'usage de ses élèves à l'Université Impériale de Moscou [Synoptic Charts of Zoognosia: Published for the Use of Students at Moscow Imperial University]*. de l'Imprimerie de l'Université Impériale, Moscou.

Flattely, F.W. (1916): Notes on the ecology of *Cirratulus (Audouinia) tentaculata* (Montagu). *Journal of the Marine Biological Association of the United Kingdom* 11: 60–70.

Ford, B.J. (2009): Charles Darwin and Robert Brown – their microscopes and the microscopic image. *Infocus* 15: 19–28.

Freycinet, L.d., Quoy, J. & Gaimard, J. (1824): *Voyage autour du monde: entrepris par ordre du roi…exécuté sur les corvettes de S. M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820*. Imprimerie en taille-douce de Langlois, Paris.

Glasby, C.J. & Bailey-Brock, J. (2001): Bait-taking fireworms (Amphinomidae: Polychaeta) and other polychaetes. *Beagle* 17: 37–41.

Glasby, C.J. & Read, G.B. (1998): A chronological review of polychaete taxonomy in New Zealand. *Journal of the Royal Society of New Zealand* 28: 347–374.

Gmelin, J.F. & [Linnaeus]. (1791): *Caroli a Linné, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. [Linnaeus 13th ed., 1788 [vol. 1(1) & 1791 for Vol. 1(6)]. Vol. tome 1 (6) [vermes etc p. 3021–3910]. G.E. Beer, Lipsiae.

Goodrich, E.S. (1901): On the structure and affinities of *Saccocirrus*. *Quarterly Journal of Microscopical Science London n.s.* 44: 413–428, pls. 27–29.

Gosse, P.H. (1853): *A Naturalists Rambles on the Devonshire Coast*. John van Voorst, London.

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

Grygier, M. (2000): Class Myzostomida. In: Beesley, P.L., Ross, G.B. & Glasby, C.J. (eds.). *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 297–329.

Gunther, A.E. (1977): *William Carmichael M'Intosh, M.D., F.R.S. [aka McIntosh]*. 1st ed. Scottish Academic Press Ltd., St. Andrews.

Gustus, R.M. & Cloney, R.A. (1973): Ultrastructure of the larval compound setae of the polychaete *Nereis vexillosa* Grube. *Journal of Morphology* 140: 355–366.

Häcker, V. (1898): Die pelagischen Polychaeten- und Achaetenlarven der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* 2: 1–50, plates 1–5.

Haeckel, E. (1866): *Generelle Morphologie der Organismen: allgemeine Grundzuge der organischen Formen-Wissenschaft, mechanisch begrundet durch die von Charles Darwin reformirte Descendenz-Theorie*. Georg Reimer, Berlin.

Haeckel, E. (1883): *A visit to Ceylon* [Translated by C. Bell]. Kegan Paul & Co., London.

Haeckel, E. (1904): *Kunstformen der Natur ("Artforms of Nature")*. Verlag des Bibliographischen Instituts, Leipzig und Wien.

Hammond, A. (1882): On *Tubifex rivulorum*. *The Journal of the Postal Microscopical Society* 1: 14–21, plate 1, continued Vol. 2, 165–175.

Hargitt, C.W. (1906): Experiments on the behaviour of tubicolous annelids. *Journal of Experimental Zoology*, 3, 295–320.

Hartman, O. (1951): *Literature of the Polychaetous Annelids. Vol. I. Bibliography*. Edwards Brothers Inc., Ann Arbor, MI.

Hartman, O. (1954): Pogonophora Johansson, 1938. *Systematic Zoology* 3: 183–185.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. Parts 1 & 2. *Allan Hancock Foundation Occasional Paper* 23: 1–628.

Hartman, O. (1965): Catalogue of the polychaetous annelids of the world. Supplement 1960–1965 and index. *Occasional Papers of the Allan Hancock Foundation* 23: 1–197.

Hatschek, B. (1878): Studien über die Entwicklungsgeschichte der Anneliden. *Arbeiten aus dem Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest* 1: 1–128.

Hatschek, B. (1893): System der Anneliden, ein vorläufiger Bericht. *Sitzungsberichte des Deutschen Naturwissenschaftlich-Medicinischen Vereines für Böhmen "Lotos" in Prag.*, Neue Folge 13: 123–126.

Herdrich, D. & Armstrong, K. (2008): *Final Report. Historic Fishing Methods in American Samoa*. Pacific Islands Fisheries Science Center, National Oceanic and Atmospheric Administration, Honolulu, HI.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Holborow, P.L. (1971): The fine structure of the trochophore of *Harmothoe imbricata*. In: Crisp, D.J. (ed.) *Fourth European Marine Biology Symposium.* Cambridge University Press, Cambridge: 237–246.

Holthuis, L.B. (1969): Albertus Seba's "Locupletissimi rerum naturalium thesauri…" (1734–1765) and the "Planches de Seba" (1827–1831). *Zoologische Mededelingen* 43: 239–252.

Horton, T., Gofas, S., Kroh, A., *et al.* (2017): Improving nomenclatural consistency: a decade of experience in the World Register of Marine Species. *European Journal of Taxonomy* 389: 1–24.

Houghton, W. (1870): *Sea-side Walks of a Naturalist with His Children*. Groombridge and sons, London.

Hudson, W.H. (1919): *The Book of a Naturalist*. 1st ed. George H. Doran Company, New York.

Humann, P.D.N. (2010): *Reef Creature Identification: Tropical Pacific*. 2nd printing 2012. New World Publications, Jacksonville, FL.

Hutchings, P.A. & Glasby, C. J. (2000): History of discovery. In: Beesley, P.L., Ross, G.B., Glasby, C.J. (eds). *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*, CSIRO Publishing, Melbourne: 3–9.

Hyman, L.H. (1959): *The Invertebrates: Smaller coelomate groups. Chaetognatha, Hemichordata, Pogonophora, Phoronida, Ectoprocta, Brachiopoda, Sipunculida, The coelomate Bilateria.* McGraw-Hill Book Co., New York.

International Commission on Zoological Nomenclature (ICZN). (1961): *Code international de nomenclature zoologique adopte par le XVe Congres international de zoologie [International Code of Zoological nomenclature adopted by the XV International Congress of Zoology]*. 1st ed. International Trust for Zoological Nomenclature, London.

International Commission on Zoological Nomenclature (ICZN). (1999): *International Code of Zoological Nomenclature*. 4th ed. The International Trust for Zoological Nomenclature, London.

Ivanov, A.V. (1963): *Pogonophora*. [Translated by D.B. Carlisle] Consultants Bureau, New York.

Jeffreys, J.G. (1863): *British Conchology*. Vol. 2. John van Voorst, London.

Johnson, J.R. (1816): *A Treatise on the Medicinal Leech: Including Its Medical and Natural History, with a Description of its Anatomical Structure: Also, Remarks upon the Diseases, Preservation and Management of Leeches*. Longman, Hurst, Rees, Orme, and Brown, London.

Johnston, G. (1865): *A Catalogue of the British Non-Parasitical Worms in the Collection of the British Museum*. 1st ed. Trustees of the British Museum, London.

Jones, M.L. (1985): On the vestimentifera, new phylum, six new species, and other taxa, from hydrothermal vents and elsewhere. *Bulletin of the Biological Society of Washington* 6: 117–158.

Keynes, R.D. (2000): *Charles Darwin's Zoology Notes & Specimen Lists from H.M.S. "Beagle"*. Cambridge University Press, Cambridge.

Kingsley, C. (1873): *Glaucus, or, The Wonders of the Shore*. 5th ed. Macmillan, London.

Knight-Jones, P. & Perkins, T.H. (1998): A revision of *Sabella*, *Bispira* and *Stylomma* (Polychaeta: Sabellidae). *Zoological Journal of the Linnean Society* 123: 385–467.

Kojima, S., Ohta, S., Yamamoto, T., (2002): Molecular taxonomy of vestimentiferans of the western Pacific and their phylogenetic relationship to species of the eastern Pacific. II. Families Escarpiidae and Arcovestiidae. *Marine Biology (Berlin)* 141: 57–64.

Krasne, F.B. & Lawrence, P.A. (1966): Structure of the photoreceptors in the compound eyespots of *Branchiomma vesiculosum*. *Journal of Cell Science*, 1, 239–248.

Kusukawa, S. (2010): The sources of Gessner's pictures for the *Historia animalium*. *Annals of Science* 67: 303–328.

Kutschera, U., Langguth, H., Kuo, D.H., Weisblat, D.A. & Shankland, M. (2013): Description of a new leech species from North America, *Helobdella austinensis* n. sp (Hirudinea: Glossiphoniidae), with observations on its feeding behaviour. *Zoosystematics and Evolution* 89: 239–246.

Kutschera, U. & Weisblat, D.A. (2015): Leeches of the genus *Helobdella* as model organisms for Evo-Devo studies. *Theory in Biosciences* 134: 93–104.

Lamarck, J.-B.d. (1802 [privately published, reprinted 1906]): Discours d'Ouverture, Prononcé le 27 floréal An 10, au Muséum dHistoire naturelle. Recherches sur l'organisation des corps vivans *Bulletin Scientifique de la France et de la Belgique* (5th series) 40: 483.

Lamarck, J.B.d. (1818): *Histoire Naturelle des animaux sans vertebres, [presentant les caracteres generaux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, etla citation des principales especes qui s'y rapportent; precedes d'une Introduction offrant la determination des caracteres essentiels de l`Animal, sa distinction du vegetal et desautres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie]*. 1 ed. Deterville, Paris.

van der Land, J. & Nørrevang, A. (1977): Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera). *Det Kongelige Danske Videnskbernes Selskab Biologiske Skrifter* 21: 1–102.

Lankester, E.R. (1890): The history and scope of zoology. In: Lankester, E.R. *The Advancement of Science. Occasional Essays & Addresses*. Macmillan, London.

Leach, W.E. (1816): Annulosa. p. 401–453 In: *Supplement to the 4th, 5th, and 6th editions of the Encyclopaedia Britannica*. Vol. 1. Archibald Constable, Edinburgh.

Leuckart, F.S. (1827): *Versuch einer naturgemässen Eintheilung der Helminthen nebst dem Entwurfe einer Verwandschafts- und Stufenfolge der Thiere überhaupt*. Neue Akademische Buchhandlung von Karl Gross, Leipzig.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Linnaeus, C. (1758): *Systema naturae per regne tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis. Editio Decima, Reformata*. Laurentii Salvii, Holmiae [Stockholm].

Linné, C.L. & Turton, W. (1806): *Volume 4. Worms. In a General System of Nature, through the Three Grand Kingdoms of Animals, Vegetables, and Minerals, Systematically Divided into Their Several Classes, Orders, Genera, Species, and Varieties, with Their Habitations, Manners, Economy, Structure and Peculiarities* [7 volumes, 1802–1806] [expanded English translated version of Gmelin's edition of Systema Naturae]. Printed for Lackington, Allen, and Co., Temple of the Muses, Finsbury Square, London.

MacGillivray, W. (1834): *Lives of eminent zoologists, from Aristotle to Linnaeus: with introductory remarks on the study of natural history, and occasional observations on the progress of zoology*. 2nd Ed. Oliver & Boyd, Edinburgh

Maerlant, J.van. (~1350): *Der Naturen Bloeme [The Flower of Nature]*. Utrecht or Flanders. In: *Medieval Manuscripts*. Koninklijke Bibliotheek, National Library of the Netherlands, Scheveningen, the Netherlands.

McIntosh, W.C. (1868): On the boring of certain annelids. *Annals and Magazine of Natural History*, (Series 4) 2, 276–295.

McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. 'Challenger' during the years 1873–76. *Report of the Scientific Results of the Exploring Voyage of H.M.S. Challenger 1873–76*, 12 [part 34 of the reports], 1–554.

McIntosh, W.C. (1923): A monograph of the British marine annelids. Vol. IV - Part II. Polychaeta, Sabellidae to Serpulidae. With additions to the British marine Polychaeta during the publication of the monograph. *Ray Society*, 4, 251–538.

Malaquin, A. & Carin, F. (1922): Tomoptérides provenant des campagnes de l'Hirondelle et la Princesse-Alice (1888–1910). *Resultats des Campagnes Sciencitifiques, Monaco* 61: 1–52.

Malmgren, A.J. (1869): Ueber die Gattung *Heteronereis* (Örst.) und ihr Verhältniss zu den Gattungen *Nereis* (Gr.) und *Nereilepas* (Gr.) *Zeitschrift fur Wissenschaftliche Zoologie* 19: 476–478.

Megenberg, K.von (1475): *Das Buch der Natur*. Johann Bämler, Augsburg.

Meyer, E. (1887): Studien über Körperbau der Anneliden. Mitteilungen der zoologische Station zu Neapel zugleich ein *repertorium für Mittelmeerkunde*, 7, 592–741.

Michaelsen, W. (1899): Oligochaeten von den Inseln des Pacific, nebst Erörterungen zur Systematik der Megascoleciden. (Esgebnisse einer Reise nach dem Pacific. Schauinsland 1896/97). *Zoologische Jahrbücher. Abteilung für Systematik, Okologie und Geographie der Tiere* 12: 211–246.

Michaelsen, W. (1900): Vermes. Oligochaeta. *Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen* 10: 1–575.

Miller, D. (1952): The insect people of the Maori. *Journal of the Polynesian Society* 61: 1–61.

Molyneux, T. (1695): Account of a not yet described Scolopendra marina, by Thomas Molyneux, M.D. S. R. S. communicated by Mr. Locke. *Philosophical Transactions* 19: 405–412.

Monro, C.C.A. (1931): Group Vermes. In: Pycraft, W.P. (ed.) *The Standard Natural History. From Amoeba to Man*. Frederick Warne and Co., London and New York: 41–67.

Montagu, G. (1803, 1804): *Testacea Britannica, or, Natural History of British Shells, Marine, Land, and Fresh-Water, Including the Most Minute: Systematically Arranged and Embellished With Figures. Pt. 1, 2*. J. White, London.

Moore, P.G. (2012): The supply of marine biological specimens (principally animals) for teaching and research in Great Britain from the nineteenth century until today. *Archives of Natural History* 39: 281–301.

Moore, P.G. (2014): Popularizing marine natural history in eighteenth- and nineteenth-century Britain. *Archives of Natural History* 41: 45–62.

Moquin-Tandon, A. (1846): *Monographie de la famille des hirudinées*. 2nd ed. J. B. Baillière, Paris.

Moquin-Tandon, A. [as Frédol, Alfred] & Lackerbauer, P.A. (1866): *Le Monde de la mer*. 2nd ed. Librairie de L. Hachette, Paris.

Mörch, O.A.L. (1863): Rivisio Critica Serpulidarum et Bidrag til Rorormenes Naturhistorie. *Naturhistorisk Tidsskrift, Kobenhavn*, (3rd series) 1, 347–470, plate 11.

Morton, J. & Miller, M. (1968): *The New Zealand Sea Shore*. 1st ed. Collins, London.

Müller, J. (1854): Ueber verschiedene Formen von Seethieren. *Archiv für anatomie physiologie und wissenschaftliche* 1854: 69–98, plates 4–6.

Neave, S.A. (1939–1946): *Nomenclator Zoologicus. A list of the Names of Genera and Subgenera in Zoology from the Tenth Edition of Linnaeus 1758 to the End of 1935*. Zoological Society of London, London.

Nissen, C. (1969 [vol 1], 1978 [vol 2]): *Die Zoologische Buchillustration. Ihre Bibliographie und Geschichte*. Anton Hiersemann, Verlag, Stuttgart.

Oliver, P.G., Morgenroth, H. & Salvador, A. (2017): Type specimens of Mollusca described by Col. George Montagu in the Royal Albert Memorial Museum & Art Gallery, Exeter and The Natural History Museum, London. *Zoosystematics and Evolution* 93: 363–412.

Örsted, A.S. (1842): Udtog af en Breskrivelse af Groenlands Annulata dorsibranchiata. *Naturhistorisk Tidsskrift* (series 1) 4: 109–127.

Parapar, J. & Hutchings, P.A. (2015): Redescription of *Terebellides stroemii* (Polychaeta, Trichobranchidae) and designation of a neotype. *Journal of the Marine Biological Association of the United Kingdom* 95: 323–337.

Parfitt, E. (1867): The annelids of Devon, with a resume of the natural history of the county. *Devonshire Association for the Advancement of Science, Literature and Art* 2: 203–208.

Park, C., Han, Y.-H., Lee, S.-G., *et al.* (2018): The developmental transcriptome atlas of the spoon worm *Urechis unicinctus* (Echiurida: Annelida). *GigaScience* 7(3): giy007–giy007.

Parker, T.J. & Haswell, W.A. (1910): *A Text-Book of Zoology*. MacMillan, London.

Pettibone, M.H. (1982): Annelida. In: Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill, New York.

Peyssonnel, J.A. (1759): [as John Andrew Peyssonel] Observations upon the sea scolopendre or sea millepes. *Philosophical Transactions of the Royal Society of London* 51: 35–37.

Pierantoni, U. (1908): *Protodrilus. Fauna und Flora des Golfes von Neapel* 31: 1–226.

Pliny the Elder. (1469): *Plinius secundus nouocomensis equestribus militiis industrie functus... [line 12] Libros Naturalis Historiæ nouitiu camenis qritiu tuo opus natu apud me proxima fetura &c. [Ends:--Colophon.] Quem modo tam rarum cupiens uix lector haber&: Quiq etiam fractus pene legendus eram: Restituit Venetis me nuper Spira Ioannes: Exscripsitq libros*

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Purschke, G., Bleidorn, C. & Struck, T. (2014): Systematics, evolution and phylogeny of Annelida – a morphological perspective. *Memoirs of Museum Victoria*, 71, 247–269.

de Quatrefages, A. (1847): Etudes sur les types inférieurs de l'embranchement des Annelés. Mémoire sur l'Echiure de Gaertner (*Echiurus gaertnerii* Nob.). *Annales des sciences naturelles, Paris, 3rd Series, Zoologie* 7: 307–343, plate 6.

de Quatrefages, A. (1857): *The rambles of a naturalist on the coasts of France, Spain, and Sicily* [Translated by E. C. Otté]. Longman, Brown, Green, Longmans, & Roberts, London.

de Quatrefages, A. (1866a): On the classification of the annelides [Translated by W. S. Dallas]. *Annals and Magazine of Natural History* 17 (series 3): 1–24.

de Quatrefages, A. (1866b [imprint 1865]): *Histoire naturelle des Anneles marins et d'eau douce. Annelides et Gephyriens. Vol. 1 & 2 (separate pagination)*. Librarie Encyclopedique de Roret, Paris.

Rainbow, P.S. (2005): From natural history to biodiversity: collections of discovery. *Archives of Natural History* 32: 221–230.

Rainbow, P.S. (2008): Marine biological collections in the 21st century. *Zoologica Scripta* 48(s1): 33–40.

Raineault, N.A., Flanders, J. & Bowman, A. (2018): New frontiers in ocean exploration: The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2017 field season. *Oceanography* 31: 1–126.

Read, G.B. & Fauchald, K. (2018): World Polychaeta database. Accessed at http://www.marinespecies.org/polychaeta/aphia.php on 2018-04-27.

Reynolds, J.W. & Cook, D.G. (1976): *Nomenclatura Oligochaetologica. A Catalogue of Names, Descriptions and Type Specimens of the Oligochaeta*. University of New Brunswick, Fredericton, New Brunswick.

Reynolds, J.W. & Wetzel, M.J. (2013–2018): Nomenclatura Oligochaetologica – Editio Secunda. Accessed at http://wwx.inhs.illinois.edu/people/mjwetzel/nomenoligo on 2018-04–27.

Röhlich, P. & Török, L.J. (1964): Elektronenmikroskopische Beobachtungen an den Sehzellen des Blutegels, *Hirudo medicinalis L. Zeitschrift für Zellforschung und Mikroskopische Anatomie*, 63, 618–635.

Rolando, L. (1822 [1821 volume]): Description d'un animal nouveau qui appartient à la classe des Echinodermes. *Memorie della Reale Accademia delle Scienze di Torino* 26: 539–556.

Rondelet, G.R. (1554–1555): *[vol.1 (1554)] Libri de piscibus marinis: in quibus verae piscium effigies expressae sunt: quae in tota piscium historia continentur, indicat elenchus pagina nona et decima: postremo accesserunt indices necessarij. [vol.2 (1555)]... Universae aquatilium historiæ pars altera, cum veris ipsorum imaginibus*. Matthiam Bonhomme, Lyon.

Rota, E. (2011): Early oligochaete science, from Aristotle to Francesco Redi. *Archives of Natural History* 38: 136–163.

Rouse, G.W. (2001): A cladistic analysis of Siboglinidae Caullery, 1914 (Polychaeta, Annelida): formerly the phyla Pogonophora and Vestimentifera. *Zoological Journal of the Linnean Society of London* 132: 55–80.

Rouse, G.W. & Giribet, G.S. (2016): *Phylum Annelida: The Segmented (and Some Unsegmented) Worms* [Chapt 14]. *In*: Brusca, R.C., Moore, W. & Shuster, S.M. (Eds.) *Invertebrates*. Sinauer Associates, Sunderland, Massachusetts.

Rouse, G.W. & Fauchald, K. (1995): The articulation of Annelids. *Zoologica Scripta* 24: 269–301.

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

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

Ruysch, F.F.R. (1710): *Thesaurus animalium primus: cum figuris aeneis = Het eerste cabinet der dieren*. Apud Joannem Wolters, Amsterdam.

Sander, K. (1994): An American in Paris and the origins of the stereomicroscope. *Roux's Archives of Developmental Biology* 203: 235–242.

Sato-Okoshi, W. (2017): Obituary: Minoru Imajima (1930–2016). *Journal of the Marine Biological Association of the United Kingdom* 97: 1203–1203.

Savigny, J.-C. (1822 [official date]): Systeme des annelides, principalement de celles des cotes de l'Egypte et de la Syrie, offrant les caracteres tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Especes. *Description de l'Égypte... Histoire Naturelle, Paris* 1: 3–128, 325–472.

Schmarda, L.K. (1859): *Neue Turbellarien, Rotatorien und Anneliden beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857 von Ludwig K. Schmarda. Erster halfte [Part.I] [New Turbellarien, Rotatorien and Anneliden observed and collected on a journey around the Earth 1853 to 1857. First half [Part.I ]*. 1st ed. Wilhelm Engelmann, Leipzig.

Schmarda, L.K. (1861a): *Ludwig K. Schmarda's Reise um die Erde in den Jahren 1853–1857*. G. Westermann, Braunschweig.

Schmarda, L.K. (1861b): *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erdr [sic] 1853 bis 1857 von Ludwig K. Schmarda. Erster Band. Turbellarien, Rotatorien und Anneliden. Zweite Hälfte.* Wilhelm Engelmann, Leipzig.

Seba, A. (1734): *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam:opus, cui, in hoc rerum genere, nullum par exstitit/ex toto terrarum orbe collegit, digessit, descripsit, et depingendum curavit Albertus Seba*. Vol. 1. Apud Janssonio-Waesbergios & J. Wetstenium & Gul. Smith, Amsterdam.

Shaw, G. & Nodder, F.P.a. (1789 [to 1813]): *Vivarium Naturae or The naturalist's Miscellany, or Coloured Figures of Natural Objects*. Nodder & Co., London.

Sherborn, C.D. (1902–1933): *Index animalium sive index nominum quae ab A.D. 1758 generibus et speciebus animalium imposita sunt [covers 1758 to 1850]*. E typographio Academico, Cantabrigiae (= Cambridge).

Shindler, K. (2016): A magpie with a card-index mind – Charles Davies Sherborn 1861–1942. *ZooKeys* 550: 33–56.

Siddall, M.E. & Burreson, E.M. (1998): Phylogeny of leeches (Hirudinea) based on mitochondrial cytochrome c oxidase subunit I. *Molecular Phylogenetics and Evolution* 9: 156–162.

Siddall, M.E., Trontelj, P., Utevsky, S., Nkamany, M. & Macdonald, K. (2007): Diverse molecular data demonstrate that commercially available medicinal leeches are not *Hirudo medicinalis*. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1481–1487.

Simakov, O., Marletaz, F., Cho, S.-J. (2013): Insights into bilaterian evolution from three spiralian genomes. *Nature* 493: 526–531.

Slabber, M. (1781): *Physikalische Belustigungen oder Mikroskopische Wahrnehmungen von drey und vierzig in- und ausländischen Wasser- und Landthierchen durch Martinus Slabber, Mitglied*

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Sloane, H. (1725): *A voyage to the islands Madera* [sic], *Barbados, Nieves, St Christophers and Jamaica: with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, &c. of the last of those islands*. Printed by B.M. for the author, London.

Solís-Weiss, V., Bertrand, Y., Helléouet, M.-N. & Pleijel, F. (2004): Types of polychaetous annelids at the Muséum national d'Histoire naturelle, Paris. *Zoosystema* 26: 377–384, appendix S1–21.

Sowerby, J. (1806): *The British Miscellany, or, Coloured Figures of New, Rare, or Little Known Animal Subjects: Many Not Before Ascertained to be Inhabitants of the British Isles: and Chiefly in the Possession of the Author, James Sowerby*. Vol. 1–2. R. Taylor & Co., London. Sold by the author, J. Sowerby, by White, Johnson, Symonds, and all other booksellers.

Spier, R. (2002): The history of the peer-review process. *Trends in Biotechnology* 20: 357–358.

Springett, J.A., Gray, R.A.J., Barker, D.J., *et al.* (1998): Population density and distribution of the New Zealand indigenous earthworm *Octochaetus multiporus* (Megascolecidae: Oligochaeta) in hill pastures. *New Zealand Journal of Ecology* 22: 87–93.

Stair, J.B. (1897): Palolo, a sea-worm eaten by the Samoans. *Journal of the Polynesian Society* 6: 141–144.

Stephen, A.C. & Edmonds, S.J. (1972): *The phyla Sipuncula and Echiura*. British Museum, London.

Stephenson, J. (1930 [reprinted 1972]): *The Oligochaeta*. Clarendon Press (reprinted by Verlag Von J. Cramer), Oxford.

Strickland, H.E. (1878): *[Strickland Code. Deceased nominal author] Rules for Zoological Nomenclature*. John Murray, London.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology*, 25, 1993–1999

Struck, T.H., Paul, C., Hill, N., *et al.* (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

Summers, M.M. & Rouse, G.W. (2014): Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Evolutionary Biology* 14: 170.

Taheri, S., James, S., Roy, V., *et al.* (2018): Complex taxonomy of the 'brush tail' peregrine earthworm *Pontoscolex corethrurus*. *Molecular Phylogenetics and Evolution* 124: 60–70.

Taylor, H.R. & Harris, W.E. (2012): An emergent science on the brink of irrelevance: a review of the past 8 years of DNA barcoding. *Molecular Ecology Resources* 12: 377–388.

Thompson, D.W. & Aristotle. (1910): *Historia Animalium*. 1st ed. Clarendon Press, Oxford.

Usselman, M.C. (2015): *Pure Intelligence: The Life of William Hyde Wollaston*. The University of Chicago Press, Chicago.

Vandepitte, L., Vanhoorne, B., Decock, W., *et al.* (2018): A decade of the World Register of Marine Species – general insights and experiences from the Data Management Team: where are we, what have we learned and how can we continue? *PLoS ONE* 13: e0194599.

Vaney, L. & Conte, A. (1898): Recherches experimentales sur la regeneration chez *Spirographis spallanzanii*. *Comptes Rendus de la Societe Biologique, Paris* 1: 973–975.

Vejdovsky, F. (1878): Beiträge zur Kenntnis der Tomopteriden. *Zeitschrift fur Wissenschaftliche Zoologie* 31: 81–100, plates 6–7.

Vejdovsky, F. (1884): *System und Morphologie des Oligochaeten*. Commissimbuchhandlung von Franz Rivnac, Prague.

Viguier, C. (1886): Etudes sur les Animaux inferieurs de la Baie d'Alger. Recherches sur les Annelides pelagiques. *Archives de Zoologie Experimentale et Generale* 4: 347–442, plates 21–27.

Walcott, C.D. (1911): Cambrian geology and paleontology. Middle Cambrian annelids. *Smithsonian Miscellanous Collections* 57: 109–144.

Wang, Y. & Xie, Q. (2014): The molecular Symplesiomorphies shared by the stem groups of Metazoan evolution: can sites as few as 1% have a significant impact on recognizing the phylogenetic position of Myzostomida? *Journal of Molecular Evolution* 79: 63–74.

Ward, L.A. & Fauchald, K. (1997): *Literature on the Polychaeta (Annelida)*. 2nd ed. (database files). Accessed at https://web.archive.org/web/20080602022426/www.annelida.net/bibliog/bibliowf.html on 2018-04-27.

Watson, G.J., Murray, J.M., Schaefer, M. & Bonner, A. (2017): Bait worms: a valuable and important fishery with implications for fisheries and conservation management. *Fish and Fisheries* 18: 374–388.

Webb, M. (1969): *Lamellibrachia barhami*, Gen. Nov. Sp. Nov. (Pogonophora), from the Northeast Pacific. *Bulletin of Marine Science* 19: 18–47.

Weigert, A. & Bleidorn, C. (2016): Current status of annelid phylogeny. *Organisms Diversity & Evolution* 16: 345–362.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Weitzmann, K. (1971): *Studies in Classical and Byzantine Manuscript Illumination*. University of Chicago Press, Chicago; London.

Wesenberg-Lund, E. (1934): Gephyreans and annelids. The Scoresby Sound Committee's 2nd East Greenland expedition in 1932 to King Christian IX's land. *Meddelelser om Groenland* 104: 1–38.

Wheeler, A. (1984): Daniel Solander and the zoology of Cook's voyage. *Archives of Natural History* 11: 505–515.

White, G. (1789): *The Natural History and Antiquities of Selborne, in the County of Southampton*. 1st ed. Printed by T. Bensley, for B. White and Son, at Horace's Head, Fleet Street, London.

Whitehead, P.J.P. (1969): Zoological specimens from Captain Cook's voyages. *The Journal of the Society for the Bibliography of Natural History* 5: 161–201.

Whitelegge, T. (1890): Report on the worm disease affecting the oysters on the coast of New South Wales. *Records of the Australian Museum, Sydney*, 1, 41–54.

Wilson, D.P. (1932): On the *Mitraria* larva of *Owenia fusiformis* delle Chiaje. *Philosophical Transactions of the Royal Society of London*, 221, 231–334.

Winnepenninckx, B., Backeljau, T. & De Wachter, R. (1995): Phylogeny of protostome worms derived from 18S rRNA sequences. *Molecular Biology and Evolution* 12: 641–649.

Wise, F.C. (1950): The development of the binocular microscope. *Monographs of the Quekett Microscopical Club* 5: 5–21.

Worsaae, K. & Rouse, G.W. (2010): The simplicity of males: Dwarf males of four species of *Osedax* (Siboglinidae; Annelida) investigated by confocal laser scanning microscopy. *Journal of Morphology*, 271, 127–142.

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Torsten H. Struck

# 2 Phylogeny

## 2.1 Phylogenetic position

The phylogenetic position of Annelida within Metazoa was uncontroversial for a long time. Ever since Cuvier (1817), the dominant hypothesis was the Articulata hypothesis, which regarded Annelida as closely related to Arthropoda. This hypothesis was still dominant in textbooks of invertebrate zoology until recently, usually placing Articulata within Spiralia (Westheide and Rieger 1996, Ax 1999, Nielsen 2001, Brusca and Brusca 2003). However, the new placement of Annelida is now also reflected in textbooks (Ruppert *et al.* 2004, Pecheni, 2010, Westheide and Rieger, 2013, Brusca *et al.* 2016, Urry *et al.* 2017). The characters supposed to strongly support the Articulata hypothesis are a segmented body organization including a rope ladder-like nervous system and segment formation by a posterior growth zone, longitudinal muscles of the body wall in distinct bundles, and presence of mushroom bodies in the brain (e.g., Westheide and Rieger 1996, Ax 1999, Scholtz 2003). Articulata was regarded as closely related to other spiralian taxa such as Mollusca based on spiral cleavage (e.g., Ax 1995, Westheide and Rieger 1996, Ax 1999), although Arthropoda show no sign of spiral cleavage in their development (Scholtz 1997, Dearden *et al.* 2002, Alwes and Scholtz 2004, Hejnol and Schnabel 2005, Hertzler 2005). During the first cell divisions of spiral cleavage, the spindle has an alternating oblique orientation in comparison to the previous one and gives rise to differently sized daughter cells in a stereotypic pattern (Nielsen 2010). Furthermore, some of the spiralian taxa (i.e., Mollusca and Entoprocta) and Annelida share a trochophore larva in their life cycle. Even Nemertea and Cycliophora might possess highly modified trochophora larvae (Funch 1996, Maslakova *et al.* 2004a,b).

Surprisingly, early phylogenetic studies based on molecular data (i.e., 18S rRNA) were not able to recover Articulata but still showed a closer relationship of Annelida to Mollusca as well as Brachiopoda, a lophophorate taxon (Field *et al.* 1988, Ghiselin 1988, Field *et al.* 1989, Patterson 1989, Raff *et al.* 1989, Lake 1990). Halanych *et al.* (1995), who included 18S rRNA data of representatives of all lophophorate lineages, confirmed these previous results with strong bootstrap support and coined the name Lophotrochozoa for this group. Lophotrochozoa is defined as including the last common ancestor of lophophorates, molluscs, and annelids, and its descendants. Hence, an apparent conflict was evident between morphological and molecular data regarding the placement of Annelida either as sister to Arthropoda or within Lophotrochozoa, respectively. Based on 18S rRNA data, Arthropoda was later placed as closely related to nematodes and their allies with strong nodal support (Aguinaldo *et al.* 1997); this placement became known as the Ecdysozoa hypothesis. Whereas previous studies (Field *et al.* 1988, Ghiselin 1988, Field *et al.* 1989, Patterson 1989, Raff *et al.* 1989, Lake 1990, Halanych *et al.* 1995) and even a morphological cladistic analysis by Eernisse *et al.* (1992) that placed Annelida as more closely related to other spiralian taxa than to Arthropoda passed more or less "unnoticed," the paper of Aguinaldo *et al.* (1997) initiated a strong controversy about the conflict between morphological and molecular data. The discussion of this conflict and the quality of both the morphological and molecular data concentrated on the topic Articulata versus Ecdysozoa and, thus, the placement of Arthropoda rather than that of Annelida (e.g., Schmidt-Rhaesa *et al.* 1998, Wägele *et al.* 1999, Wägele and Misof 2001, Zrzavy 2001, Scholtz 2002, Giribet 2003, Scholtz 2003, Schmidt-Rhaesa 2006).

Of the characters supporting Articulata, segmentation is regarded as a key character due to its complexity (Scholtz 2002, 2003). Scholtz (2002, 2003) defined a segment as an anteroposteriorly repeated body unit, which can be defined by a set of substructures occurring together. These substructures per body unit are an outer annulus, one pair of coelomic sacs, one pair of metanephridia, one pair of ventral ganglia with commissures, lateral nerves and connectives (i.e., the rope ladder-like ventral nerve cord), one pair of appendages, and a set of muscles. Strictly applied, several annelid and arthropod taxa would not fulfill this definition.

With regard to annelids, some taxa have no appendages or even chaetae (e.g., Capitellidae, Clitellata, Protodrilida, and Dinophilidae). Coelomic sacs are fused to varying degrees (e.g., Arenicolidae and Tomopteridae). The nervous system shows a high degree of variability affecting all elements of the nerve cord, even possessing a medullary nerve cord or an orthogonal-like organization (Bullock and Horridge 1965, Golding 1992, Hessling and Westheide 1999, Orrhage and Müller 2005, Müller 2006, Purschke 2016). Moreover, segmentation is strongly reduced in several interstitial polychaete taxa due to paedomorphosis (for review, see Worsaae and Kristensen

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2005, Struck 2006). For further review of the variability of morphological characters in Annelida, see Purschke *et al.* (2014). Similar cases can be shown for arthropods with respect to the nervous system, lack of transitory coelomic sacs, or a different development of the nephridial system (Tiegs 1947, Arnaud and Bamber 1987, Klag and Ksiazkiewicz Kapralska 1989, Schwalm 1997, Mayer 2006, Mayer and Harzsch 2007, Bartolomaeus *et al.* 2009). However, it has been argued that this high plasticity in Annelida and Arthropoda reveals the high complexity of the complex segmentation, as substructures are independent from each other (Scholtz 2002).

On the other hand, other protostome taxa also exhibit a repetitive organization in different organ systems. Kinorhyncha possess repeated body units with an outer annulus, one pair of ganglia, and a set of muscles (Schmidt-Rhaesa and Rothe 2006). Monoplacophora (Mollusca) are repetitively arranged in their musculature, excretory organs, gills, and gonads (Friedrich *et al.* 2002, Wanninger and Haszprunar 2002). Serial repetition in one or more tissues or organs occurs also in several other taxa, i.e., eucestodes, other platyhelminths, Polyplacophora, some nematodes and nematomorphs, and a nemertean (e.g., Westheide and Rieger 1996, Schmidt-Rhaesa 2007). Therefore, from a structural point of view, these bilaterian taxa would fulfill the definition of segmentation by Scholtz (2002, 2003), if the definition is not strictly applied. On the other hand, a strict application of the definition would exclude most of the annelid and arthropod taxa as well. In summary, within Protostomia, as well as within both Annelida and Articulata, serial repetition is exhibited with different degrees of complexity ranging from just one or few organs or tissues being affected to more or less the complete body. Hence, a common origin of segmentation of Annelida and Arthropoda cannot be derived with certainty from the structural components and an independent origin in both taxa is as likely.

Other characters supporting Articulata is longitudinal muscles of the body wall in distinct bundles and the presence of mushroom bodies in the brain (e.g., Westheide and Rieger 1996, Ax 1999, Scholtz 2003). However, these characters also exhibit a high variability in Annelida and thus call their presence in the ground pattern of Annelida or the homology to arthropod structures into question (e.g., Tzetlin and Filippova 2005, Loesel and Heuer 2010). For example, mushroom bodies as seen in arthropods can be observed only in Nereididae and Aphroditiformia. Slightly different or less prominent ones are present in Hesionidae, Nephtyidae, and Phyllodocidae, whereas all other taxa investigated to date show no evidence for mushroom bodies (i.e., Syllidae, Tomopteridae, Opheliidae, Eunicidae, Lumbrineridae, Arenicolidae, Terebelliformia, Sabellidae, and Clitellata) (Heuer *et al.* 2010). However, this character is in need of a more comprehensive and detailed reinvestigation (see Purschke 2016). Furthermore, longitudinal muscles are also concentrated in other bilaterian taxa like Nematoda or Kinorhyncha.

While some cladistic analyses of morphological data recovered Articulata (Meglitsch and Schram 1991, Rouse and Fauchald 1995, Sørensen *et al.* 2000, Nielsen 2001, Brusca and Brusca 2003), others reveal a closer relationship of Annelida to spiralian taxa like Mollusca rather than to Arthropoda (Eernisse *et al.* 1992, Zrzavy *et al.* 1998, Giribet *et al.* 2000, Peterson and Eernisse 2001, Zrzavy *et al.* 2001, Zrzavy 2003). This might be indicative of the homoplasious nature of the characters supporting Articulata as well as Lophotrochozoa and Ecdysozoa. However, the practice of character and taxon selection, character coding and scoring, or usage of exemplar or ground pattern characters for terminals in such studies is controversially discussed and strongly contributes to the differences in these studies (e.g., Jenner 2000, Prendini 2001, Jenner 2004a,b). Finally, the assessment if a character is primarily absent or secondarily lost can be problematic in morphological cladistic analyses (e.g., Purschke *et al.* 2000, Jenner 2004c, Struck 2006, Bleidorn 2007).

The suitability of the 18S rRNA data used in the first molecular studies regarding bilaterian relationships has been criticized, and support for Ecdysozoa been attributed to chance similarity only (e.g., Philippe *et al.* 1994, Wägele *et al.* 1999, Wägele and Misof 2001). However, since then, an impressive array of different molecular markers has been used. None supported monophyly of Articulata, but all favored the placement of Annelida close to or within the lophotrochozoans, although not all recovered monophyly of Lophotrochozoa or Ecdysozoa. This array comprises larger 18S rRNA datasets (e.g., Van de Peer *et al.* 2000), 28S rRNA (Mallatt and Winchell 2002, Telford *et al.* 2005, Passamaneck and Halanych 2006, Baguñà *et al.* 2008, Paps *et al.* 2009b), Hox gene data (de Rosa *et al.* 1999, Balavoine *et al.* 2002, Passamaneck and Halanych 2004, Baguñà *et al.* 2008), mitochondrial genomes (e.g., Boore and Brown 2000, Helfenbein and Boore 2004, Podsiadlowski *et al.* 2009), myosin II heavy chain (Ruiz-Trillo *et al.* 2002), Na-K ATPase α-subunit (Anderson *et al.* 2004), aldolase, triosephosphate isomerase, phosphofructokinase, methionine adenosyltransferase, elongation factor 1α, ATP synthase β chain, catalase (Peterson *et al.* 2004, Peterson and Butterfield 2005, Helmkampf *et al.* 2008a, Sperling *et al.* 2009a), glyceraldehyde-3-phosphate dehydrogenase, histone H3, intermediate filaments, tropomyosin, phosphofructokinase (Baguñà *et al.* 2008, Paps *et al.* 2009a) or dyskerin, vacuolar ATP synthase subunit, carnitine palmytoyltransferase, enolase, RNA polymerase II

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(Bourlat *et al.* 2008), microRNA data (Sempere *et al.* 2007, Baguñà *et al.* 2008, Sperling *et al.* 2009b, Wheeler *et al.* 2009), and phylogenomic datasets consisting of more than 50 genes mostly derived from transcriptomic data (Philippe *et al.* 2005a,b, Marletaz *et al.* 2006, Matus *et al.* 2006, Hausdorf *et al.* 2007, Roeding *et al.* 2007, Dunn *et al.* 2008, Helmkampf *et al.* 2008b, Struck and Fisse 2008, Witek *et al.* 2008, Hejnol *et al.* 2009, Roeding *et al.* 2009, Witek *et al.* 2009, Hausdorf *et al.* 2010, Nesnidal *et al.* 2010, Struck *et al.* 2014, Laumer *et al.* 2015, Kocot *et al.* 2017). Based on topology testing, a closer relationship of Annelida and Arthropoda could be significantly rejected (Hausdorf *et al.* 2007, Struck and Fisse 2008). Thus, molecular data clearly support the placement of Annelida within Lophotrochozoa, although the position within Lophotrochozoa is controversially discussed (Halanych 2004). However, based on the recent phylogenomic studies, a consensus is emerging (Edgecombe *et al.* 2011). In this emerging consensus, Annelida is part of a group comprising at least also Mollusca, Nemertea, Brachiopoda, and Phoronida (Struck *et al.* 2014, Kocot *et al.* 2017). It remains uncertain if Annelida is the sister taxon to either Nemertea or Mollusca, Brachiopoda, and Phoronida (Kocot *et al.* 2017), although a sister group relationship of Annelida and Mollusca can be rejected (Hausdorf *et al.* 2010).

To summarize, the molecular data unequivocally reject a close relationship of Annelida to Arthropoda but place Annelida close to Mollusca, Nemertea, Brachiopoda, and Phoronida.

## 2.2 Phylogeny of Annelida

In the following, the phylogeny of Annelida will be discussed in two sections. First, the monophyly and taxon composition of Annelida will be addressed with respect to taxa such as Myzostomida, Siboglinidae, Echiura, and Sipuncula, which, at different times, had been regarded as separate phyla in the Linnean hierarchical system. This section closes with a consideration of taxa that have been traditionally regarded as Annelida, such as *Diurodrilus*, but were also suggested for exclusion from Annelida. In the second section, different classificatory, systematic, or phylogenetic schemes of annelid relationships at a higher taxonomic level over the past two centuries will be reviewed, including detailed discussions about the positions of Clitellata, as well as Archiannelida, within Annelida and the phylogenetic relationships of higher polychaete taxa. This review focuses on the relationships or groups of taxa, which different authors put forward, and to some degree the arguments that the authors provided for these groups. The motivations of the authors for their schemes, such as being purely classificatory or systematic-evolutionary, are not discussed. Similarly, major debates about annelid evolution, for example, the one initiated by Dales (1963, 1977), are not addressed in detail either. Detailed discussions about individual taxa, such as families, are also not provided. This section is restricted in this manner to allow a better comparison to recent results based on tree-based morphological or molecular studies. For the same reason of better comparison, graphical depictions of some of these schemes are provided in Fig. 2.1 as trees even if the schemes were not proposed in a phylogenetic context. Readers interested in the history of the debate about annelid evolution in general, as well as in more details about individual taxa, should refer to the corresponding chapters. This section is concluded with a discussion of recent molecular phylogenetic studies, which allow the proposal of a working hypothesis of annelid relationship for future studies shown in Fig. 2.2. This tree is a meta-tree derived from recent phylogenomic studies (Weigert *et al.* 2014, Laumer *et al.* 2015, Struck *et al.* 2015) as well as the nuclear rRNA-based analyses of Struck *et al.* (2008) and the total-evidence analyses of six genes and morphological data by Zrzavy *et al.* (2009) for taxa not covered by these phylogenomic studies. The placement of Fabriciidae and *Travisia* is based on recent molecular phylogenetic studies (Kupriyanova and Rouse 2008, Paul *et al.* 2010), and taxa lacking molecular data are included entirely based on morphological considerations.

## 2.3 Monophyly and taxon composition of Annelida

The monophyly of Annelida has long been a controversial issue. Placed within Articulata, only very few characters such as a foregut with dorsolateral folds and capillary chaetae of β-chitin in four groups support the monophyly of Annelida (Rouse and Fauchald 1995, Ax 1999, Purschke 2002). Some regarded these as being present already in the stem lineage of Articulata and discussed the placement of arthropod taxa within Annelida (Anderson 1973, Sawyer 1984, Jamieson 1986, 1987, Sawyer 1986, Rouse and Fauchald 1995). However, due to the placement within Lophotrochozoa, the monophyly of Annelida is well supported by several morphological characters, like segmentation with a praepygidial proliferation zone, a dorsal brain and a ventral nerve cord, longitudinal muscle bands, capillary chaetae of β-chitin in four groups, and nuchal organs (for a detailed review, see Purschke 2002, Purschke *et al.* 2014). Based on molecular data, recovering the monophyly of Annelida within Lophotrochozoa was difficult in earlier

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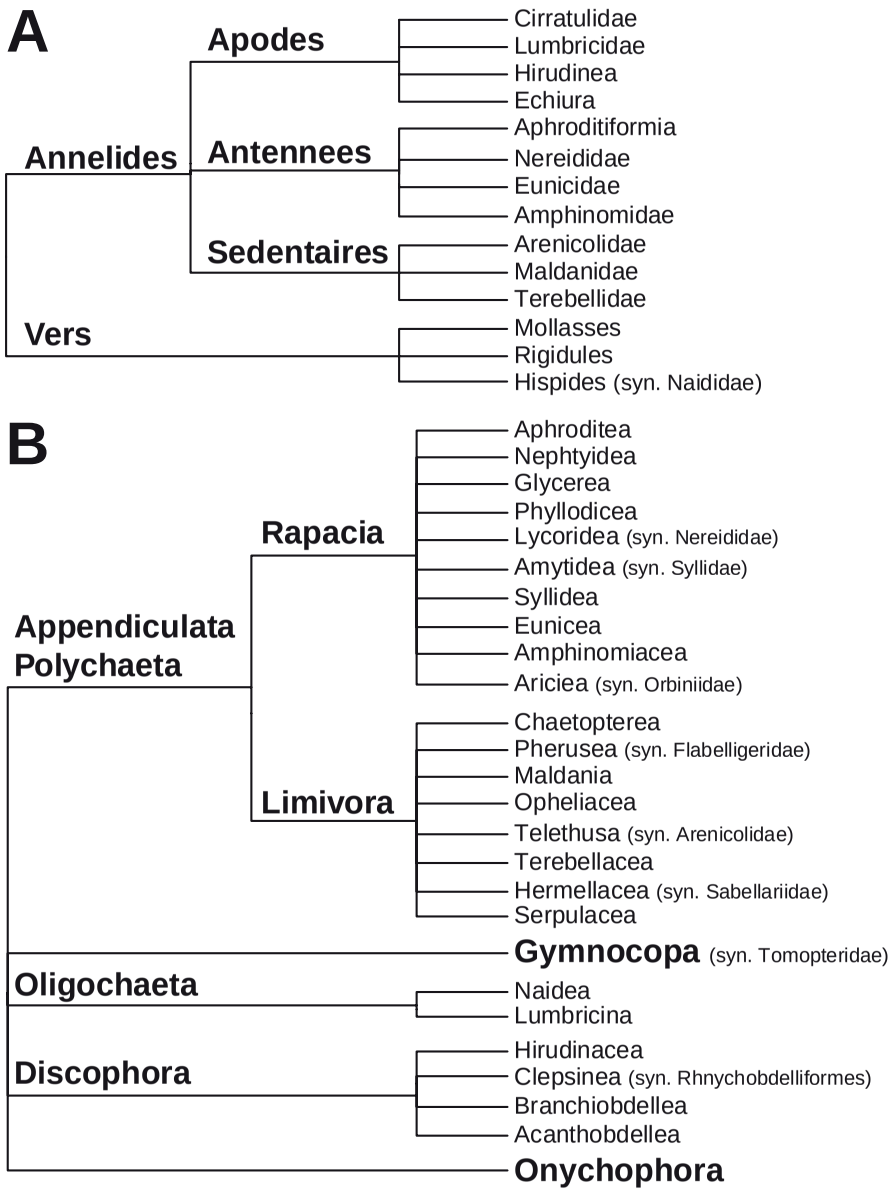


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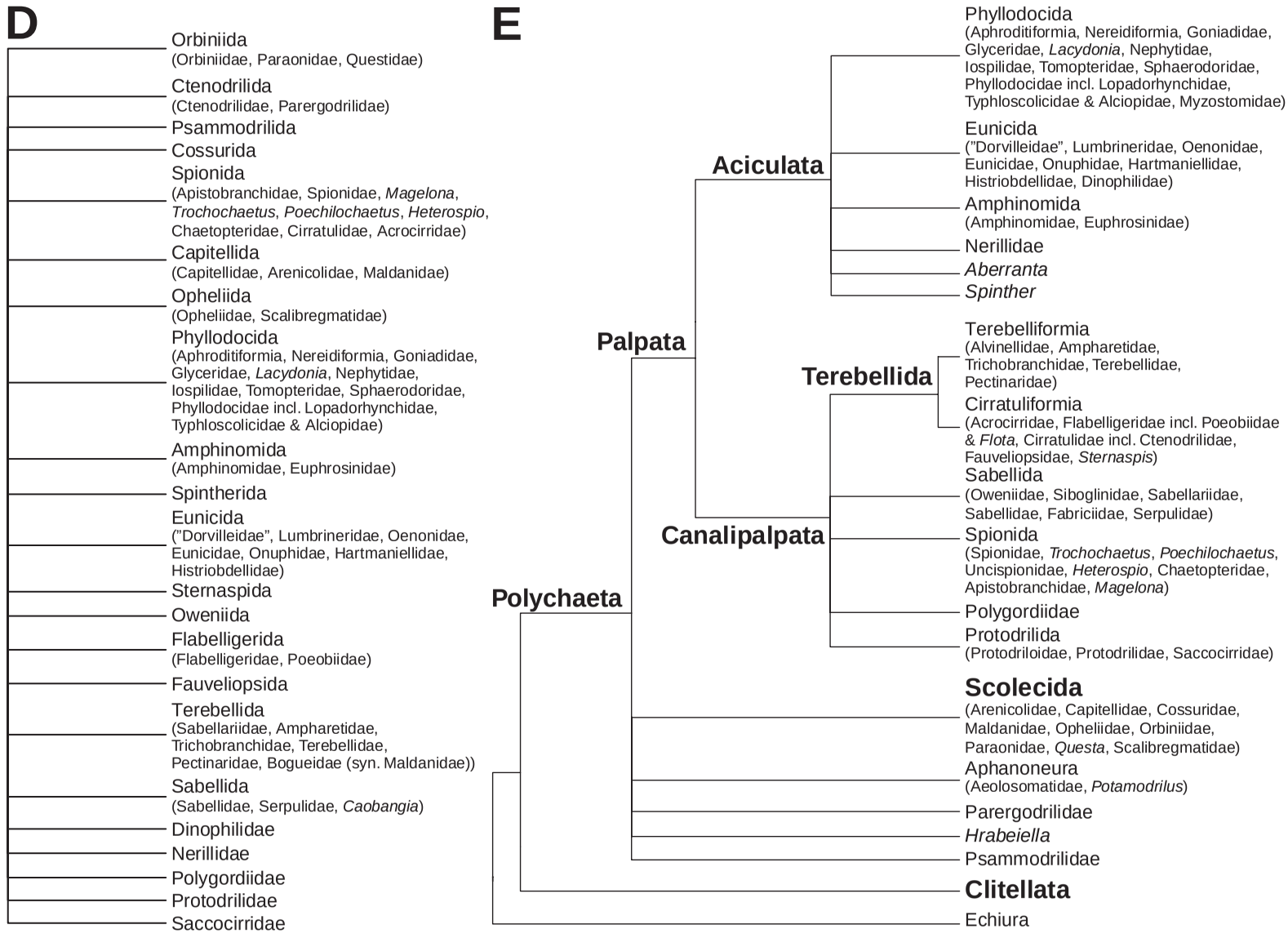


**Fig. 2.1:** Systematic or classificatory schemes of annelids or polychaetes, respectively, based on different authors. Although some of the authors did not put their schemes in an evolutionary or phylogenetic framework, but a classificatory one, the depiction of all schemes is as trees to facilitate comparisons with recent tree-based studies. The taxon composition and name of higher taxonomic ranks such as orders in a scheme follow the corresponding authors. A, Lamarck (1816, 1818); B, Grube (1850); C, Fauvel (1923, 1927); D, Fauchald (1977); E, Rouse and Fauchald (1997), Rouse (1999, 2000), and Rouse and Pleijel (2001). Syn. = synonym of.

studies (for review see McHugh 2000, 2005). However, recent studies with increased numbers of taxa and characters and improved reconstruction methods consistently recovered the monophyly of Annelida, several even with strong nodal support (Bleidorn *et al.* 2006, 2007, Hausdorf *et al.* 2007, Struck *et al.* 2007, 2011, 2015, Dunn *et al.* 2008, Struck and Fisse 2008, Zhong *et al.* 2008, Hejnol *et al.* 2009, Mwinyi *et al.* 2009, Shen *et al.* 2009, Wu *et al.* 2009, Dordel *et al.* 2010, Hartmann *et al.* 2012, Riesgo *et al.* 2012, Struck 2013, Weigert *et al.* 2014, Andrade *et al.* 2015, Laumer *et al.* 2015). Furthermore, most annelids share a unique and conserved order of mitochondrial protein coding genes (Vallès and Boore 2006, Weigert *et al.* 2016).

Traditionally, Annelida comprised Clitellata and polychaetes (Fauchald 1977, Fauchald and Rouse 1997). However, both morphological and molecular data revealed that other taxa, formerly considered as separate phyla, have to be included within the annelid radiation (for review, see Halanych *et al.* 2002).

### 2.3.1 Myzostomida

Myzostomids, flat-bodied marine ectocommensals or parasites of echinoderms, were first described by Leuckart (1827) and placed in close relationship to different metazoan taxa throughout the nineteenth century (for review, see Rouse and Fauchald 1995, Eeckhaut and Lanterbecq 2005, Bleidorn *et al.* 2014). For most of the twentieth century, a close relationship to Annelida or placement within polychaetes has been generally accepted (e.g., Benham 1896, Fedotov 1929, Jägersten 1940, Kato 1952, Prenant 1959, Hartman 1969, Brusca and Brusca 1990, Rouse and Pleijel 2001). Although the body plan of Myzostomida is unique due to their ectocommensalic/parasitic life history, several morphological features support an inclusion of Myzostomida within Annelida: parapodia with chitinous chaetae (aciculae and hooks) and cirri, chaetogenesis, similarities in larval development via trochophore- and nectochaeta-like larvae, structure of the nervous system, hypertrophied axial pharynx, and serial arrangement of protonephridia (Jägersten 1936, Pietsch and Westheide 1987, Rouse and Fauchald 1997, Müller and Westheide 2000, Eeckhaut *et al.* 2003, Jenner 2003, Eeckhaut and Lanterbecq 2005, Lanterbecq *et al.* 2008, Helm *et al.* 2014, Helm and Bleidorn 2016). In contrast, spermatozoon ultrastructure (i.e., the sperm flagellum attaches anteriorly and curves backward) seems to suggest a closer relationship to Syndermata (Mattei and Marchand 1987, Zrzavy *et al.* 2001, but see Jenner 2003). However, sperm ultrastructure is one of the most variable features in animals as it is tightly linked to the mode of reproduction (e.g., Rouse 2006).

Elongation factor 1α, 18S, and 28S rRNA seemed to support the latter hypothesis by placing Myzostomida close to platyzoan taxa or Bryozoa (Eeckhaut *et al.* 2000, Zrzavy *et al.* 2001, Passamaneck and Halanych 2006). Subsequent and careful analyses of the molecular data showed that the results were due to either limited taxon sampling or long branch artifacts (Bleidorn *et al.* 2007). Sequences of myzostomid species very often exhibit highly increased substitution rates resulting in a long branch leading to Myzostomida. In phylogenetic reconstructions, such branches tend to group together and/or are placed close to the outgroup, known as long branch attraction (Felsenstein 1978, Bergsten 2005). Even in larger datasets of more than 10 genes, the placement of Myzostomida is affected by this problem (Bleidorn *et al.* 2009c, Dordel *et al.* 2010, Struck *et al.* 2011). For example, in the phylogenomic analyses of Dunn *et al.* (2008) based on more than 150 genes, Myzostomida is placed together with the platyzoan taxa, which also exhibit strongly increased substitution rates. Increasing both the taxon sampling, especially of acoelomorphan taxa, and the number of positions placed Myzostomida within Annelida (Hejnol *et al.* 2009). Molecular markers of Myzostomida not or less affected by increased substitution rates such as myosin II heavy chain and mitochondrial proteins, as well as mitochondrial gene order data, strongly support a close relationship of Myzostomida and Annelida (Bleidorn *et al.* 2007, 2009c, Mwinyi *et al.* 2009, Shen *et al.* 2009). Hox gene, small RNA, and phylogenomic data also substantiate this position (Bleidorn *et al.* 2009b, Hartmann *et al.* 2012, Helm *et al.* 2012).

The myosin II heavy chain data found Myzostomida as sister to Nereididae, although the taxon sample is limited (additionally only Echiura and Clitellata: Bleidorn *et al.* 2007). A Bayesian taxon-exclusion analysis of combined morphological and molecular data with reinclusion of problematic taxa such as Myzostomida in a one-by-one manner placed Myzostomida within Phyllodocida (Zrzavy *et al.* 2009). These results are congruent with the morphological cladistic analyses of Rouse and Fauchald (1997) placing Myzostomida within Aciculata or, more specifically, within Phyllodocida mainly due to the possession of a hypertrophied axial pharynx and aciculae. In contrast, a Bayesian analysis of the combined morphological and molecular dataset including all taxa from the very beginning found Myzostomida in a basal polytomy comprising, among some other annelids, also Sipuncula, which branched off after Chaetopteridae (Zrzavy *et al.* 2009). Similarly, the mitochondrial protein data recovered Myzostomida as sister to all other annelid taxa of these analyses (including Sipuncula and Echiura, but without Chaetopteridae), with strong nodal support, and not as closely related to a phyllodocidan taxon (Bleidorn *et al.*

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2007, 2009c, Mwinyi *et al.* 2009, Shen *et al.* 2009). Finally, in a phylogenomic study of 231 genes, Myzostomida is also placed in the basal part of the annelid tree (Struck *et al.* 2011). In contrast, Andrade *et al.* (2015), using datasets of up to 1,473 genes, were unable to resolve their position due to long-branch attraction. Weigert and Bleidorn (2016), considering all available evidence, placed Myzostomida within Errantia with uncertain affinity, and herein, this conclusion is followed (Fig. 2.2).

## 2.3.2 Siboglinidae

Siboglinidae, also known as Pogonophora and Vestimentifera, Frenulata and Afrenulata, or Perviata and Obturata, has had a controversial taxonomic history and nowadays also comprises *Sclerolinum* and *Osedax* (Rouse *et al.* 2004, Halanych 2005). Caullery (1914) described the first siboglinid species, *Siboglinum weberi*, and compared it to hemichordates. Uschakov (1933), describing another species, *Lamellisabella zachsi*, regarded it as an aberrant sabellid polychaete. This set the stage for future discussions. Some regarded Pogonophora as closely related to deuterostomes because they presumably had a dorsal nerve cord, radial cleavage, and tripartite body with prosoma, mesosoma, and a modified metasoma (e.g., Dawydoff 1948, Ulrich 1950, Ivanov 1954, 1975, Jägersten 1956, Webb 1964a, von Salvini-Plawen 2000), whereas others placed them within protostomes, specifically close to Annelida, due to the possession of a ventral nerve cord, spiral cleavage, metameric segmentation, and homology of their chaetae with uncini of polychaetes (e.g., Hartman 1954, Liwanow and Porfirjewa 1967, Nørrevang 1970a,b, van der Land and Nørrevang 1975, Southward 1988, Southward 1993, Halanych 2005). The placement of Siboglinidae with respect to other metazoan taxa was problematic due to several reasons. The cleavage of the yolk-rich eggs was interpreted as either modified radial or spiral and the lecithotrophic larvae as a modified trochophora larvae (Nørrevang 1970a,b; Ivanov 1975, Bakke 1976). As adults, Siboglinidae lack a mouth and a gut, and thus, it was uncertain if they possessed a dorsal nerve cord like deuterostomes or a ventral one like protostomes. Moreover, until 1964, all observations relied on incomplete specimens and only the anterior parts were known, which are not segmented. It was Webb (1964b) who discovered and described the comparatively short segmented posterior end for which the terms "metasoma" or "opisthosoma" were applied (Webb 1964a,b, 1969). The development of larvae with a mouth and a gut showed that the nerve cord is indeed ventral and connected to the brain via circumesophageal connectives (Southward 1988, 1993, 1999, Young *et al.* 1996). The discovery of the posterior segmented body region, or opisthosoma (Webb 1964a,b, 1969), revealed that, without a doubt, Siboglinidae possess a segmented body organization. Ultrastructural analyses further supported the homology of the chaetae of Siboglinidae with uncini of Sabellida and Terebellida (Bartolomaeus 1995). Morphological cladistic analyses also supported a closer relationship of Annelida and Siboglinidae (Rouse and Fauchald 1995, 1997). Based on morphological data, to date, placement of Siboglinidae within Annelida is generally accepted and beyond discussion.

To date, different molecular data more or less strongly support a close relationship to or placement within Annelida: elongation factor 1α (e.g., McHugh 1997, Kojima 1998), cytochrome oxidase c subunit I (Black *et al.* 1997), hemoglobin (e.g., Negrisolo *et al.* 2001, Bailly *et al.* 2002, 2003), 18S and 28S rRNA (e.g., Halanych *et al.* 2001, Bleidorn *et al.* 2003b, Passamaneck and Halanych 2006, Struck *et al.* 2008), multigene analyses (e.g., Brown *et al.* 1999, Colgan *et al.* 2006, Rousset *et al.* 2007, Struck *et al.* 2007), mitochondrial genomes (Boore and Brown 2000, Jennings and Halanych 2005), and phylogenomic data (Dordel *et al.* 2010, Struck *et al.* 2011, 2015, Struck 2013, Weigert *et al.* 2014, Andrade *et al.* 2015). Additionally, topology testing significantly rejected the exclusion of Siboglinidae from Annelida (Struck *et al.* 2007). Analyses of combined morphological and molecular data also placed Siboglinidae within Annelida (Zrzavy *et al.* 2009). For more detailed reviews of the early taxonomic history of Siboglinidae, see Rouse and Fauchald (1995) and Halanych *et al.* (2002).

Whereas all data, both morphological and molecular, clearly support a placement within Annelida, the exact phylogenetic position of Siboglinidae within Annelida is uncertain. The morphological cladistic analyses of Rouse and Fauchald (1997) placed Siboglinidae within Sabellida as sister to a clade comprising Fabriciidae, Sabellidae, Serpulidae, and Sabellariidae. Oweniidae was sister to this clade. However, supporting characters, such as the fusion of the peristomium with the prostomium, were either reversals or homoplastic, and thus, support was weak for this clade. Bartolomaeus (1995) also regarded Siboglinidae as more closely related to Sabellida than to Terebellida due to the possession of a pair of anterior nephridia. However, this is a homoplastic character as it can also be found in Acrocirridae, Cirratulidae, Flabelligeridae, and Sternapsidae (Rouse and Fauchald 1997). Rousset *et al.* (2004) conducted a morphological cladistic analysis restricted to the taxa of Canalipalpata and found Siboglinidae as sister to a clade comprising Terebellida and Oweniidae. The remaining sabellidan taxa were sister to this clade. In a combined analysis with 18S and 28S rRNA data, Siboglinidae was sister to Oweniidae (Rousset *et al.* 2004). According to these authors, morphological characters supporting this

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position are chaetae emerging from the body wall in the posterior segments and the presence of an intraepidermal nerve cord. However, at least the last character is subjected to homoplasy, since such a position of the ventral nerve cord is widespread among polychaetes. Recent combined analyses of morphological and molecular data found Siboglinidae in different positions, among others, as sister to Clitellata or together with Oweniidae in the basal part of the tree (Zrzavy *et al.* 2009). Molecular phylogenetic analyses with appropriate taxon sampling were generally inconsistent with each other with respect to the sister group relationship of Siboglinidae, and nodal support was generally low (Brown *et al.* 1999, Bleidorn *et al.* 2003a,b, Hall *et al.* 2004, Struck *et al.* 2005, 2007, 2008, Struck and Purschke 2005, Colgan *et al.* 2006, 2008, Rousset *et al.* 2007).

Nonetheless, two possible placements for Siboglinidae are emerging from these analyses based on more than one gene, although support is still weak for both. Several analyses found a close relationship of Siboglinidae to Clitellata (Brown *et al.* 1999, Colgan *et al.* 2008, Zrzavy *et al.* 2009). The determined part of the mitochondrial gene order of Siboglinidae is identical to that of the clitellate *Lumbricus terrestris,* including the tRNAs. However, the same is true for the complete mitochondrial genome of the arenicolid *Arenicola marina* (T. Struck, unpublished data). Moreover, the mitochondrial gene order of Maldanidae differs by only one tRNA transposition and the ground pattern of Terebellida by one tRNA duplication (Jennings and Halanych 2005, Zhong *et al.* 2008, Zhong *et al.* 2011). Thus, this is more likely a symplesiomorphy than an autapomorphy uniting Siboglinidae and Clitellata. Other analyses placed them as sister either to Spionidae/Fabriciidae/Sabellidae/Serpulidae/Sabellariidae or to Oweniidae (Struck *et al.* 2005, 2007, 2008). In the first phylogenomic study, Siboglinidae was firmly placed within Sedentaria, but their exact position within Sedentaria remained uncertain due to low data coverage and/or long-branch issues for Siboglinidae (Struck *et al.* 2011, Struck 2013, Andrade *et al.* 2015). Phylogenomic studies with substantially increased taxon sampling of about 100 taxa robustly placed Siboglinidae as sister to Cirratulida (Weigert *et al.* 2014, Struck *et al.* 2015). Therefore, in the metatree (Fig. 2.2), Siboglinidae was placed as sister to Cirratulida within Sedentaria. Future studies have to provide further support for this sister group relationship.

### 2.3.3 Echiura

Echiura, a clade of unsegmented marine worms, was first described by Pallas (1766) as belonging to *Lumbricus* (see Hessling and Westheide 2002). Lamarck (1801) grouped Echiura together with polychaetes and Clitellata. Throughout the nineteenth century, Echiura was treated as part of the annelid radiation (e.g., Cuvier 1817, 1830, Lamarck 1818, Hatschek 1880). Quatrefages (1847) transferred Echiura to Gephyrea, which also comprised Sipuncula, Sternaspidae, and Priapulida. According to its name, this group was supposed to form a bridge between annelids and echinoderms. However, Sedgwick (1898) eliminated this taxon and transferred Echiura back to Annelida. Several features support a close affinity of Echiura with Annelida (Purschke *et al.* 2000, Hessling 2002): a typical annelid-like collagenous cuticle, trochophore larva (Baltzer 1932), chaetogenesis and ultrastructure of the chaetae (Storch 1984, Pilger 1993), structure and organization of the blood vascular system (Clark 1969), and development and ultrastructure of spermatozoa (Franzén and Ferraguti 1992). However, Echiura also lack any sign of segmentation as adults as well as nuchal organs. Thus, whereas some regarded these latter characters as secondarily absent, i.e., lost or reduced (Nielsen 1995, Eibye-Jacobsen and Nielsen 1996, Ax 1999, Purschke *et al.* 2000), others judged them as primarily absent and accordingly excluded Echiura from Annelida but still advocated a close relationship to Annelida or Articulata (Newby 1940, Clark 1969, Stephen and Edmonds 1972). This latter view seemed to be supported by morphological cladistic analyses of Annelida (Rouse and Fauchald 1995, 1997, Rouse 1999, 2000). However, the distinction between primary or secondary absence in cladistic analyses based on morphological data might be problematic (e.g., Purschke *et al.* 2000, Jenner 2004c, Struck 2006, Bleidorn 2007). Moreover, the development of the nervous system in Echiura reveals traces of an ancestral segmentation pattern (Hessling 2002, 2003, Hessling and Westheide 2002).

▸ **Fig. 2.2:** Metatree of annelid taxa of this volume. This tree is based on recent phylogenomic studies (Weigert *et al.* 2014, Struck *et al.* 2015), which served as a backbone tree, as well as Laumer *et al.* (2015) for the placement of *Lobatocerebrum*, fig. 10 of Struck *et al.* (2008), and fig. 2 of Zrzavy *et al.* (2009) for taxa not covered by these phylogenomic studies. Taxa not covered by these studies (i.e., Fabriciidae and *Travisia*) were included based on recent molecular phylogenetic studies (Kupriyanova and Rouse 2008, Paul *et al.* 2010). Moreover, a question mark indicates lack of molecular data to date and taxa were included based on morphological considerations. The taxon composition and name of higher taxonomic ranks, such as orders, follow the corresponding chapters of this book. This metatree should be regarded as a working hypothesis for future studies rather than the annelid tree of life. Dashed lines indicate uncertain placement. Color of the branches refers to results of the morphological cladistic analyses of Rouse and Fauchald (1997): blue = Aciculata, green = Canalipalpata, red = Scolecida.

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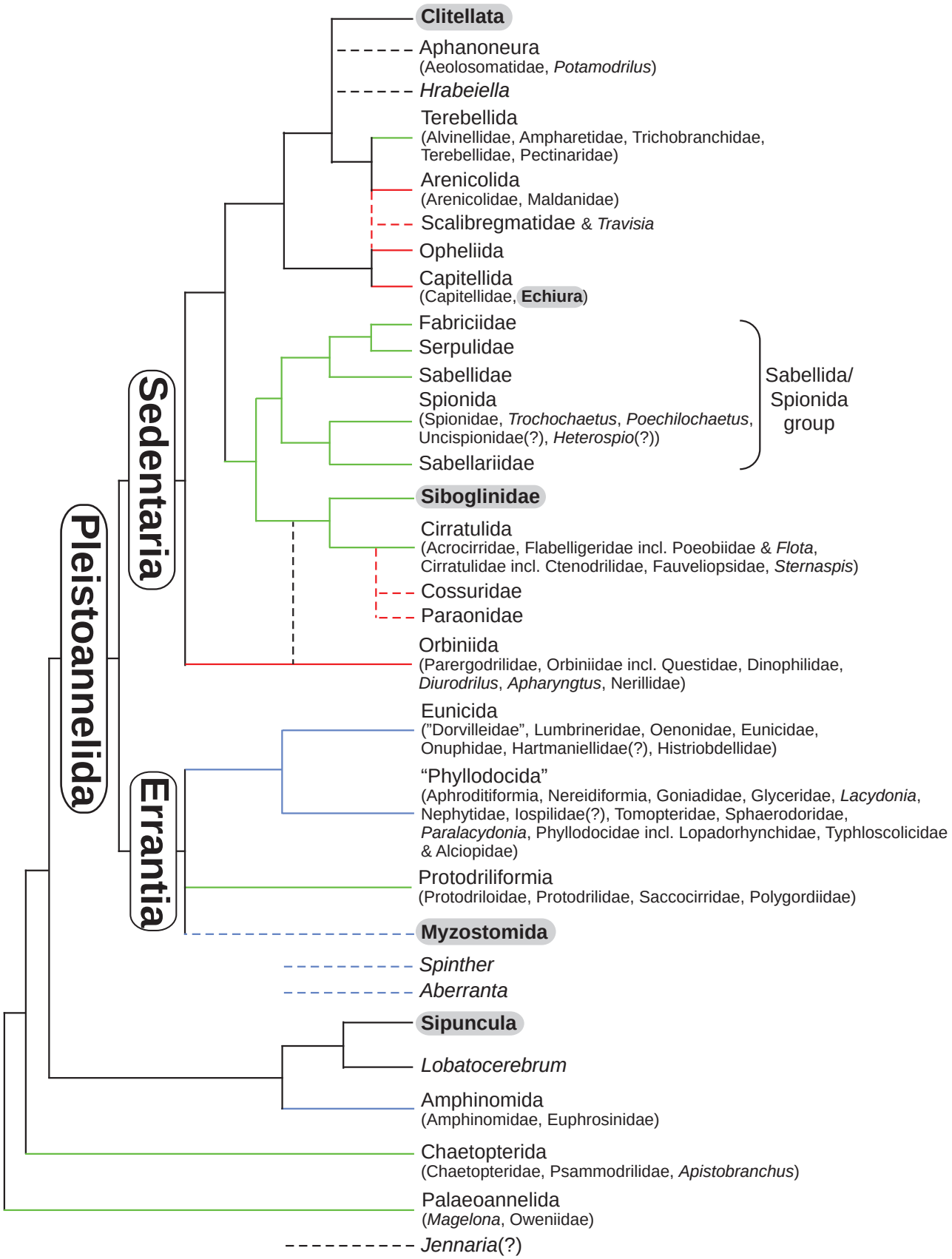


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First support from molecular data for an inclusion of Echiura within Annelida was derived from elongation factor 1α data (McHugh 1997). To date, ample molecular data support the inclusion of Echiura within Annelida, ranging from single genes like myosin II heavy chain or 18S rRNA via multiple genes and mitochondrial genomes to phylogenomic data (Brown *et al.* 1999, McHugh 2000, Mallatt and Winchell 2002, Ruiz-Trillo *et al.* 2002, Bleidorn *et al.* 2003a,b, 2006, 2007, 2009c, Hall *et al.* 2004, Jördens *et al.* 2004, McHugh 2005, Struck *et al.* 2005, 2007, 2008, 2011, 2015, Struck and Purschke 2005, Colgan *et al.* 2006, 2008, Passamaneck and Halanych 2006, Rousset *et al.* 2007, Bourlat *et al.* 2008, Dunn *et al.* 2008, Zhong *et al.* 2008, Hejnol *et al.* 2009, Mwinyi *et al.* 2009, Shen *et al.* 2009, Wu *et al.* 2009, Zrzavy *et al.* 2009, Dordel *et al.* 2010, Golombek *et al.* 2013, Struck 2013, Weigert *et al.* 2014, Andrade *et al.* 2015, Weigert *et al.* 2016). Topology tests significantly rejected the exclusion of Echiura from Annelida (Struck *et al.* 2007). Moreover, of all four taxa discussed in this section to be included into Annelida, Echiura is the only one for which the exact annelid sister group could be named relatively early on. Based on 18S rRNA data, a sister group relationship to Capitellidae was first proposed with strong nodal support (Bleidorn *et al.* 2003a,b). Later studies based on 18S rRNA, 28S rRNA, elongation factor 1α, histone H3, cytochrome oxidase c subunit I, and 16S rRNA data, as well as phylogenomic data, strongly confirmed this placement (Hall *et al.* 2004, Jördens *et al.* 2004, Struck and Purschke 2005, Halanych *et al.* 2007, Struck *et al.* 2007, 2008, 2011, 2015, Dunn *et al.* 2008, Bleidorn *et al.* 2009c, Hejnol *et al.* 2009, Zrzavy *et al.* 2009, Golombek *et al.* 2013, Struck 2013, Weigert *et al.* 2014, Andrade *et al.* 2015). Thus, Echiura is the sister group of Capitellidae (Fig. 2.2).

### 2.3.4 Sipuncula

Sipuncula are relatively large, unsegmented worms without chaetae (more than 90% are >5 mm), which burrow in marine sediments, live in crevices of various hard substrates, or inhabit abandoned tubes, shells, or tests of other organisms. Sipuncula, first recognized by Linneaus (1767), was considered to be closely related to Holothuroida at the beginning of the nineteenth century (Lamarck 1816, Cuvier 1830, see Schulze *et al.* 2005). Later on, Sipuncula was placed in Gephyrea (de Quatrefages 1847). However, deuterostome affinities of Sipuncula were rejected based on developmental data such as spiral cleavage and a typical trochophore larva, and they were placed within Protostomia (e.g., Rice 1985, Eernisse *et al.* 1992, Cutler 1994). Molluscan affinities have repeatedly been proposed based on the so-called molluscan cross during spiral cleavage (e.g., Scheltema 1993). However, the concepts of molluscan and annelid crosses have been criticized and regarded as being without any phylogenetic significance (Guralnick and Lindberg 2001, Guralnick 2002, Maslakova *et al.* 2004a). Rice (1985) suggested a close affinity to Annelida based on developmental features, but the homology of some of the features has been doubted (Nielsen 1987). The early development of the nervous system of Sipuncula in an anteroposterior progression is indicative of a posterior growth zone and shows strong similarities to the early development of Annelida; later in development, this metameric pattern is distorted due to cell migration (Kristof *et al.* 2008). Sipuncula and Terebellida exhibit similarities in the lining of the nephridial podocytes (Bartolomaeus and Quast 2005). Moreover, similarities to annelids can also be found in the ultrastructure of the foregut of the pelagosphera larva and the cuticle (Tzetlin and Purschke 2006). In contrast, morphological cladistic analyses of annelid taxa did not place Sipuncula within Annelida, but close to Mollusca (Rouse and Fauchald 1997, Rouse 1999, 2000).

Early molecular phylogenetic studies based on only one or a few genes, and some in combination with morphological data, generally placed Sipuncula within Lophotrochozoa (e.g., Winnepenninckx *et al.* 1998, Giribet *et al.* 2000, Halanych 2004, Schulze *et al.* 2007). Among others, closer relationships to either Mollusca, Annelida, or Mollusca plus Annelida were suggested, but the position of Sipuncula remained generally unresolved (for a detailed review, see Schulze *et al.* 2005). However, increasing amounts of molecular data for both Sipuncula and other lophotrochozoan taxa in recent years have achieved some substantial progress. Recent studies consistently placed Sipuncula within or as sister to Annelida, with more or less strong nodal support, and the order of mitochondrial protein-coding genes of Sipuncula is similar to the order found in other annelid taxa such as Nereididae or Clitellata (Bleidorn *et al.* 2006, Colgan *et al.* 2006, 2008, Hausdorf *et al.* 2007, Rousset *et al.* 2007, Struck *et al.* 2007, 2008, 2011, 2015, Dunn *et al.* 2008, Mwinyi *et al.* 2009, Shen *et al.* 2009, Zrzavy *et al.* 2009, Dordel *et al.* 2010, Riesgo *et al.* 2012, Struck 2013, Andrade *et al.* 2014, Weigert *et al.* 2014, Laumer *et al.* 2015). A recent study of microRNAs also supported a close relationship of Sipuncula and Annelida (Sperling *et al.* 2009b). Moreover, topology tests significantly rejected the exclusion of Sipuncula from Annelida, even as their sister group (Hausdorf *et al.* 2007, Struck *et al.* 2007, Mwinyi *et al.* 2009, Dordel *et al.* 2010).

Whereas the position of Sipuncula within Annelida was generally inconsistent and lacked strong nodal

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support, several analyses placed Sipuncula in the basal part of the annelid tree (Hausdorf *et al.* 2007, Dunn *et al.* 2008, Struck and Fisse 2008, Struck *et al.* 2008, Mwinyi *et al.* 2009, Dordel *et al.* 2010, Struck *et al.* 2011, Struck 2013, Andrade *et al.* 2015). Recent phylogenomic studies with an increased number of genes and taxa, as well as better quality control for artificial signal, placed Sipuncula as sister to Amphinomida (Weigert *et al.* 2014, Struck *et al.* 2015). Laumer *et al.* (2015) also included *Lobatocerebrum* and found these as sister to Sipuncula. Following these phylogenomic studies, Sipuncula were placed in a clade together with Amphinomida and *Lobatocerebrum* in the basal part of the metatree (Fig. 2.2).

In summary, Myzostomida, Siboglinidae, Echiura, and Sipuncula all had been excluded from Annelida at a time and regarded as so-called distinct phyla due to their unique bauplan. However, all taxa have to be included within Annelida and their unique bauplan is derived from the annelid ground pattern, revealing that the annelid bauplan has been highly variable in the course of annelid evolution.

### 2.3.5 Taxa to be excluded?

Whereas these former taxa have to be included within Annelida, a few interstitial taxa (species) possibly have been suggested to be excluded from Annelida. One example is the genus *Diurodrilus*, an unsegmented, minute, interstitial worm-like organism, first described by Remane (1925), who placed it within Dinophilidae. Later on, *Diurodrilus* was removed from Dinophilidae but was still placed in Annelida and regarded as a highly aberrant interstitial polychaete, which eventually evolved due to progenesis (Kristensen and Niilonen 1982, Westheide 1990). However, *Diurodrilus* possesses a very unique body organization, which renders its placement within Spiralia problematic (Kristensen and Niilonen 1982, Worsaae and Rouse 2008). Support for a placement within Annelida derives only from similarities in the structure of the cuticle (Kristensen and Niilonen 1982, Worsaae and Rouse 2008). On the other hand, *Diurodrilus* resembles Micrognathozoa in the presence, position, and ultrastructure of ciliophores, as well as in the anterior position of two pairs of protonephridia (Worsaae and Rouse 2008). First molecular data based on 18S and 28S rRNA did not place them within Annelida, but as part of the basal radiation of Lophotrochozoa (Worsaae and Rouse 2008). However, a following study showed that the molecular analyses were heavily affected by long-branch attraction, inadequate taxon sampling, and missing data for key taxa (Golombek *et al.* 2013). Amending these issues placed *Diurodrilus* within Annelida, and this was further supported by data from the mitochondrial genome, both at the gene order and the nucleotide level (Golombek *et al.* 2013). Two recent phylogenomic studies independently found *Diurodrilus* as closely related to Orbiniidae (Laumer *et al.* 2015, Struck *et al.* 2015). Hence, in the metatree, *Diurodrilus* was placed in Orbiniida (Fig. 2.2).

The position of two other unsegmented interstitial worm-like genera, *Lobatocerebrum* and *Jennaria*, is also contentious. *Lobatocerebrum* was first described by Rieger (1980). *Lobatocerebrum* generally resembles turbellarian flatworms (Platyhelminthes), but most of these similarities are superficial. Only the cytology of the musculature and the structure of the foregut possibly substantiate a relationship to Platyhelminthes (Rieger 1980, 1981). On the other hand, several cytological characters, such as the structure of the cuticle, epidermal glands, the basal granule cell system, the position and structure of the ECM (extracellular matrix) with respect to the epidermal cells, the serially arranged pairs of protonephridia, the general structure of the anus-hindgut system, and the male gonoduct, point to annelid affinities, promoting their placement within Annelida (Rieger 1980, 1981, Nielsen 1995). Moreover, the ultrastructure of the spermatozoa is similar to that of Clitellata (Rieger 1991b, Nielsen 1995). In contrast, morphological cladistic analyses including *Lobatocerebrum* did not recover a close relationship to annelid taxa but placed them basal within Trochozoa or as sister to Entoprocta (Zrzavy *et al.* 1998, 2001, Zrzavy 2003). However, a phylogenomic study by Laumer *et al.* (2015) clearly placed them within Annelida as sister to Sipuncula.

Similar to *Lobatocerebrum*, *Jennaria* also shares similarities with Annelida as well as with turbellarian flatworms and Gnathostomulida (Rieger 1991a,b,). For example, the structure of the serial arranged protonephridia and the cuticle arrangement of cilia and enteronephridia are similar to those of other interstitial annelids. However, in morphological cladistic analyses, *Jennaria* is not closely related to Annelida, but a basal trochozoan taxon (Zrzavy 2003). In summary, no convincing synapomorphy is known to group *Jennaria* with any spiralian taxon to date (Rieger 1991a,b, Nielsen 1995, Zrzavy 2003), and molecular data are lacking.

## 2.4 Phylogenetic relationships of annelid taxa

The first scientific recognition of annelid taxa like *Nereis*, *Aphrodita*, *Lumbricus*, *Hirudo*, and *Serpula* occurred in

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the *Systema Naturae* of Linneaus (1758). They were placed together with other soft-bodied worm-like organisms such as nematodes in the class Vermes, worms. In the following century, the main emphasis was on descriptions of new annelid species and suggestions about the delineation of a taxon Annelida. Lamarck (1801, 1802) was the first to recognize a taxon Annélides, the segmented worms (or "Vers exterieurs avec des organes exterieurs," free-living worms with external organs), comprising polychaetes, earthworms, and echiurans, but not leeches, which he placed together with nematomorphs and flatworms in the group "Vers exterieurs sans organes exterieurs," free-living worms without external organs. However, later on, Lamarck (1818) included the leeches within Annelida as part of the Apodes, which also comprised echiurans, earthworms, and cirratulids and was characterized by the lack of appendages (Fig. 2.1 A). In this publication, the other annelids were subdivided into two further groups, Antennées and Sédentaires. The former comprised scale worms, nereidids, eunicids, and amphinomids and thus were essentially free-living worms with anterior antennae and dorsal branchiae. The latter comprised arenicolids, maldanids, and terebellids, which are characterized by a more sedentary mode of life. Cuvier (1812) and Savigny (1822) also recognized Annélides, comprising polychaetes, earthworms, and leeches, although Cuvier (1812) additionally included the nematomorph *Gordius*. Savigny (1822) split Annelida in two groups, with the second group ("Deuxième Division") consisting only of leeches. The "Première Division" was divided into three subtaxa: Nereideae, comprising phyllodocidan,[1] eunicidan, and amphinomidan taxa; Serpuleae, consisting of sabellidan, terebellidan, and arenicolidan taxa; and Lumbricinae, including echiurans and earthworms. Hence, the two first subdivisions correspond to the Antennées and Sédentaires of Lamarck (1818).

Cuvier (1812) split the annelid taxa into three groups. The first one, Dorsibranchiata, contained most free-living polchaetes and is similar to Antennées and Nereideae except that it additionally comprised spionids and arenicolids. The second one, Tubicoles, comprised sabellids and serpulids and is characterized by the presence of dorsal branchiae only in the anterior region, if at all. The third group, Abranches, included echuirans, earthworms, leeches, and *Gordius*, all of which did not possess any branchiae. Cuvier (1816) refined his systematization of Annelida by replacing *Gordius* by capitellids within Abranches and by including the scaphopod *Dentalium* and the green algae *Penicillus*, which superficially resembles a serpulid, within Tubicoles. Audouin and Milne Edwards (1834) slightly modified this systematization by changing the name of Dorsibranchiata to "Annélides errantes" and including additionally paraonids, chaetopterids, and onychophorans. Moreover, "Annélides tubicoles" was synonymized with Sédentaires and Abranches split into "Annélides terricoles" comprising capitellids and earthworms and "Annélides souceuses," the leeches. Finally, Blainville (1816) also recognized polychaetes and oligochaetes as one group and coined the name Sétipodes (later changed to Chaetopoda) based on the presence of chaetae in the parapodia but placed leeches together with other worm-like organisms in Apoda. Blainville (1828) then provided a detailed systematization of Chaetopoda based on body organization; Hétérocriniens comprising the taxa of Sabellida, Terebellida, Flabelligeridae, Spionidae, and Capitellidae; Paromocriniens with arenicolidan taxa; and Homocriniens comprising the remaining polychaetes, oligochaetes and echiurans. Therefore, at this time, a consensus was emerging that Annelida at least comprised polychaetes, oligochaetes, and leeches, although the two former names had not been proposed yet. The inclusion of Echiura and Onychophora within Annelida was uncertain at that time.

Whereas Ehlers (1864) more or less followed Blainville (1828) in grouping earthworms within Chaetopoda, Grube (1850) separated both clitellate taxa from polychaetes and coined the names Polychaeta and Oligochaeta in his systematization of Annelida. Grube split Annelida into five taxa (Fig. 2.1 B): (1) Polychaeta, comprising all taxa, which were henceforth referred to as polychaetes (i.e., without Echiura, Sipuncula, Myzostomida, and later Siboglinidae); (2) the holopelagic Tomopteridae, for which he erected the taxon Gymnocopa; (3) Onychophora; (4) Oligochaeta, comprising both earthworms and microdrilids; and (5) Discophora comprising leeches, acanthobdellids and branchiobdellids.

Johnston (1865), Levinsen (1884), Hatschek (1893), Benham (1896), and Perrier (1897) also recognized a separate annelid taxon Polychaeta, although some still placed Tomopteridae in a separate taxon Gymnocopa (Johnston 1865, Levinsen 1884) or grouped both Polychaeta and Oligochaeta within a taxon Chaetopoda to the exclusion of Discophora/Hirudinea (Levinsen 1884, Hatschek 1893,

**1** The taxon composition and name of orders herein follow the corresponding chapters of this *Handbook of Zoology* instead of the widely adopted schemes of Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, New York: 1–354 or Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.

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Perrier 1897). Since the beginning of the twentieth century, most annelid researchers treated Clitellata and Polychaeta as two separate taxa usually referred to as classes (e.g., Fauvel 1923, Fauvel 1927, Uschakov 1955, Dales 1963, Fauchald 1977, George and Hartmann-Schröder 1985, Rouse and Fauchald 1995).

### 2.4.1 Position of Clitellata

Michaelsen (1928–1932) coined the name Clitellata and included aeolosomatids, hirudineans, and oligochaetes in this taxon. Whereas it is still controversially discussed whether or not Aeolosomatidae (Aphanoneura) is the sister taxon or very closely related to Clitellata comprising oligochaetes and hirudineans (Timm 1981, Brinkhurst and Nemec 1987, Bunke 1994, 1998, 2003, Moon *et al.* 1996, Hessling and Purschke 2000, Rota *et al.* 2001, Purschke and Hessling 2002, Struck *et al.* 2002a, 2007, 2008, Marotta *et al.* 2003, Hall *et al.* 2004, Struck and Purschke 2005, Rousset *et al.* 2007, Zrzavy *et al.* 2009), support for the monophyly of Clitellata comprising oligochaetes and hirudineans is overwhelming (e.g., Purschke 2002, Erséus and Kallersjo 2004, Erséus 2005 Struck *et al.* 2011). With respect to Polychaeta, some had the opinion that polychaetes were the more "primitive" annelids and that clitellates derived from polychaetes (e.g., Fauchald 1974). Nonetheless, throughout most of the twentieth century, Polychaeta and Clitellata were treated as separated classes even by these authors. This is most likely the case because a strict phylogenetic Hennigian rigor was not advocated in annelid systematics during this time. Instead, the authors rather applied the philosophy of Linnean categories and hierarchies. Rouse and Fauchald (1995) noted that the monophyly of Polychaeta had never been tested by morphological-cladistic analyses and is supported only by the presence of nuchal organs. Therefore, Rouse and Fauchald (1997) conducted morphological-cladistic analyses comprising all polychaete families and Clitellata, among others, and found Clitellata as sister to a monophyletic Polychaeta (Fig. 2.1 E). In their analyses with reduced taxon sampling, monophyly of Polychaeta is supported either by the presence of palps and mixonephridia or the presence of nuchal organs, parapodia, and mixonephridia based on multistate or absence/presence coding, respectively. However, none of the characters is free of homoplasy, considering all polychaete families. Later studies by Rouse (1999, 2000) also recovered a monophyletic Polychaeta. These analyses were based on a more appropriate sampling of outgroups given the placement of Annelida within Lophotrochozoa, slightly modified or updated characters due to new results, and additional larval characters. Thus, the morphological-cladistic analyses seem to support the traditional split of Annelida in Clitellata and Polychaeta.

However, in parallel, the inclusion of Clitellata within polychaetes was explicitly proposed in the 1990s based on both molecular data and functional morphology. Nielsen (1995) suggested incorporating Clitellata within polychaetes based on similarities to Capitellidae. Westheide (1997) discussed the direction of evolution within polychaetes based on the functional morphology of the coelom and coelothels and concluded that Clitellata is a highly derived polychaete subtaxon and that many of the differences between Clitellata and polychaetes, such as the reduction of appendages in Clitellata, are related to their reproduction. Purschke (2002) and Bartolomaeus *et al.* (2005) seconded these conclusions. Lack or strong reduction and modification of nuchal organs in terrestrial polychaetes gave further credentials to the view that nuchal organs in clitellates might have been lost instead of being primary absent (Purschke 1997, 1999, Purschke *et al.* 2000). Differentiating between primary absence or secondary loss of a character is problematic in morphological-cladistic analyses, if the relationship is not supported by a sufficient number of other synapomorphies not effected by loss (Westheide *et al.* 1999, Purschke *et al.* 2000). For example, the loss of nuchal organs in Pisionidae can be easily detected in morphological cladistic analyses (Bartolomaeus *et al.* 2005). However, if large numbers of characters are affected by loss due to, for example, loss of segmentation or paedomorphic evolution, the correct detection as such might not be possible by morphological-cladistic analyses (Struck 2006, Bleidorn 2007, Bleidorn *et al.* 2009a).

Morphology-based analyses have not been able to determine a polychaete subtaxon as sister taxon to Clitellata. Questidae had been suggested as a possible sister group of Clitellata due to the presence of a clitellum-like structure forming a cocoon and the limitation of the reproductive organs to a few body segments in combination with clearly polychaete characters like nuchal organs and the position of the brain in the prostomium (Giere and Riser 1981, Almeida *et al.* 2003). However, several characters, such as the ventral pharyngeal pad and the accessory musculature, raised serious doubts for such a placement (Giere and Riser 1981, Rouse and Fauchald 1997, Rouse and Pleijel 2001, Giere *et al.* 2008). Molecular data strongly and unambiguously place Questidae within Orbiniidae (Erséus *et al.* 2000, Rota *et al.* 2001, Bleidorn

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*et al*. 2003a,b, 2009a, Bleidorn 2005). In the meantime, several morphological characters like a ventral buccal organ composed of large interstitial cells and transverse muscle fibers and surrounded by an investing muscle system can substantiate such a positioning as well (Beermann *et al*. 2011).

Similar to Aphanoneura, *Hrabeiella* is another taxon that is still controversially discussed as a sister taxon to Clitellata based on both molecular and morphological data (Rota and Lupetti 1996, 1997, Rota 1998, Purschke 1999, 2003, Purschke *et al*. 2000, Rota *et al*. 2001, Jördens *et al*. 2004, Struck and Purschke 2005, Rousset *et al*. 2007, Struck *et al*. 2008, Zrzavy *et al*. 2009). Clitellate-like features such as hermaphroditism, simple chaetae, or lack of parapodia characterize both taxa. However, the homology between these structures and the corresponding characters in Clitellata has not been established. On the other hand, the dorsal pharynx of *Hrabeiella* shows a surprisingly high degree of correspondence to Clitellata (Purschke 2003). Even the structure of the central nervous system is similar to Clitellata, although nuchal organs are present in *Hrabeiella* (Purschke 2000). In contrast, spermatozoal ultratstructure did not indicate any clitellate relationship (Rota and Lupetti 1997, Rota 1998). In summary, based on morphological data, it remains controversial whether or not to place Clitellata within polychaetes.

This is different with respect to molecular data. The first molecular study to address this issue was the one by Kim *et al*. (1996), who used 18S rRNA and included more than one polychaete (i.e., *Neanthes* and *Aphrodita*). They found a sister group relationship of these two polychaetes to Clitellata. However, taxon sampling of polychaetes was still very limited and the 18S rRNA sequences of both polychaetes are problematic (Martin 2001). Winnepenninckx *et al*. (1998) increased the taxon sampling of polychaetes, but their results were inconclusive in that Clitellata and polychaete taxa were scattered throughout the protostome tree of life with low nodal support. Kojima (1998) and McHugh (1997) placed Clitellata within polychaetes based on elongation factor 1α, but nodal support was weak or assessed only by Bremer support values; the latter do not provide levels of statistical significance. All later studies based on 18S rRNA also congruently recovered the placement of Clitellata within polychaetes, albeit given weak nodal support (Martin 2001, Rota *et al*. 2001, Struck *et al*. 2002a,b, Bleidorn *et al*. 2003a,b, Hall *et al*. 2004). This placement of Clitellata within polychaetes was further substantiated by mitochondrial genomes (Boore and Brown 2000, Jennings and Halanych 2005, Bleidorn *et al*. 2006, 2007, 2009c, Vallès and Boore 2006, Zhong *et al*. 2008, Mwinyi *et al*. 2009) and multigene analyses utilizing nuclear 18S rRNA, 28S rRNA (parts or nearly complete), histone H3, U2 snRNA, and mitochondrial cytochrome oxidase subunit I and 16S rRNA in different combinations (Brown *et al*. 1999, Jördens *et al*. 2004, Struck *et al*. 2005, 2007, 2008, Struck and Purschke 2005, Colgan *et al*. 2006, Rousset *et al*. 2007). Nodal support at basal nodes in the annelid tree remained weak, and the analyses provided no support for a polychaete sister group or a larger group of polychaete families also comprising Clitellata. Moreover, placement of Clitellata is often incongruent between these analyses. Nonetheless, topology testing significantly rejected a sister group relationship of Polychaeta and Clitellata based on nuclear 18S rRNA, 28S rRNA, and elongation factor 1α, as well as mitochondrial genome data (Struck *et al*. 2007). In the first phylogenomic study of annelids (Struck *et al*. 2011), Clitellata was placed within Annelida or, more specifically, within Sedentaria. The placement was strongly supported by a maximal bootstrap value of 100. Later, phylogenomic studies (Weigert *et al*. 2014, Andrade *et al*. 2015, Struck *et al*. 2015) strongly corroborated this placement and more specifically found strong support for a placement within a clade consisting also of Arenicolida, Terebellida, Capitellida, and Opheliida. In this clade, Clitellata is sister to a clade of Terebellida and Arenicolida (Fig. 2.2). Additionally, the analyses of Struck *et al*. (2008) also found a clade including Clitellata, Arenicolida, Terebellida, Capitellida, Opheliida, and Scalibregmatidae based on 18S and 28S rRNA data. This analysis had a much more comprehensive taxon sampling than the phylogenomic studies so far, which, for example, did not cover Scalibregmatidae. However, the actual polychaete sister group of Clitellata is still, to some degree, contentious as the relationship of *Hrabeiella* and Aphanoneura to Clitellata has yet to be resolved.

In summary, in the last two decades, evidence has been accumulating that Clitellata is indeed a highly derived subtaxon of Polychaeta, and hence, "Polychaeta" is a paraphyletic assemblage.

### 2.4.2 Position of "Archiannelida"

Besides Polychaeta and Clitellata, another class that has been considered within Annelida is Archiannelida, an assemblage of small, interstitial worms. Hatschek (1878) proposed Archiannelida as a separate group from Chaetopoda, based on a simpler organization and lack of

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several characters such as chaetae or external segmentation. Archiannelida contained Polygordiida, which at that time also included Protodrilidae. Within Chaetopoda, he differentiated three groups: Archichaetopoda (later named Protochaeta), consisting of Saccocirridae; Polychaeta; and Oligochaeta. Archichaetopoda was regarded as the most primitive of the three. Generally, this scheme reflected the view that evolution progressed from simple to complex in annelids. In the following years, several authors adopted the same line of argumentation and some also included Dinophilida and Histriobdellidae within Archiannelida (von Graff 1882, Lang 1884, Repiachoff 1886, Weldon 1886, Fraipont 1887, Hatschek 1888, 1893, Harmer 1889, Schimkewitsch 1895, Benham 1896, Salensky 1907, Pierantoni 1908, Shearer 1910, MacBride 1914, Iwanoff 1928). Others advocated the hypotheses that Polygordiida and/or Saccocirridae are more closely related to Opheliidae (Giard 1880, Langerhans 1880), Dinophilida is a paedomorphic eunicidan taxon or secondarily reduced (Metschnikoff 1866, Salensky 1907, Nachtsheim 1919) and Histriobdellidae is a taxon of degenerated, parasitic polychaetes (Eisig 1898, Salensky 1907, Mesnil *et al.* 1922, Lang 1950). Goodrich (1901) showed that *Protodrilus* is more similar to Saccocirridae than to *Polygordius* and hence erected the new family Protodrilidae, which was closely related to Saccocirridae. Moreover, he regarded the archiannelidan taxa as secondarily degenerated rather than primitive. However, this did not result in the placement of Polygordiida and Protodrilidae within Polychaeta but led to the consideration of Saccocirridae as archiannelids as well (Hermans 1969). On the basis of the resemblance of Nerillida to Dinophilida, de Beauchamp (1910) transferred the former, which had originally been placed close to Nereididae (Schmidt 1848), to Archiannelida. Goodrich (1912) and Heider (1922) also supported the inclusion of Nerillida within Archiannelida.

Reisinger (1925) constituted a taxon Archiannelida comprising Polygordiida, Ctenodrilidae, Aeolosomatidae, Saccocirridae, Protodrilidae, Nerillida, Histriobdellidae, Dinophilida, and Parergodrilidae. However, the placement of Ctenodrilidae, Aeolosomatidae, Histriobdellidae, and Parergodrilidae in Archiannelida was soon criticized (Hermans 1969). For example, both Aeolosomatidae and Parergodrilidae were seen as closely related to Clitellata (Meyer 1927, Michaelsen 1928–1932, Stephenson 1930). Whereas the position of Aeolosomatidae within Annelida is still contentious, Parergodrilidae has now been determined to be the sister to Orbiniidae (Struck *et al.* 2002a, 2008, 2015, Bleidorn *et al.* 2003b, Jördens *et al.* 2004, Bleidorn 2005, Struck and Purschke 2005, Zrzavy *et al.* 2009). Similarly, Ctenodrilidae is now placed within Cirratulidae (Bleidorn *et al.* 2003b, Hall *et al.* 2004, Struck and Purschke 2005, Rousset *et al.* 2007), and Histriobdellidae, within Eunicida (see Orensanz 1990). Hempelmann (1931) listed only Polygordiidae, Saccocirridae, Protodrilidae, Nerillida, and Dinophilida as being part of Archiannelida. He also voiced concerns regarding the exclusion of Archiannelida from Polychaeta but did not include Archiannelida within Polychaeta. Others followed this view and regarded these taxa as archiannelids separate from Polychaeta (Remane 1932, Jägersten 1947, Dales 1963, Mileikovsky 1968). Jägersten (1947) pointed to the morphological similarities in the structure of the pharynx in Dinophilida, Protodrilidae, Saccocirridae, and Nerillida and that these could support a closer relationship among the archiannelidan taxa. On the basis of the pharyngeal organs, Hermans (1969) regarded the archiannelids as a monophyletic assemblage but placed them within polychaetes as an order adapted to the interstitial life. The last to advocate a primitive position for the archiannelids was Mettam (1985) in a critique of Clark's hydrostatic hypothesis about the direction of evolution within Annelida (Clark 1964, 1969). Mettam's argumentation in favor of an ancestral meio-annelid is based mainly on the assumptions that evolution progresses from simple to complex and that reduction and simplification would result in maladapted degenerates.

Giangrande and Gambi (1998) followed Mettam's critique of Clark's hydrostatic hypothesis by pointing out the different functions of complete septa in relation to the presence of well-developed parapodia and circular musculature as well as the way of living in annelid worms. In contrast, Giangrande and Gambi (1998) proposed that the evolution of a metameric coelom and, hence, of complete septa was driven by developmental constraints as the size of annelid worms increased. Assuming modular developmental processes, they argued that "greater length in annelids … was attained by the addition of segmental units by duplication of existing modules" (Giangrande and Gambi 1998: 48). On the basis of the absence of larval segments in the pelagic trochophora larvae of Polygordiidae, as well as the lifelong addition of segments at the posterior end, they concluded that Polygordiidae was most similar to the ancestral condition in Annelida, although some derived features such as a thick cuticle and lack of external segmentation and chaetae related to the adaptation to the interstitial realm

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are present. On the other hand, other archiannelid taxa such as Dinophilidae were regarded as highly derived, paedomorphic polychaetes.

In the meantime, support for the Archiannelida-hypothesis strongly dwindled. Several authors showed similarities of different archiannelidan taxa to larval stages of larger, macrofaunal polychaetes and hence regarded archiannelids as simplified polychaetes adapted to the interstitial realm probably by means of paedomorphic evolution and placed them within polychaetes (Livanov 1940, Beklemischev 1952, Svesnikov 1958, Westheide 1971a, 1984, 1985a,b, 1987, 1990, Åkesson 1977, Kristensen and Niilonen 1982, Westheide and Riser 1983, Eibye-Jacobsen and Kristensen 1994, Westheide and Purschke 1996, Rouse and Pleijel 2001, Worsaae and Kristensen 2005, Worsaae *et al.* 2005, Struck 2006). Ultrastructural investigations by Purschke and coauthors showed that the ventral pharyngeal organs are very different between the archiannelidan taxa and hence are not synapomorphic homologous structures (Purschke 1985a,b, 1987, Purschke and Jouin 1988, Purschke and Tzetlin 1996, Tzetlin and Purschke 2005). No other characters supporting the monophyly of Archiannelida were detected (Brandenburg 1970, Westheide 1971b, 1984, Rieger and Rieger 1975, 1976, Eakin *et al.* 1977, Jouin 1978a,b, Brandenburger and Eakin 1981, Purschke 1990). Following the considerations based on Clark's hydrostratic hypothesis (Clark 1964, 1969), others placed the archiannelidan taxa as separate taxa of uncertain affinity within polychaetes (Fauchald 1977, Pettibone 1982, George and Hartmann-Schröder 1985) (Fig. 2.1 D). Neither morphological cladistic analyses nor molecular phylogenetic studies recovered support for the Archiannelida hypothesis (Rouse and Fauchald 1997, Rouse 1999, 2000, Struck *et al.* 2002b, 2008, Struck and Purschke 2005, Worsaae *et al.* 2005, Rousset *et al.* 2007, Zrzavy *et al.* 2009). Recently, two phylogenomic studies (Andrade *et al.* 2015, Struck *et al.* 2015) independently supported that Polygordiidae and Protodrilida are within Errantia. The more comprehensive study by Struck *et al.* (2015) found them as a clade named Protodriliformia as sister to Eunicida and Phyllodocida (Fig. 2.2). In contrast, while the study of Andrade *et al.* (2015) was inconclusive concerning the placement of Dinophilidae due to long-branch issues and lacked key taxa, the study of Struck *et al.* (2015) strongly placed Dinophilidae, Nerillidae, *Diurodrilus*, and *Apharyngtus* as closely related to Orbiniidae and Parergodrilidae (Fig. 2.2) Hence, the Archiannelida hypothesis is rejected. Polygordiidae and Protodrilida as Protodriliformia are sister to Eunicida and Phyllodocida, while Nerillidae, *Diurodrilus*, *Apharyngtus*, and Dinophilidae are part of Orbiniida.

## 2.4.3 Phylogenetic relationships of polychaete taxa

The placement of Clitellata and archiannelids within polchaetes renders Polychaeta and Annelida synonymous. In the following, the history of the systematization of Polychaeta after Grube (1850) will be reviewed because it is relevant for all annelids. Grube (1850) split Polychaeta into two major groups, Rapacia and Limivora (Fig. 2.1 C). Rapacia (Raubanneliden in Grube 1850) comprised Amphinomida, Eunicida, Phyllodocida (except for Tomopteridae, which was placed in Gymnocopa), and Orbiniidae, and the name referred to their carnivorous lifestyle. Limivora (Schlammfresser, mudeater), consisting of all remaining polychaetes, was characterized by a microphagous diet. Grube (1850) did not provide any morphological features separating these two taxa from each other. Others followed Grube by splitting Polychaeta into two major groups or adopted Grube's general systematic scheme. Hatschek (1893) proposed the group Cirrifera based on the presence of dorsal parapodial cirri. This group included Rapacia, Spionida, Chaetopterida, Opheliida, and Flabelligeridae (as Pherusidae). The remaining polychaetes were grouped into Acirra. However, some of the taxa of Cirrifera, such as Spionida, do not possess dorsal cirri (Fauchald and Rouse 1997). Benham (1894, 1896) divided Polychaeta into Phanerocephala and Cryptocephala, the latter comprising Fabriciidae, Sabellariidae, Sabellidae, and Serpulidae. Cryptocephala was characterized by a peristomium overgrowing and hiding the prostomium, but no feature was provided to group Phanerocephala together. Quatrefages (1866) developed a systematic scheme, which was adopted by many following authors; he considered only polychaete taxa as Annelida, but no clitellate ones. He split Annelida (identical to Polychaeta herein in taxon composition) into Annelidae erraticae (later named Errantia) and Annelidae sedentariae (later named Sedentaria), referring to names already being used by Audouin and Milne Edwards (1834) (as Annélides errantes and Annélides tubicoles [ou sédentaires]) and Lamarck (1818) (as Sédentaires). The names refer to their mode of living as either errant, more vagile worms or sedentary, more sessile ones, but the systematization itself was based on the presence or absence of distinct body regions also known as tagmatization (de Quatrefages 1866). Hence, Annelidae erraticae comprised, besides Amphinomida, Eunicida, and Phyllodocida, also Cirratulida and some spionids and opheliids, as these taxa lack any obvious body regions. Annelidae sedentariae was characterized by the presence of distinct body regions. However,

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several of these taxa, such as Maldanidae or Scalibregmatidae, show little or no sign of tagmatization; on the other hand, Onuphidae clearly possess distinct body regions but are also obviously closely related to the errant polychaete taxon Eunicidae (Fauchald and Rouse 1997). Nonetheless, several authors adopted this scheme with slight modifications. Perrier (1897) used the names Errantia and Sedentaria and transferred Cirratulida (except for Ctenodrilidae) and the spionid and opheliid taxa to Sedentaria. Fauvel (1923, 1927, 1953), Hempelmann (1937), Uschakov (1955), Day (1967a,b), Hartmann-Schröder (1971), and Barnes (1987) used a similar scheme as Perrier (1897) but also included Ctenodrilidae within Sedentaria (Fig. 2.1 C). Thus, Errantia, comprising Eunicida, Phyllodocida, and Amphinomida, is similar in taxon composition to Rapacia of Grube (1850) and Sedentaria comprising the remaining polychaetes to Limivora of Grube (1850) (Fig. 2.1 B, C).

Since the middle of the last century, this scheme has been heavily criticized. It had been argued that the groupings reflect the mode of living rather than evolutionary history and are valuable only for practical purposes. Nonetheless, some adopted the scheme (Uschakov 1955, Day 1967a,b, Hartman 1968, 1969). Dales (1963, 1977) rejected the system and grouped the polychaete families into several orders of equal rank without higher taxonomic groups, as no morphological characters unequivocally supported any higher groupings. In that, he followed Levinsen (1884), who also had grouped the polychaete families into equally ranked orders, but the work was not very influential at that time. Storch (1968), Fauchald (1977), Pettibone (1982), George and Hartmann-Schröder (1985), Hartmann-Schröder (1996), and Westheide (1996, 2007) followed Dales' example and grouped families into equally ranked orders, but number of orders and their composition varied among the authors (Fig. 2.1 D). Thus, by the end of the last century, the old systematic scheme of Errantia and Sedentaria had been completely abandoned, but a new scheme had not arisen yet, so the phylogeny of Polychaeta was regarded as unresolved.

### 2.4.4 Morphological-cladistic analyses

Rouse and Fauchald (1997) tried a new approach to reconcile the different polychaete families into higher taxonomic groupings based on morphological data. They used a cladistic method that considered all data simultaneously instead of only a single or a few characters as previously done (de Quatrefages 1866, Hatschek 1893, Benham 1894, 1896, Dales 1963, 1977). They coded 124 morphological characters as absent/present or 55 characters as multistate for 80 polychaete families. Different strategies were used to analyze the data, for example, by weighing the characters differentially or by excluding symbiotic, pelagic, interstitial, and poorly known taxa. These taxa often show highly aberrant morphologies, and character states are often unknown in the case of poorly described species, leading to unstable placements of these taxa in the reconstructed trees. On the basis of the restricted absent/presence analysis with a priori character weights and successive a posteriori weighing, Rouse and Fauchald (1997) proposed that Polychaeta split into Scolecida and Palpata. Scolecida comprised Arenicolida, Capitellida, Opheliida, Orbiniida, Paraonidae, and Cossuridae (Fig. 2.1 E). The name for these earthworm-like taxa is derived from the Greek word *scolex*, for worm. Monophyly of Scolecida is supported by the presence of parapodia with similar rami and the possession of two or more pairs of pygidial cirri in the analyses of Rouse and Fauchald (1997). Palpata was characterized by the possession of palps and the limitation of the peristomium to the lips. Palpata was further divided into Canalipalpata and Aciculata. Canalipalpata comprised Chaetopterida, Oweniida, Sabellida, Spionida, Terebellida, and the remaining Cirratulida and was supported by the presence of peristomial palps, grooved the name giving feature. Aciculata consisted of Amphinomida, Eunicida, and Phyllodocida (Fig. 2.1 E) and hence was, in its composition, similar to Errantia of Fauvel (1923) and Perrier (1897) (Fig. 2.1 C) or Rapacia of Grube (1850) (Fig. 2.1 B). The name Aciculata is based on the presence of acicula, aciculae (internalized supporting chaetae). Other supporting characters were the presence of median and lateral prostomial antennae and prostomial palps, cirriform dorsal cirri, ventral cirri, and one pair of pygidial cirri, as well as nephridia and coelomoducts, in most segments. Moreover, some taxa were placed as *incertae sedis* by Rouse and Fauchald (1997): Aphanoneura, Parergodrilidae, *Hrabeiella*, and Psammodrilidae as *incertae sedis* within Polychaeta; Nerillida and *Spinther* as *incertae sedis* within Aciculata; and Polygordiidae and Protodrilida as *incertae sedis* within Canalipalpata (Fig. 2.1 E). Rouse (1999, 2000) modified the data matrix by including 16 larval characters and additional lophotrochozoan outgroup taxa and corrected some misscorings in the original dataset. These analyses retrieved similar results as Rouse and Fauchald (1997) in all aspects (i.e., including the deviations from this scheme using different strategies to analyze the data). Rouse and Pleijel (2001) adopted this new systematic scheme for their book on polychaetes, as did others for reviews (e.g., Rouse and Pleijel 2003, 2007), textbooks on polychaetes (e.g., Glasby *et al.* 2000, Rouse and Pleijel 2006), on general invertebrate zoology

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(e.g., Ax 1999, Ruppert *et al.* 2004), or for the taxonomic database of National Center for Biotechnology Information GenBank (www.ncbi.nlm.nih.gov). Within a short time, this scheme of annelid phylogeny was generally accepted, but see Bartolomaeus *et al.* (2005) and Westheide (2007).

As mentioned earlier, the position of Clitellata as sister group to Polychaeta has been strongly criticized right from the beginning and proven to be incorrect due to a misplacement of Clitellata based on secondary absence of characters in Clitellata instead of primary absence like in the outgroup taxa (e.g., Purschke *et al.* 2000, Bleidorn 2007, Struck *et al.* 2007, 2011, Zrzavy *et al.* 2009). Others pointed out that the character reconstructions are inconsistent and structural integrity is not given for all stem species (Bartolomaeus *et al.* 2005). For example, one of the two supporting characters of Palpata is the possession of palps. The two highest ranked taxa within Palpata are Canalipalpata and Aciculata, which are sister taxa to each other (Fig. 2.1 E). Canalipalpata are characterized by peristomial, grooved palps, whereas Aciculata are characterized by prostomial, sensory palps. At least one of the two conditions assumed to be an autapomorphy of either Canalipalpata or Aciculata, respectively, must be plesiomorphic and an autapomorphy for Palpata (Bartolomaeus *et al.* 2005). Moreover, of the characters supporting Scolecida, Palpata, Canalipalpata, and Aciculata, only the characters aciculae and ventral cirri supporting Aciculata are free of homoplasy. All others are affected by either parallelism, reversal within the group, or both (Rouse and Fauchald 1997; see also Bartolomaeus *et al.* 2005 for more detailed discussion of this point). However, internalized supporting chaetae very similar to aciculae (and sometimes called as such) are also known in Chaetopteridae, Orbiniidae, and Apistobranchidae (Rouse and Pleijel 2001) but were not coded as homologous to aciculae in Rouse and Fauchald (1997). Finally, only the absent/presence analysis with a restricted taxon sampling, a priori character weights, and successive a posteriori weighing recovered the monophyly of Scolecida, Palpata, Canalipalpata and Aciculata. The monophyly of Aciculata was corroborated in all of their 11 different analyses, but Canalipalpata, only in two additional ones (i.e., the absent/presence analysis with a restricted taxon sampling, equal character weights, and successive a posteriori weighing, and the absent/presence analysis with a complete taxon sampling, a priori character weights, and successive a posteriori weighing), and Palpata only, in one additional one (i.e., the absent/presence analysis with a restricted taxon sampling, equal character weights, and successive a posteriori weighing) (Rouse and Fauchald 1997). The monophyly of Scolecida was never recovered in any of their other analyses. Thus, weighing strategies were crucial in the recovery of all clades except Aciculata.

### 2.4.5 Molecular analyses

Early molecular studies based on either 18S rRNA or elongation factor 1α sequences covered too little of the polychaete biodiversity to adequately address the evolution and phylogeny of Annelida in general and polychaetes in particular (Kim *et al.* 1996, McHugh 1997, Kojima 1998, Winnepenninckx *et al.* 1998, McHugh 2000). Brown *et al.* (1999) had a comprehensive taxon sampling of 35 annelid species and was based on sequences of three genes (U2 snRNA, histone H3, and the D1 and D9–10 expansion elements of the 28S rRNA) instead of only 18S rRNA or elongation factor 1α. The analysis recovered Eunicida and Terebellida as well as a closer relationship of cirratulidan taxa to each other and a placement of Spionidae within Sabellida (Fig. 2.2). However, nodal support with bootstrap values below 50 at all basal nodes was way too low to substantiate a robust alternative hypothesis of annelid phylogeny based on molecular data. Ensuing studies based on 18S rRNA sequences included a steadily increasing number of taxa but also suffered from low-resolution power as judged by low nodal support and incongruencies among each other and previous molecular and morphological analyses (Martin 2001, Rota *et al.* 2001, Struck *et al.* 2002a,b, Bleidorn *et al.* 2003,a,b, Hall *et al.* 2004). In addition, using different methods to analyze the data (e.g., maximum parsimony, maximum likelihood, or neighbor joining) could result in different trees for the same dataset. Annelid monophyly could not be recovered, and outgroup taxa were dispersed throughout the annelid radiation. The low number of positions in these datasets, which ranged from 1413 (Brown *et al.* 1999) to 1770 (Rota *et al.* 2001) nucleotides, might be partially responsible for the low molecular phylogenetic signal. Therefore, McHugh (2005) suggested increasing the number of positions in the datasets in addition to the number of taxa.

More recent studies sampled additional genes in different combinations, namely, 28S rRNA (complete or parts of it), elongation factor 1α, histone H3, U2 snRNA, cytochrome oxidase I, and 16S rRNA (Jördens *et al.* 2004, Struck *et al.* 2005, 2007, 2008, Struck and Purschke 2005, Colgan *et al.* 2006, Rousset *et al.* 2007). Due to these additional gene fragments, up to 2.5 times more data were available for more than 70 annelid species (Struck *et al.* 2007). Although nodal support still remained low, slight progresses could be achieved in some analyses using the most suitable maximum likelihood approach. For example, the monophyly of Annelida was recovered

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even with a comprehensive outgroup sampling (Struck *et al.* 2005, 2007, Colgan *et al.* 2006). On the other hand, topology testing significantly rejected monophyly of Scolecida, Palpata, Canalipalpata, and Aciculata sensu Rouse and Fauchald (1997) (Struck *et al.* 2007). Moreover, results became more consistent among different studies. The analyses of Struck *et al.* (2007, 2008) both recovered a clade of Phyllodocida, Eunicida, and Orbiniidae plus Parergodrilidae, a clade Terebellida, a close relationship of Terebellida, Arenicolida, Clitellata, Opheliida, and Capitellida to each other as well as basal positions of Amphinomida and Chaetopterida and Spionida as a subgroup of paraphyletic Sabellida. Basal Chaetopterida and a placement of Spionida within Sabellida had also been shown in the analyses of Colgan *et al.* (2006). Struck *et al.* (2008), and Rousset *et al.* (2007) have in common a sister group relationship of Arencolida and Terebellida. Struck *et al.* (2008) recovered Cirratuliformia with low support, a group also proposed by Rouse and Fauchald (1997). Finally, a total evidence analysis of Zrzavy *et al.* (2009) based on six genes and morphological data using a Bayesian approach was highly congruent to the results of Struck *et al.* (2008). Both studies found basal positions of Oweniida, Chaetopterida, Amphinomida, Sipuncula, Myzostomida, and the former archiannelidan taxa Protodrilida, Polygordiida, Nerillida, and Dinophilida. The remaining annelids split into two major groups. One comprised Phyllodocida, Eunicida, and Orbiniidae plus Parergodrilidae, and the other one, the remaining annelids, including Clitellata and Echiura. The placement of Spionida within Sabellida and a sister group relationship of Arenicolida and Terebellida is similar to Struck *et al.* (2008). However, as for the other analyses, nodal support is low, especially given that posterior probabilities had been estimated, which tend to overestimate the support (e.g., Suzuki *et al.* 2002, Simmons *et al.* 2004, Lewis *et al.* 2005). Due to the lack of strong nodal support in these studies, no alternative hypothesis of annelid phylogeny could be suggested, but simulation studies by Struck *et al.* (2008) showed that annelid phylogeny could be resolved using more data. Moreover, Dordel *et al.* (2010) revealed that amino acid data would be better suited to achieve this goal than nucleotide data. Therefore, Struck *et al.* (2011) conducted a first phylogenomic study of Annelida generating EST (Expressed Sequence Taq) data for a comprehensive set of 34 annelids.

Using this phylogenomic approach, Struck *et al.* (2011) were able to compile a dataset of nearly 48,000 amino acid positions and data coverage of 41.7% per taxon, which is relatively high for a phylogenomic study. With this large dataset, they obtained a well-supported phylogeny with several basal nodes showing bootstrap values of 70 or higher. Some even obtained the maximal support value of 100. Andrade *et al.* (2015) generally confirmed the results with datasets comprising up to 37 different annelids and 337,236 positions with a coverage of 95%. However, Struck (2013) also showed how influential erroneously assigned paralogous sequences can be on the reconstruction of the annelid tree using phylogenomic datasets. Accordingly, Weigert *et al.* (2014) and Struck *et al.* (2015) adjusted the procedure to compile and analyze such datasets to mitigate this and other problems. In these studies, up to 81 annelid taxa and 189,193 positions with a coverage of up to 75.6% were analyzed. These two studies substantially increased the robustness of the analyses, including maximal nodal support for almost all nodes, as well as generally confirming the major groupings of Struck *et al.* (2011) and also found by Andrade *et al.* (2015). The results of these studies are used as a backbone tree in Fig. 2.2.

In these studies, Oweniidae, *Magelona*, Chaetopterida, Amphinomida, and Sipuncula were part of the first annelid radiation (Weigert *et al.* 2014, Struck *et al.* 2015) (Fig. 2.2). The first clade to branch off is Oweniidae plus *Magelona*, which was named Palaeoannelida (Weigert and Bleidorn 2016). Zrzavy *et al.* (2009) additionally recovered *Aberranta* as part of the basal radiation as well. For *Spinther*, the placement in the analyses of Andrade *et al.* (2015) was inconsistent, and hence, it is regarded as uncertain herein (Fig. 2.2).

The remaining annelids split into two well-supported groups; one clade comprised Eunicida, Phyllodocida, and Protodriliformia, and the other one, Orbiniida, Siboglinidae, Sabellida, Spionida, Cirratulida, Terebellida, Arenicolida, Opheliida, Capitellida, and Clitellata (Weigert *et al.* 2014, Struck *et al.* 2015). These two clades had also been generally recovered in the analyses of Struck *et al.* (2008) and Zrzavy *et al.* (2009). As the taxon compositions of these two clades were very similar to the taxon compositions of the traditional Errantia and Sedentaria, respectively (Fauvel 1923, 1927), Struck *et al.* (2011) resurrected these names for these two clades with some modifications. Besides Phyllodocida and Eunicida, Errantia also included Protodriliformia and excluded Amphinomida. Hence, using a stem-based definition, the composition of the clade Errantia can be defined by the last common ancestor of Eunicida, Phyllodocida, and all organisms or species that share a more recent common ancestor with these two taxa than with Clitellata and Spionidae. Struck *et al.* (2011) refrained from extending the definition of Aciculata of Rouse and Fauchald (1997) because ancestral state reconstructions in their study revealed that internalized supporting chaetae such as aciculae were part of the annelid ground pattern. Thus, it should not be used as a defining character for a subclade.

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Sedentaria now also includes Clitellata and Echiura (as part of Capitellida) and excludes Chaetopterida, Oweniidae, and *Magelona*. Therefore, using a stem-based definition, the composition of the clade Sedentaria can be defined by consisting of Clitellata, Echiura, Spionidae, and all organisms or species that share a more recent common ancestor with these three taxa than with Phyllodocida or Eunicida. The clade consisting of Errantia and Sedentaria received substantial bootstrap support ranging from about 90 up to 100 (Struck *et al.* 2011, 2015, Weigert *et al.* 2014). Struck (2011) named this clade Pleistoannelida as it comprises most of the recent annelid biodiversity and defined it by the last common ancestor of Sedentaria and Errantia *sensu* Struck *et al.* (2011) and all the descendants of that ancestor. However, as Struck *et al.* (2011) did not provide formal definitions of Errantia and Sedentaria, the definition of Pleistoannelida should be slightly adjusted to reflect the more precise definitions for these two taxa given herein. Therefore, Pleistoannelida can be defined by the last common ancestor of Sedentaria and Errantia as defined herein and all the descendants of that ancestor.

Within Errantia, the most surprising result was the inclusion of Protodriliformia (Struck *et al.* 2015), which were previously regarded as sedentary polychaetes. In Struck *et al.* (2011), Phyllodocida was not monophyletic, as Aphroditiformia, the scale worms, was sister to Orbiniida with strong bootstrap support of 100. However, Struck (2013) could show that this placement of Aphroditiformia, Orbiniidae, and Amphinomida was due to erroneously assigned paralogous sequences. Following studies (Weigert *et al.* 2014, Struck *et al.* 2015) found monophyletic Phyllodocida as sister to Eunicida (Fig. 2.2).

Within Sedentaria, the recent phylogenomic studies (Weigert *et al.* 2014, Struck *et al.* 2015) provided well-supported nodes. In the more comprehensive study by Struck *et al.* (2015), Orbiniida, including also several former archiannelid taxa, is sister to the other Sedentaria. Fauvel (1927) already regarded Orbiniidae as intermediate forms between Errantia and Sedentaria. The remaining Sedentaria split into two major clades (Struck *et al.* 2015). One clade consists of Siboglinidae and Cirratulida as sister to each other, as well as Spionida placed within Sabellida. In Weigert *et al.* (2014), which had no archiannelid taxa included, Cirratulida and Siboglinidae were sister to Orbinidae instead. In Struck *et al.* (2008), Cirratulida also includes Paraonidae. Similarly, Paraonidae and Cossuridae are also closely related to Cirratulida in Zrzavy *et al.* (2009). Moreover, Spionida is placed as sister to Sabellariidae in the Sabellida/Spionida clade in both Struck *et al.* (2008) and Zrzavy *et al.* (2009). Finally, Kupriyanova and Rouse (2008) found Fabriciidae to be more closely related to Serpulidae than to Sabellidae.

The other clade, comprising Terebellida, Arenicolida, Opheliida, Capitellida, and Clitellata (Struck *et al.* 2011, 2015, Weigert *et al.* 2014), is also recovered in Struck *et al.* (2008) (Fig. 2.2). Within this clade, a well-supported sister group relationship of Arenicolida and Terebellida was recovered (Struck *et al.* 2011, 2015, Weigert *et al.* 2014). This sister group relationship was also found by Struck *et al.* (2008) and Zrzavy *et al.* (2009). In Struck *et al.* (2008), Arenicolida also included Scalibregmatidae, congruent with the results of Paul *et al.* (2010), whereas in Zrzavy *et al.* (2009), Scalibregmatidae was sister to Opheliida. Arenicolida and Terebellida are the sisters of Clitellata (Weigert *et al.* 2014, Struck *et al.* 2015). However, in Zrzavy *et al.* (2009), Aphanoneura and *Hrabeiella* are sisters to Clitellata congruent with Struck *et al.* (2007). Finally, Opheliida and Capitellida are sisters to each other (Weigert *et al.* 2014, Struck *et al.* 2015). In summary, based on the recent phylogenomic analyses outlined earlier, a new classification of Annelida can be proposed based on molecular data (Fig. 2.2) as an alternative to that of Rouse and Fauchald (1997) (Fig. 2.1 E).

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## 2.6 References

Aguinaldo, A.M.A., Turbeville, J.M., Linford, L.S., Rivera, M.C., Garey, J.R., Raff, R.A. & Lake, J.A. (1997): Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* 387: 489–493.

Åkesson, B. (1977): Parasite-host relationships and phylogenetic systematics. The taxonomic position of dinophilids. *Mikrofauna des Meeresbodens* 61: 19–28.

Almeida, W.d.O., Christoffersen, M.L., Amorim, D.d.S., Garraffoni, A.R.S. & Silva, G.S. (2003): Polychaeta, Annelida, and Articulata are not monophyletic: articulating the Metameria (Metazoa, Coelomata). *Revista Brasileira de Zoologia* 20: 23–57.

Alwes, F. & Scholtz, G. (2004): Cleavage and gastrulation of the euphausiacean *Meganyctiphanes norvegica* (Crustacea, Malacostraca). *Zoomorphology* 123: 125–137.

Anderson, D. (1973): *Embryology and Phylogeny in Annelids and Arthropods*. Pergamon Press Ltd., Oxford.

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Anderson, F.E., Córdoba, A.J. & Thollesson, M. (2004): Bilaterian phylogeny based on analyses of a region of the sodium-potassium ATPase ß-subunit gene. *Journal of Molecular Evolution* 58: 252–268.

Andrade, S.C.S., Montenegro, H., Strand, M., Schwartz, M., Kajihara, H., Norenburg, J.L., Turbeville, J.M., Sundberg P. & Giribet, G. (2014): A transcriptomic approach to ribbon worm systematics (Nemertea): resolving the Pilidiophora problem. *Molecular Biology and Evolution* 31: 3206–3215.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Arnaud, F. & Bamber, R.N. (1987): The biology of Pycnogonida. *Advances in Marine Biology* 24: 1–96.

Audouin, J.V. & Milne Edwards, H. (1834): *Recherches pour servir a l'histoire naturelle du littoral de la France, ou Recueil de mémoires sur l'anatomie, la physiologie, la classification et les moeurs des animaux de nos côtes; ouvrage accompagné de planches faites d'après nature*. Crochard, Paris.

Ax, P. (1995): *Das System der Metazoa I*. Gustav Fischer Verlag, Stuttgart.

Ax, P. (1999): *Das System der Metazoa II*. Fischer, Stuttgart.

Baguñà, J., Martinez, P., Paps, J. & Riutort, M. (2008): Back in time: a new systematic proposal for the Bilateria. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 1481–1491.

Bailly, X., Jollivet, D., Vanin, S., Deutsch, J., Zal, F., Lallier, F. & Toulmond, A. (2002): Evolution of the sufilde-binding function within the globin multigenic family of the deep-sea hydrothermal vent tubeworm *Riftia pachyptila*. *Molecular Biology and Evolution* 19: 1421–1433.

Bailly, X., Leroy, R., Carney, S., Collin, O., Zal, F., Toulmond, A. & Jollivet, D. (2003): The loss of hemoglobin $H_2S$-binding function in annelids from sulfide-free habitats reveals molecular adaptation driven by Darwinian positive selection. *Proceedings of the National Academy of Sciences of the United States of America* 100: 5885–5890.

Bakke, T. (1976): The early embryos of *Siboglinum fiordicum* Webb (Pogonophora) reared in the laboratory. *Sarsia* 60: 1–11.

Balavoine, G., de Rosa, R. & Adoutte, A. (2002): Hox clusters and bilaterian phylogeny. *Molecular Phylogenetics and Evolution* 24: 366–373.

Baltzer, F. (1932): Echiurida. In: Kükenthal, W. (ed.) *Handbuch der Zoologie*. Vol. 2. Walter De Gruyter, Berlin: 62–168.

Barnes, R.D. (1987): *Invertebrate Zoology.* Saunders College Publishing, Fort Worth, TX.

Bartolomaeus, T. (1995): Structure and formation of the uncini in *Pectinaria koreni*, *Pectinaria auricoma* (Terebellida) and *Spirorbis spirorbis* (Sabellida): implications for annelid phylogeny and the position of the Pogonophora. *Zoomorphology* 115: 161–177.

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

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

Bartolomaeus, T., Quast, B. & Koch, M. (2009): Nephridial development and body cavity formation in *Artemia salina* (Crustacea: Branchiopoda): no evidence for any transitory coelom. *Zoomorphology* 128: 247–262.

de Beauchamp, P. (1910): Sur l'organisation de la *Nerilla*. *Bulletin Biologique de la France et de la Belgique* 44: 11–22.

Beermann, A., Giere, O. & Purschke, G. (2011): Ultrastructure of the ventral pharynx in the interstitial annelid *Questa paucibranchiata* (Orbiniidae) and its phylogenetic significance. *Zoomorphology* 130: 167–180.

Beklemischev, V.N. (1952): *Principles of Comparative Anatomy of Invertebrates*. Soviet Science, Moscow.

Benham, W.B. (1894): Suggestions for a new classification of the Polychaeta. *Report of the British Association for the Advancement of Science* 1984: 696–697.

Benham, W.B. (1896): Archiannelida, Polychaeta, Myzostomidaria. In: Farmer, S.F. & Shipley, A.E. (eds.) *The Cambridge Natural History*. Macmillan, London: 241–334.

Bergsten, J. (2005): A review of long-branch attraction. *Cladistics* 21: 163–193.

Black, M., Halanych, K., Maas, P., Hoeh, W., Hashimoto, J., Desbruyeres, D., Lutz, R. & Vrijenhoek, R. (1997): Molecular systematics of vestimentiferan tubeworms from hydrothermal vents and cold-water seeps. *Marine Biology* 130: 141–149.

de Blainville, H.M.D. (1816): Prodrome d'une nouvelle distribution systématiques du règne animal. *Bulletin de la Société Philomathique de Paris* 8: 113–124.

de Blainville, H.M.D. (1828): *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des differens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connaisance, soit relativement a l'utilité qu'en peuvent retirer la médicine, l'agriculture, le commerce et les arts. Suivi d'une biographie des plus célèbres naturalistes*. FG Levrault, Strasbourg & Paris.

Bleidorn, C. (2005): Phylogenetic relationships and evolution of Orbiniidae (Annelida, Polychaeta) based on molecular data. *Zoological Journal of the Linnean Society* 144: 59–74.

Bleidorn, C. (2007): The role of character loss in phylogenetic reconstruction as exemplified for the Annelida. *Journal of Zoological Systematic and Evolutionary Research* 45: 299–307.

Bleidorn, C., Eeckhaut, I., Podsiadlowski, L., Schult, N., McHugh, D., Halanych, K.M., Milinkovitch, M.C. & Tiedemann, R. (2007): Mitochondrial genome and nuclear sequence data support Myzostomida as part of the annelid radiation. *Molecular Biology and Evolution* 24: 1690–1701.

Bleidorn, C., Helm, C., Weigert, A., Eeckhaut, I., Lanterbecq, D., Struck, T.H., Tiedemann, R. & Hartmann, S. (2014): From morphology to phylgenomics: placing the enigmatic Myzostomida in the tree of life. In: Wägele, J.W. & Bartolomaeus, T. (eds.) *Deep Metazoan Phylogeny: The Backbone of the Tree of Life – New Insights from Analyses of Molecules, Morphology, and Theory of Data Analysis*. De Gruyter, Berlin: 161–172.

Bleidorn, C., Hill N., Ersèus, C. & Tiedemann, R. (2009a): On the role of character loss in orbiniid phylogeny (Annelida): molecules vs. morphology. *Molecular Phylogenetics and Evolution* 52: 57–69.

Bleidorn, C., Lanterbecq, D., Eeckhaut, I. & Tiedemann, R. (2009b): A PCR survey of Hox genes in the myzostomid *Myzostoma cirriferum*. *Development Genes and Evolution* 219: 211–216.

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Bleidorn, C., Podsiadlowski, L. & Bartolomaeus, T. (2006): The complete mitochondrial genome of the orbiniid polychaete *Orbinia latreilli* (Annelida, Orbiniidae) – a novel gene order for Annelida and implications for annelid phylogeny. *Gene* 370: 96–103.

Bleidorn, C., Podsiadlowski, L., Zhong, M., Eeckhaut, I., Hartmann, S., Halanych, K. & Tiedemann, R. (2009c): On the phylogenetic position of Myzostomida: can 77 genes get it wrong? *BMC Evolutionary Biology* 9: 150.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003a): A contribution to sedentary polychaete phylogeny using 18S rRNA sequence data. *Journal of Systematic Zoology and Evolutionary Research* 41: 186–195.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003b): New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 29: 279–288.

Boore, J.L. & Brown, W.M. (2000): Mitochondrial genomes of *Galathealinum*, *Helobdella* and *Platynereis*: sequence and gene arrangements comparisons indicate that Pogonophora is not a phylum and Annelida and Arthropoda are not sister taxa. *Molecular Biology and Evolution* 17: 87–106.

Bourlat, S.J., Nielsen, C., Economou, A.D. & Telford, M.J. (2008): Testing the new animal phylogeny: a phylum level molecular analysis of the animal kingdom. *Molecular Phylogenetics and Evolution* 49: 23–31.

Brandenburg, J. (1970): Die Cuticula des *Dinophilus* (Archiannelida). *Zeitschrift für Morphologie der Tiere* 68: 300–307.

Brandenburger, J.L. & Eakin, R.M. (1981): Fine structure of ocelli in larvae of an archiannelid, *Polygordius* cf *appendiculatus*. *Zoomorphology* 99: 23–36.

Brinkhurst, R.O. & Nemec, A.F.L. (1987): A comparison of phenetic and phylogenetic methods applied to the systematics of Oligochaeta. *Hydrobiologia* V155: 65–74.

Brown, S., Rouse, G.W., Hutchings, P. & Colgan, D. (1999): Assessing the usefullness of histone H3, U2 snRNA and 28S rDNA in analyses of polychaete relationships. *Australian Journal of Zoology* 47: 499–516.

Brusca, R.C. & Brusca, G.J. (1990): *Invertebrates*. 1st ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

Brusca, R.C. & Brusca, G.J. (2003): *Invertebrates*. 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

Brusca, R.C., Moore, W. & Shuster, S.M. (2016): *Invertebrates*. 3rd ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

Bullock, T.H. & Horridge, G.A. (1965): *Structure and Function in the Nervous System of Invertebrates*. Freeman, San Francisco.

Bunke, D. (1994): Ultrastructure of the metanephridial system in *Aeolosma bengalense* (Annelida). *Zoomorphology* 114: 247–258.

Bunke, D. (1998): Ultrastructure of the nephrostome in *Enchytraeus albidus* (Annelida, Clitellata). *Zoomorphology* 118: 177–182.

Bunke, D. (2003): Early development of the metanephridia in the caudal budding zone of a clitellate annelid, *Dero digitata* (Naididae): an electron-microscopical study. *Acta Zoologica* 84: 87–97.

Caullery, M. (1914): Sur les Siboglinidae, type nouveau d'invertébrés recueilli par l'expédition du Siboga. *Comptes Rendus de L'Academie des Sciences* 158: 2014–2017.

Clark, R.B. (1964): *Dynamics in Metazoan Evolution. The Origin of the Coelom and Segments*. Clarendon Press, Oxford.

Clark, R.B. (1969): Systematics and phylogeny: Annelida, Echiura, Sipuncula. In: Florkin, M. & Scheer, B.T. (eds.) *Chemical Zoology*. Vol. 4. Academic Press, New York: 1–68.

Colgan, D.J., Hutchings, P.A. & Beacham, E. (2008): Multi-gene analyses of the phylogenetic relationships among the Mollusca, Annelida, and Arthropoda. *Zoological Studies* 47: 338–351.

Colgan, D.J., Hutchings, P.A. & Braune, M. (2006): A multigene framework for polychaete phylogenetic studies. *Organisms, Diversity and Evolution* 6: 220–235.

Cutler, E.B. (1994): *The Sipuncula. Their Systematics, Biology and Evolution*. Cornell University Press, Ithaca, NY.

Cuvier, G. (1812): Sur un nouveau rapprochment à établir entre les classes qui composant le Règne Animal. *Annales du Muséum d'Histoire naturelle Paris* 19: 73–84.

Cuvier, G. (1816): *Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides*. Deterville, Paris.

Cuvier, G. (1817): *Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Deterville, Paris.

Cuvier, G. (1830): *Le regne animal distribue d'apres son oranisation, pour servir de base a l'histoire naturelle de animaux et d'introduction a l'anatomie comparee*. Ser. 2, Vol. 3. Deterville, Paris.

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

Dales, R.P. (1977): The polychaete stomatodeum and phylogeny. In: Reish, D.J. & Fauchald, K. (eds.) *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles: 525–546.

Dawydoff, C. (1948): Contribution á la coinnaissance de *Siboglinum* Caullery. *Bulletin Biologique de la France et de la Belgique* 82: 141–163.

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

Day, J.H. (1967b): *A Monograph on the Polychaeta of Southern Africa. Part 1. Errantia*. British Museum (Natural History), London.

Dearden, P.K., Donly, C. & Grbic, M. (2002): Expression of pair-rule gene homologues in a chelicerate: early patterning of the two-spotted spider mite *Tetranychus urticae*. *Development* 129: 5461–5472.

Dordel, J., Fisse, F., Purschke, G. & Struck, T.H. (2010): Phylogenetic position of Sipuncula derived from multi-gene and phylogenomic data and its implication for the evolution of segmentation. *Journal of Zoological Systematics and Evolutionary Research* 48: 197–207.

Dunn, C.W., Hejnol, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., Sorensen, M.V., Haddock, S.H.D., Schmidt-Rhaesa, A., Okusu, A., Kristensen, R.M., Wheeler, W.C., Martindale, M.Q. & Giribet, G. (2008): Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452: 745–750.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Eakin, R.M., Martin, G.G. & Reed, C.T. (1977): Evolutionary significance of fine structure of archiannelid eyes. *Zoomorphology* 88: 1–18.

Edgecombe, G., Giribet, G., Dunn, C., Hejnol, A., Kristensen, R., Neves, R., Rouse, G., Worsaae, K. & Sørensen, M. (2011): Higher-level metazoan relationships: recent progress and remaining questions. *Organisms Diversity & Evolution* 11: 151–172.

Eeckhaut, I., Fievez, L. & Müller, M.C.M. (2003): Larval development of *Myzostoma cirriferum* (Myzostomida). *Journal of Morphology* 258: 269–283.

Eeckhaut, I. & Lanterbecq, D. (2005): Myzostomida: A review of the phylogeny and ultrastructure. *Hydrobiologia* 535–536: 253–275.

Eeckhaut, I., McHugh, D., Mardulyn, P., Tiedemann, R., Monteyne, D., Jangoux, M. & Milinkovitch, M.C. (2000): Myzostomida: a link between trochozoans and flatworms? *Proceedings of the Royal Society of London, Series B: Biological Sciences* 267: 1383–1392.

Eernisse, D.J., Albert, J.S. & Anderson, F.E. (1992): Annelida and Arthropoda are not sister taxa: a phylogenetic analysis of spiralian metazoan morphology. *Systematic Biology* 41: 305–330.

Ehlers, E. (1864): *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Wilhelm Engelmann, Leipzig.

Eibye-Jacobsen, D. & Kristensen, R.M. (1994): A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta* 23: 107–131.

Eibye-Jacobsen, D. & Nielsen, C. (1996): The rearticulation of annelids. *Zoologica Scripta* 25: 275–282.

Eisig, H.D. (1898): Zur Entwicklungsgeschichte der Capitelliden. *Mittheilungen aus der zoologischen Station zu Neapel* 13: 1–292.

Erséus, C. (2005): Phylogeny of oligochaetous Clitellata. *Hydrobiologia* 535–536: 357–372.

Erséus, C. & Kallersjo, M. (2004): 18S rDNA phylogeny of Clitellata (Annelida). *Zoologica Scripta* 33: 187–196.

Erséus, C., Prestegaard, T. & Källersjö, M. (2000): Phylogenetic analysis of Tubificidae (Annelida, Clitellata) based on 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 15: 381–389.

Fauchald, K. (1974): Polychaete phylogeny: a problem in protostome evolution. *Systematic Zoology* 23: 493–506.

Fauchald, K. (1977): The polychaete worms. *Definitions and Keys to the Orders, Families and Genera*. Natural History Museum of Los Angeles County. Science Series, Los Angeles.

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

Fauvel, P. (1923): Polychètes Errantes. *Faune de France* 5: 1–488.

Fauvel, P. (1927): Polychètes Sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. *Faune de France* 16: 1–494.

Fauvel, P. (1953): *The Fauna of India, including Pakistan, Ceylon, Burma and Malaya. Annelida. Polychaeta*. The Indian Press, Allahabad.

Fedotov, D. (1929): Beiträge zur Kenntnis der Morphologie der Myzostomiden. *Zeitschrift für Morphologie und Ökologie der Tiere* 15: 156–191.

Felsenstein, J. (1978): Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* 27: 401–410.

Field, K.G., Olsen, G.J., Giovannoni, S.J., Raff, E.C., Pace, N.R. & Raff, R.A. (1989): Response: phylogeny and molecular data. *Science* 243: 550–551.

Field, K.G., Olsen, G.J., Lane, D.J., Giovannoni, S.J., Ghiselin, M.T., Raff, E.C., Pace, N.R. & Raff, R.A. (1988): Molecular phylogeny of the animal kingdom. *Science* 239: 748–753.

Fraipont, J. (1887): Le genre *Polygordius*. *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte* 14: 1–125.

Franzén, A. & Ferraguti, M. (1992): Ultrastructure of spermatozoa and spermatids in *Bonellia viridis* and *Hamingia arctica* (Echiura) with some phylogenetic considerations. *Acta Zoologica* 73: 25–31.

Friedrich, S., Wanninger, A., Brueckner, M. & Haszprunar, G. (2002): Neurogenesis in the mossy chiton, *Mopalia muscosa* (Gould) (Polyplacophora): evidence against molluscan metamerism. *Journal of Morphology* 253: 109–117.

Funch, P. (1996): The chordoid larva of *Symbion pandora* (Cycliophora) is a modified trochophore. *Journal of Morphology* 230: 231–263.

George, J.D. & Hartmann-Schröder, G. (1985): *Polychaetes: British Amphinomida, Spintherida and Eunicida. Keys and Notes for the Identification of the Species*. EJ Brill/Dr. W. Backhuys, London.

Ghiselin, M.T. (1988): The origin of molluscs in the light of molecular evidence. *Oxford Surveys in Evolutionary Biology* 5: 66–95.

Giangrande, A. & Gambi, M.C. (1998): Metamerism and life-style within polychaetes: Morpho-functional aspects and evolutionary implications. *Italian Journal of Zoology* 65: 39–50.

Giard, A. (1880): Sur les affinités du genre *Polygordius* avec les Annélides de la famille des Opheliidae. *Comptes Rendus de l'Académie des Science, Paris* 91: 341–326.

Giere, O., Ebbe, B. & Erseus, C. (2008): *Questa* (Annelida, Polychaeta, Orbiniidae) from Pacific regions—new species and reassessment of the genus *Periquesta*. *Organisms Diversity & Evolution* 7: 304–319.

Giere, O.W. & Riser, N.W. (1981): Questidae – polychaetes with oligochaetoid morphology and development. *Zoologica Scripta* 10: 95–103.

Giribet, G. (2003): Molecules, development and fossils in the study of metazoan evolution; Articulata versus Ecdysozoa revisited. *Zoology* 106: 303–326.

Giribet, G., Distel, D.L., Polz, M., Sterrer, W. & Wheeler, W.C. (2000): Triploblastic relationships with emphasis on the acoelomates and the position of Gnathostomulida, Cycliophora, Plathelminthes, and Chaetognatha: a combined approach of 18S rDNA sequences and morphology. *Systematic Biology* 49: 539–562.

Glasby, C.J., Hutchings, P.A., Fauchald, K., Paxton, H., Rouse, G.W., Watson Russell, C. & Wilson, R.S. (2000): Class polychaeta. In: Beesly, P.L., Ross, G.J. & Glasby, C.J. (eds.) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. Vol. 4. CSIRO Publishing, Melbourne: 1–296.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Golding, D.W. (1992): Polychaeta: nervous system. In: Harrison, F.W. & Gardiner, S.L. (eds.) *Microscopic Anatomy of Invertebrates 7: Annelida*. Wiley-Liss, New York: 153–179.

Golombek, A., Tobergte, S., Nesnidal, M.P., Purschke, G. & Struck, T.H. (2013): Mitochondrial genomes to the rescue – Diurodrilidae in the myzostomid trap. *Molecular Phylogenetics and Evolution* 68: 312–326.

Goodrich, E.S. (1901): On the structure and affinities of *Saccocirrus*. *Quarterly Journal of Microscopical Science* 44: 413–428.

Goodrich, E.S. (1912): *Nerilla* an Archiannelid. *Quarterly Journal of Microscopical Science* 57: 397–319.

von Graff, L. (1882): *Monographie der Turbellarien*. I. Rhabdocoelida. W. Engelmann, Leipzig.

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

Guralnick, R. (2002): A recapitulation of the rise and fall of the cell lineage research program: the evolutionary developmental relationships of cleavage to homology, body plans and life history. *Journal of History of Biology* 35: 527–567.

Guralnick, R.P. & Lindberg, D.R. (2001): Reconnecting cell and animal lineages: what do cell lineages tell us about the evolution and development of Spiralia? *Evolution* 55: 1501–1519.

Halanych, K. (2005): Molecular phylogeny of siboglinid annelids (a.k.a. pogonophorans): a review. *Hydrobiologia* 535–536: 297–307.

Halanych, K.M. (2004): The new view of animal phylogeny. *Annual Review of Ecology, Evolution, and Systematics* 35: 229–256.

Halanych, K.M., Bacheller, J.D., Aguinaldo, A.M.A., Liva, S.M., Hillis, D.M. & Lake, J.A. (1995): Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science* 267: 1641–1643.

Halanych, K.M., Cox, L.N. & Struck, T.H. (2007): A brief review of holopelagic annelids. *Integractive Comparative Biol*ogy 47: 872–879.

Halanych, K.M., Dahlgren, T.G. & McHugh, D. (2002): Unsegmented Annelids? Possible Origins of Four Lophotrochozoan Worm Taxa. *Integrative and Comparative Biology* 42: 678–684.

Halanych, K.M., Feldman, R.A. & Vrijenhoek, R.C. (2001): Molecular evidence that *Sclerolinum brattstromi* is closely related to Vestimentiferans, not to Frenulate Pogonophorans (Siboglinidae, Annelida). *Biological Bulletin* 201: 65–75.

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

Harmer, S.F. (1889): Notes on the anatomy of *Dinophilus*. *Journal of the Marine Biological Association of the United Kingdom* 1: 119–142.

Hartman, O. (1954): Pogonophora Johansson, 1938. *Systematic Zoology* 3: 183–185.

Hartman, O. (1968): *Atlas of Errantiate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles.

Hartman, O. (1969): *Atlas of the Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles.

Hartmann, S., Helm, C., Nickel, B., Meyer, M., Struck, T.H., Tiedemann, R., Selbig, J. & Bleidorn, C. (2012): Exploiting gene families for phylogenomic analysis of myzostomid transcriptome data. *PLoS ONE* 7: e29843.

Hartmann-Schröder, G. (1971): *Teil 58. Annelida, Borstenwürmer, Polychaeta*. VEB Gustav Fischer Verlag, Jena: 594.

Hartmann-Schröder, G. (1996): Teil 58. *Annelida, Borstenwürmer, Polychaeta*. Gustav Fischer, Stuttgart: 648.

Hatschek, B. (1878): Studien über die Entwicklungsgeschichte der Anneliden. Ein Beitrag zur Morphologie der Bilateralien. *Arbeiten des Zoologischen Institutes zur Universität Wien* 1: 277–404.

Hatschek, B. (1880): Ueber die Entwicklungsgeschichte von *Echiurus* und die systematische Stellung der Echiuridae (Gephyrei chaetiferi). *Arbeiten der Zoologischen Station Triest* 3: 45–79.

Hatschek, B. (1888): *Lehrbuch der Zoologie. Eine morphologische Übersicht des Thiereiches zur Einführung in das Studium dieser Wissenschaft*. Gustav Fischer, Jena.

Hatschek, B. (1893): System der Anneliden, ein vorlaufiger Bericht. *Lotos* 13: 123–126.

Hausdorf, B., Helmkampf, M., Meyer, A., Witek, A., Herlyn, H., Bruchhaus, I., Hankeln, T., Struck, T.H. & Lieb, B. (2007): Spiralian phylogenomics supports the resurrection of Bryozoa comprising Ectoprocta and Entoprocta. *Molecular Biology and Evolution* 24: 2723–2729.

Hausdorf, B., Helmkampf, M., Nesnidal, M.P. & Bruchhaus, I. (2010): Phylogenetic relationships within the lophophorate lineages (Ectoprocta, Brachiopoda and Phoronida). *Molecular Phylogenetics and Evolution* 55: 1121–1127.

Heider, K. (1922): Über Archianneliden. *Sitzungsberichte der Königlichen Preussischen Akademie der Wissenschaften* 6: 39–44.

Hejnol, A., Obst, M., Stamatakis, A., Ott, M., Rouse, G.W., Edgecombe, G.D., Martinez, P., Baguñà, J., Bailly, X., Jondelius, U., Wiens, M., Müller, W.E.G., Seaver, E., Wheeler, W.C., Martindale, M.Q., Giribet, G. & Dunn, C.W. (2009): Assessing the root of bilaterian animals with scalable phylogenomic methods. *Proceedings of the Royal Society B: Biological Sciences* 276: 4261–4270.

Hejnol, A. & Schnabel, R. (2005): The eutardigrade *Thulinia stephaniae* has an indeterminate development and the potential to regulate early blastomere ablations. *Development* 132: 1349–1361.

Helfenbein, K.G. & Boore, J.L. (2004): The Mitochondrial Genome of *Phoronis architecta* – comparisons demonstrate that Phoronids are Lophotrochozoan protostomes. *Molecular Biology and Evolution* 21: 153–157.

Helm, C., Bernhart, S.H., Siederdissen, C.H.Z., Nickel, B. & Bleidorn, C. (2012): Deep sequencing of small RNAs confirms an annelid affinity of Myzostomida. *Molecular Phylogenetics and Evolution* 64: 198–203.

Helm, C. & Bleidorn, C. (2016): Annelida: Myzostomida. In: Schmidt-Rhaesa, A., Harzsch, S. & Purschke, G. (eds.) *Structure and Evolution of invertebrate Nervous Systems*. Oxford University Press, Oxford: 241–247.

Helm, C., Stevenson, P.A., Rouse, G.W. & Bleidorn, C. (2014): Immunohistochemical investigations of *Myzostomum cirriferum* and *Myzostomum* cf. *katoi* (Myzostomida, Annelida) with implications for the evolution of the emyzostomid body plan. *Zoomorphology* 133: 257–271.

Helmkampf, M., Bruchhaus, I. & Hausdorf, B. (2008a): Multigene analysis of lophophorate and chaetognath phylogenetic relationships. *Molecular Phylogenetics and Evolution* 46: 206–214.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Helmkampf, M., Bruchhaus, I. & Hausdorf, B. (2008b): Phylogenomic analyses of lophophorates (brachiopods, phoronids and bryozoans) confirm the Lophotrochozoa concept. *Proceedings of the Royal Society B: Biological Sciences* 275: 1927–1933.

Hempelmann, F. (1931): Erste und zweite Klasse der Vermes Polymera (Annelida). Archiannelida und Polychaeta. In: Kükenthal, W. & Krumbach, T. (eds.) *Handbuch der Zoologie, Band 2*. Leif, Berlin: 1–112.

Hempelmann, F. (1937): *Buch 2: Polychaeta.* Akademische Verlagsgesellschaft Geest & Portig, Leipzig.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

Hertzler, P.L. (2005): Cleavage and gastrulation in the shrimp *Penaeus* (*Litopenaeus*) *vannamei* (Malacostraca, Decapoda, Dendrobranchiata). *Arthropod Structure & Development* 34: 455–469.

Hessling, R. (2002): Metameric organisation of the nervous system in developmental stages of *Urechis caupo* (Echiura) and its phylogenetic implications. *Zoomorphology* 121: 221–234.

Hessling, R. (2003): Novel aspects of the nervous system of *Bonellia viridis* (Echiura) revealed by the combination of immunohistochemistry, confocal laser-scanning microscopy and three-dimensional reconstruction. *Hydrobiologia* 496: 225–239.

Hessling, R. & Purschke, G. (2000): Immunohistochemical (cLSM) and ultrastructural analysis of the central nervous system and sense organs in *Aeolosoma hemprichi* (Annelida, Aeolosomatidae). *Zoomorphology* 120: 65–78.

Hessling, R. & Westheide, W. (1999): CLSM analysis of development and structure of the central nervous system of *Enchytraeus crypticus* ('Oligochaeta', Enchytraeidae). *Zoomorphology* 119: 37–47.

Hessling, R. & Westheide, W. (2002): Are Echiura derived from a segmented ancestor? Immunohistochemical analysis of the nervous system in developmental stages of *Bonellia viridis*. *Journal of Morphology* 252: 100–113.

Heuer, C., Muller, C., Todt, C. & Loesel, R. (2010): Comparative neuroanatomy suggests repeated reduction of neuroarchitectural complexity in Annelida. *Frontiers in Zoology* 7: 13.

Ivanov, A.V. (1954): New Pogonophora from the Far Eastern Seas. *Systematic Zoology* 3: 69–79.

Ivanov, A.V. (1975): Embryonalentwicklung der Pogonophora und ihre systematische Stellung. *Zeitschrift für zoologische Systematik and Evolutionsforschung Sonderheft* 1975: 10–44.

Iwanoff, P.P. (1928): Die Entwicklung der Larvalsegmente bei den Anneliden. *Zeitschrift für Morphologie und Ökologie der Tiere* 10: 62–161.

Jägersten, G. (1936): Zur Kenntnis der Parapodialborsten bei *Myzostomum*. *Zoologiska Bidrag från Uppsala* 16: 283–294.

Jägersten, G. (1940): Zur Kenntnis der Morphologie, Enwicklung und Taxonomie der Myzostomida. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 11: 1–84.

Jägersten, G. (1947): On the structure of the pharynx of the Archiannelida with special reference to there occurring muscle of aberrant type. *Zoologiska Bidrag från Uppsala* 25: 551–570.

Jägersten, G. (1956): Investigations on *Siboglinum ekmani*, n.sp., encountered in Skagerrak with some general remarks on the group Pogonophora. *Zoologiska Bidrag från Uppsala* 31: 211–252.

Jamieson, B.G.M. (1986): Onychophoran-euclitellate relationships: evidence from spermatozoal ultrastructure. *Zoologica Scripta* 15: 141–155.

Jamieson, B.G.M. (1987): *The Ultrastructure and Phylogeny of Insect Spermatozoa*. Cambridge University Press, London.

Jenner, R.A. (2000): Evolution of animal body plans: the role of metazoan phylogeny at the interface between pattern and process. *Evolution and Development* 2: 208–221.

Jenner, R.A. (2003): Unleashing the force of cladistics? Metazoan phylogenetics and hypothesis testing. *Integrative and Comparative Biology* 43: 207–218.

Jenner, R.A. (2004a): The scientific status of metazoan cladistics: why current research practice must change. *Zoologica Scripta* 33: 293–310.

Jenner, R.A. (2004b): Towards a phylogeny of the Metazoa: evaluating alternative phylogenetic positions of Platyhelminthes, Nemertea, and Gnathostomulida, with a critical reappraisal of cladistic characters. *Contributions to Zoology* 73: 3–163.

Jenner, R.A. (2004c): When molecules and morphology clash: reconciling conflicting phylogenies of the Metazoa by considering secondary character loss. *Evolution and Development* 6: 372–378.

Jennings, R.M. & Halanych, K.M. (2005): Mitochondrial genomes of *Clymenella torquata* (Maldanidae) and *Rifta pachyptila* (Siboglinidae): evidence for conserved gene order in Annelida. *Molecular Biology and Evolution* 22: 210–222.

Johnston, G. (1865): *A Catalogue of the British Non-parasitical Worms in the Collection of the British Museum*. British Museum, London.

Jördens, J., Struck, T.H. & Purschke, G. (2004): Phylogenetic inference regarding Parergodrilidae and *Hrabeiella periglandulata* ("Polychaeta", Annelida) based on 18S rDNA, 28S rDNA and COI sequences. *Journal of Zoological Systematics and Evolutionary Research* 42: 270–280.

Jouin, C. (1978a): Anatomical and ultrastructural study of the pharyngeal bulb in *Protodrilus* (Polychaeta, Annelida). I. Muscles and myoepithelial junctions. *Tissue and Cell* 10: 269–287.

Jouin, C. (1978b): Anatomical and ultrastructural study of the pharyngeal bulb in Protodrilus (Polychaeta, Archiannelida). II. The stomodeal epithelium and its cuticle. *Tissue and Cell* 10: 289–301.

Kato, K. (1952): On the development of myzostome. *Science Reports of the Saitama University, Series B* 1: 1–16.

Kim, C., Moon, S., Gelder, S. & Kim, W. (1996): Phylogenetic relationships of annelids, molluscs, and arthropods evidenced from molecules and morphology. *Journal of Molecular Evolution* 43: 207–215.

Klag, J. & Ksiazkiewicz Kapralska, M. (1989): Embryonic hemocytes and body cavity formation in *Tetrodontophora bielanensis* (Insecta, Collembola). In: Dallai, R. (ed.) *The Third International Seminar on Apterygota*. University of Siena, Siena: 215–219.

Kocot, K.M., Struck, T.H., Merkel, J., Waits, D.S., Todt, C., Brannock, P.M., Weese, D.A., Cannon, J.T., Moroz, L.L., Lieb, B. & Halanych, K.M. (2017): Phylogenomics of Lophotrochozoa with consideration of systematic error. *Systematic Biology* 66: 256–282.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Kojima, S. (1998): Paraphyletic status of polychaeta suggested by phylogenetic analysis based on the amino acid sequences of elongation factor-1[alpha]. *Molecular Phylogenetics and Evolution* 9: 255–261.

Kristensen, R.M. & Niilonen, T. (1982): Structural evidence on *Diurodrilus* Remane (Diurodrilidae fam.n.), with description of *Diurodrilus westheidei* sp.n. from the artic interstitial meiobenthos, W. Greenland. *Zoologica Scripta* 11: 1–12.

Kristof, A., Wollesen, T. & Wanninger, A. (2008): Segmental mode of neural patterning in Sipuncula. *Current Biology* 18: 1129–1132.

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

Lake, J.A. (1990): Origin of Metazoa. *Proceedings of National Academy of Science of the United States of America* 87: 763–766.

Lamarck, J.P.B.A.d.M. (1801): *Systême des Animaux sans Vertèbres*. Deterville, Paris.

Lamarck, J.P.B.A.d.M. (1802): *La nouvelle classes des Annélides*. Bulletin du Muséum d'Histoire Naturelle, Paris.

Lamarck, J.P.B.A.d.M. (1816): *Histoire naturelle des animaux sans vertebres*. Verdiere, Paris.

Lamarck, J.P.B.A.d.M. (1818): *Histoire naturelle des animaux sans vertebres*. Deterville, Verdiere, Paris.

Lang, A. (1884): *Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrenzenden Meeresabschnitte*. Eine Monographie. W. Engelmann, Leipzig: 1–688.

Lang, K. (1950): A contribution to the morphology of *Stratodrilus platensis* Cordero (Histriobdellidae). *Arkiv för Zoologi* 42: 1–30.

Langerhans, P. (1880): Die Wurmfauna Madeiras. I. *Zeitschrift für wissenschaftliche Zoologie* 34: 87–143.

Lanterbecq, D., Bleidorn, C., Michel, S. & Eeckhaut, I. (2008): Locomotion and fine structure of parapodia in *Myzostoma cirriferum* (Myzostomida). *Zoomorphology* 127: 59–68.

Laumer Christopher, E., Bekkouche, N., Kerbl, A., Goetz, F., Neves, Ricardo, C., Sørensen Martin, V., Kristensen Reinhardt, M., Hejnol, A., Dunn, Casey, W., Giribet, G. & Worsaae, K. (2015): Spiralian Phylogeny informs the evolution of microscopic lineages. *Current Biology* 25: 2000–2006.

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

Lewis, P.O., Holder, M.T. & Holsinger, K.E. (2005): Polytomies and Bayesian phylogenetic inference. *Systematic Biology* 54: 241–253.

Linneaus, C.V. (1758): *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentii Salvii, Holmiæ.

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

Livanov, N.A. (1940): *Class Polychaeta. Handbook of Zoology 2*. Soviet Science, Moscow, Leningrad.

Liwanow, N.A. & Porfirjewa, N.A. (1967): Die Organisation der Pogonophoren und deren Beziehungen zu den Polychaeten. *Biologisches Zentralblatt* 86: 177–204.

Loesel, R. & Heuer, C.M. (2010): The mushroom bodies – prominent brain centres of arthropods and annelids with enigmatic evolutionary origin. *Acta Zoologica* 91: 29–34.

MacBride, E.W. (1914): *Text-Book of Embryology, Invertebrata*. Vol. I. Macmillan and Co., Ltd., London.

Mallatt, J. & Winchell, C.J. (2002): Testing the new animal phylogeny: first use of combined large-subunit and small-subunit rRNA gene sequences to classify the protostomes. *Molecular Biology and Evolution* 19: 289–301.

Marletaz, F., Martin, E., Perez, Y., Papillon, D., Caubit, X., Lowe, C.J., Freeman, B., Fasano, L., Dossat, C. & Wincker, P. (2006): Chaetognath phylogenomics: a protostome with deuterostome-like development. *Current Biology* 16: R577–R578.

Marotta, R., Ferraguti, M. & Martin, P. (2003): Spermiogenesis and seminal receptacles in *Aeolosoma singulare* (Annelida, Polychaeta, Aeolosomatidae). *Italian Journal of Zoology* 70: 123–132.

Martin, P. (2001): On the origin of the Hirudinea and the demise of the Oligochaeta. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268: 1089–1098.

Maslakova, S.A., Martindale, M.Q. & Norenburg, J.L. (2004a): Fundamental properties of the spiralian developmental program are displayed by the basal nemertean *Carinoma tremaphoros* (Palaeonemertea, Nemertea). *Developmental Biology* 267: 342–360.

Maslakova, S.A., Martindale, M.Q. & Norenburg, J.L. (2004b): Vestigial prototroch in a basal nemertean, *Carinoma tremaphoros* (Nemertea; Palaeonemertea). *Evolution & Development* 6: 219–226.

Mattei, X. & Marchand, B. (1987): Les spermatozoides des acanthocephales et des myzostomides. Resemblances et conséquences phylétiques. *Comptes de l´Academie des Sciences, Paris, Series III* 305: 525–529.

Matus, D.Q., Copley, R.R., Dunn, C.W., Hejnol, A., Eccleston, H., Halanych, K.M., Martindale, M.Q. & Telford, M.J. (2006): Broad taxon and gene sampling indicate that chaetognaths are protostomes. *Current Biology* 16: R575–R576.

Mayer G. (2006): Origin and differentiation of nephridia in the Onychophora provide no support for the Articulata. *Zoomorphology* 125: 1–12.

Mayer, G. & Harzsch, S. (2007): Immunolocalization of serotonin in Onychophora argues against segmental ganglia being an ancestral feature of arthropods. *BMC Evolutionary Biology* 7: 118.

McHugh, D. (1997): Molecular evidence that echiurans and pogonophorans are derived annelids. *Proceedings of the National Academy of Sciences of the United States of America* 94: 8006–8009.

McHugh, D. (2000): Molecular Phylogeny of the Annelida. *Canadian Journal of Zoology* 78: 1873–1884.

McHugh, D. (2005): Molecular systematics of polychaetes (Annelida). *Hydrobiologia* 535–536: 309–318.

Meglitsch, P.A. & Schram, F.R. (1991): *Invertebrate Zoology.* Oxford University Press, Oxford.

Mesnil, F., Caullery, M. & Hebd, C.R. SÃ©anc. Acad. Sd. Paris (1922): L'appareil maxillaire d'*Histriobdella homari*; affinités des Histriobdellides avec les Euniciens. *Comptes Rendus de l'Academie des Sciences* 174: 913–917.

Metschnikoff, E. (1866): Apsilus lentiformis, ein Räderthier. *Zeitschrift fuer Wissenschaftliche Zoologie* 16: 346–356.

Mettam, C. (1985): Functional constraints in the evolution of the Annelida. In: Morris, S.C., George, J.D., Gibson, R. & Platt, H.M. (eds.) *The Origins and Relationships of Lower Invertebrates.*

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

*The Systematics Association Special Volume Ed*. Clarendon Press, Oxford: 297–309.

Meyer, A. (1927): Ist *Parergodrilus heideri* (Reisinger) ein Archiannelide? Zoologischer Anzeiger 72: 19–35.

Michaelsen, W. (1928–1932): Clitellata = Gürtelwürmer. In: Kükenthal, W. (ed.) *Handbuch der Zoologie*. DeGruyter, Berlin: 1–118.

Mileikovsky, S.A. (1968): Morphology of larvae and systematics of Polychaeta. *Zoologiceskij Zhurnal* 47: 49–59.

Moon, S.Y., Chang, B.K., Gelder, S.R. & Won, K. (1996): Phylogenetic position of the aberrant branchiobdellidans and aphanoneurans within the Annelida as derived from 18S ribosomal RNA gene sequences. *Hydrobiologia* 324: 229–236.

Müller, M.C.M. (2006): Polychaete nervous systems: ground pattern and variations – cLS microscopy and the importance of novel characteristics in phylogenetic analysis. *Integrative and Comparative Biology* 46: 125–133.

Müller, M.C.M. & Westheide, W. (2000): Structure of the nervous system of *Myzostoma cirriferum* (Annelida) as revealed by immunohistochemistry and cLSM analyses. *Journal of Morphology* 245: 87–98.

Mwinyi, A., Meyer, A., Bleidorn, C., Lieb, B., Bartolomaeus, T. & Podsiadlowski, L. (2009): Mitochondrial genome sequence and gene order of *Sipunculus nudus* give additional support for an inclusion of Sipuncula into Annelida. *BMC Genomics* 10: 27.

Nachtsheim, H. (1919): Zytologische und experimentelle Untersuchungen über die Geschlechtsbestimmung bei *Dinophilus apatris* Korsch. *Archiv für mikroskopische Anatomie* 93: 17–140.

Negrisolo, E., Pallavicini, A., Barbato, R., Dewilde, S., Ghiretti-Magaldi, A., Moens, L. & Lanfranchi, G. (2001): The evolution of extracellular hemoglobins of annelids, vestimentiferans, and pogonophorans. *Journal of Biological Chemistry* 276: 26391–26397.

Nesnidal, M.P., Helmkampf, M., Bruchhaus, I. & Hausdorf, B. (2010): Compositional heterogeneity and phylogenomic inference of Metazoan relationships. *Molecular Biology and Evolution* 27: 2095–2104.

Newby, W.W. (1940): The embryology of the echiuroid worm *Urechis caupo*. *Memoirs of the American Philosophical Society* 16: 1–219.

Nielsen, C. (1987): Structure and function of metazoan ciliary bands and their phylogenetic significance. *Acta Zoologica* 68: 205–262.

Nielsen, C. (1995): *Animal Evolution. Interrelationships of the Living Phyla*. Oxford University Press, Oxford.

Nielsen, C. (2001): *Animal Evolution. Interrelationships of the Living Phyla*. 2nd ed. Oxford University Press, Oxford.

Nielsen, C. (2010): Some aspects of spiralian development. *Acta Zoologica* 91: 20–28.

Nørrevang, A. (1970a): On the embryology of *Siboglinum* and its implications for the systematic position of the Pogonophora. *Sarsia* 42: 7–16.

Nørrevang, A. (1970b): The position of Pogonophora in the phylogenetic system. *Zeitschrift für zoologische Systematik and Evolutionsforschung* 8: 161–172.

Orensanz, J.M. (1990): The eunicemorph polychaete annelids from Antarctic and Subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Biology of the Antarctic Seas* 21: 1–183.

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

Paps, J., Baguna, J. & Riutort, M. (2009a): Bilaterian phylogeny: a broad sampling of 13 nuclear genes provides a new Lophotrochozoa phylogeny and supports a paraphyletic basal Acoelomorpha. *Molecular Biology and Evolution* 26: 2397–2406.

Paps, J., Baguñà, J. & Riutort, M. (2009b): Lophotrochozoa internal phylogeny: new insights from an up-to-date analysis of nuclear ribosomal genes. *Proceedings of the Royal Society B: Biological Sciences* 276: 1245–1254.

Passamaneck, Y. & Halanych, K.M. (2006): Lophotrochozoan phylogeny assessed with LSU and SSU data: evidence of lophophorate polyphyly. *Molecular Phylogenetics and Evolution* 40: 20–28.

Passamaneck, Y.J. & Halanych, K.M. (2004): Evidence from *Hox* genes that bryozoans are lophotrochozoans. *Evolution and Development* 6: 275–281.

Patterson, C. (1989): Phylogenetic relations of major groups: conclusions and prospects. In: Fernholm, B., Bremer, K. & Jörnvall, H. (eds.) *The Hierarchy of Life*. Elsevier Science B.V., Amsterdam: 471–488.

Paul, C., Halanych, K.M., Tiedemann, R. & Bleidorn, C. (2010): Molecules reject an opheliid affinity for *Travisia* (Annelida). *Systematics and Biodiversity* 8: 507–512.

Pechenik, J.A. (2010): *Biology of the Invertebrates*. 5th ed. McGraw-Hill Higher Education, New York.

Perrier, E. (1897): *Traité de Zoologie, fasc. 4*. Masson & Cie, Paris.

Peterson, K.J. & Butterfield, N.J. (2005): From the cover: origin of the Eumetazoa: testing ecological predictions of molecular clocks against the Proterozoic fossil record. *Proceedings of National Academy of Science of the United States of America* 102: 9547–9552.

Peterson, K.J. & Eernisse, D.J. (2001): Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18S rDNA gene sequences. *Evolution and Development* 3: 170–205.

Peterson, K.J., Lyons, J.B., Nowak, K.S., Takacs, C.M., Wargo, M.J. & McPeek, M.A. (2004): Estimating metazoan divergence times with a molecular clock. *Proceedings of the National Academy of Sciences of the United States of America* 101: 6536–6541.

Pettibone, M.H. (1982): Annelida, Polychaeta. In: Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill, New York: 1–43.

Philippe, H., Chenuil, A. & Adoutte, A. (1994): Can the Cambrian explosion be inferred through molecular phylogeny? *Development* Supplement: 15–25.

Philippe, H., Delsuc, F., Brinkman, H. & Lartillot, N. (2005a): Phylogenomics. *Annual Review of Ecology, Evolution, and Systematics* 36: 541–562.

Philippe, H., Lartillot, N. & Brinkmann, H. (2005b): Multigene analyses of bilaterian animals corroborate the monophyly of Ecdysozoa, Lophotrochozoa, and Protostomia. *Molecular Biology and Evolution* 22: 1246–1253.

Pierantoni, U. (1908): Protodrilus. *Fauna und Flora des Golfes von Neapel: Und der Angrenzenden Meeres-Abschnitte* 31: 1–226.

Pietsch, A. & Westheide, W. (1987): Protonephridial organs in *Myzostoma cirriferum* (Myzostomida). *Acta Zoologica* 68: 195–203.

Pilger, J. (1993): Echiura. In: Harrison, F.W. (ed.) *Microscopic Anatomy of Invertebrates*. Vol. 12. Wiley-Liss, New York: 185–236.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Podsiadlowski, L., Braband, A., Struck, T.H., Döhren, J.V. & Bartolomaeus, T. (2009): Phylogeny and mitochondrial gene order variation in Lophotrochozoa in the light of new mitogenomic data from Nemertea. *BMC Genomics* 10: 364.

Prenant, M. (1959): Classe des Myzostomides. In: Grasse, P.P. (ed.) *Traite de Zoologie. Anatomie, Systematique, Biologie. V (1). Annelides-Sipunculiens-Echiuriens-Priapuliens-Endoproctes-Phoronidiens*. Masson et Cie, Paris: 714–784.

Prendini, L. (2001): Species or supraspecific taxa as terminals in cladistic analysis? Groundplans Versus exemplars revisited. *Systematic Biology* 50: 290–300.

Purschke, G. (1985a): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida) – I. The pharynx of the Dinophilidae. *Zoomorphology* 105: 223–239.

Purschke, G. (1985b): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida) – II. The pharynx of the Nerillidae. *Mikrofauna Marina* 2: 23–60.

Purschke, G. (1987): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida) – IV. The pharynx and jaws of the Dorvilleidae. *Acta Zoologica* 68: 83–105.

Purschke, G. (1990): Comparative electron microscopic investigation of the nuchal organs in *Protodriloides*, *Protodrilus* and *Saccocirrus* (Annelida, Polychaeta). *Canadian Journal of Zoology* 68: 325–338.

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

Purschke, G. (1999): Terrestrial polychaetes – models for the evolution of the Clitellata (Annelida)? *Hydrobiologia* 406: 87–99.

Purschke, G. (2000): Sense organs and central nervous system in an enigmatic terrestrial polychaete, *Hrabeiella perigandulata* (Annelida) – implications for annelid evolution. *Invertebrate Biology* 119: 329–341.

Purschke, G. (2002): On the ground pattern of Annelida. *Organisms, Diversity and Evolution* 2: 181–196.

Purschke, G. (2003): Is *Hrabeiella periglandulata* (Annelida, "Polychaeta") the sister group of Clitellata? Evidence from an ultrastructural analysis of the dorsal pharynx in *H. periglandulata* and *Enchytraeus minutus* (Annelida, Clitellata). *Zoomorphology* 122: 55–66.

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

Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Systematics, evolution and phylogeny of Annelida – a morphological perspective. *Memoirs of Museum Victoria* 71: 247–269.

Purschke, G. & Hessling, R. (2002): Analysis of the central nervous system and sense organs in *Potamodrilus fluviatilis* (Annelida: Potamodrilidae). *Zoologischer Anzeiger* 241: 19–35.

Purschke, G., Hessling, R. & Westheide, W. (2000): The phylogenetic position of the Clitellata and the Echiura – on the problematic assessment of absent characters. *Journal of Zoological Systematic and Evolutionary Research* 38: 165–173.

Purschke, G. & Jouin, C. (1988): Anatomy and ultrastructure of the ventral pharyngeal organs of *Saccocirrus* (Saccocirridae) and *Protodriloides* (Protodriloidae fam. n.) with remarks on the phylogenetic relationships within Protodrilida (Annelida: Polychaeta). *Journal of Zoology* 215: 405–432.

Purschke, G. & Tzetlin, A.B. (1996): Dorsolateral ciliary folds in the polychaete foregut: structure, prevalence and phylogenetic significance. *Acta Zoologica* 77: 33–49.

de Quatrefages, A. (1847): Memoires sur l'echine de Gaertner. *Annales des Sciences Naturelles, Zoologie* 3: 307.

de Quatrefages, A. (1866): *Histoire Naturelle des Annelides, Marine et d'Eau Douce. Annelides et gephyriens*. Librairie Encyclopedique de Roret, Paris.

Raff, R.A., Field, K.G., Olsen, G.J., Giovannoni, S.J., Lane, D.J., Ghiselin, M.T., Pace, N.R. & Raff, E.C. (1989): Metazoan phylogeny based on analysis of 18S ribosomal RNA. In: Fernholm, B., Bremer, K. & Jörnvall, H. (eds.) *The Hierarchy of Life*. Elsevier Science B.V., Amsterdam: 247–260.

Reisinger, E. (1925): Ein landbewohnender Archiannelide. Zugleich ein Beitrag zur Systematik der Archianneliden. *Zeitschrift für Morphologie und Ökologie der Tiere* 3: 197–254.

Remane, A. (1925): Diagnosen neuer Archianneliden. *Zoologischer Anzeiger* 65: 15–17.

Remane, A. (1932): Archiannelida. In: Grimpe, G. (ed.) *Die Tierwelt Nord- und Ostsee*. Akademischer Verlag, Leipzig.

Repiachoff, W. (1886): On the anatomy and developmental history of *Dinophilus gardineri* O. Schmidt [in Russian]. *Zapiski Novorossiiskago Obshchestva Estestvoispytatelei, Odessa* 10: 1–77.

Rice, M.E. (1985): Sipuncula: developmental evidence for phylogenetic inference. In: Morris, S.C., George, J.D., Gibson, R. & Platt, H.M. (eds.) *The Origins and Relationships of Lower Invertebrates*. Oxford University Press, Oxford: 274–296.

Rieger, R.M. (1980): A new group of interstitial worms, Lobatocerebridae nov. fam. (Annelida) and its significance for metazoan phylogeny. *Zoomorphology* 95: 41–84.

Rieger, R.M. (1981): Fine structure of the body wall, nervous system, and digestive tract in the Lobatocerebridae Rieger and the organization of the gliointerstitial system in Annelida. *Journal of Morphology* 167: 139–165.

Rieger, R.M. (1991a): *Jennaria pulchra*, nov. gen. nov. spec., eine neue psammobionte Annelide aus dem Küstengrundwasser von North Carolina. *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck* 78: 203–215.

Rieger, R.M. (1991b): Neue Organisationstypen aus der Sandlückenraumfauna: die Lobatocerebriden und *Jennaria pulchra*. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 84: 247–259.

Rieger, R.M. & Rieger, G.E. (1975): Fine structures of the pharyngeal bulb in *Trilobodrilus* and its phylogenetic significance within Archiannelida. *Tissue Cell* 7.

Rieger, R.M. & Rieger, G.E. (1976): Fine structure of the archiannelid cuticle and remarks on the evolution of the cuticle within the Spiralia. *Acta Zoologica* 57: 53–68.

Riesgo, A., Andrade, S.C., Sharma, P., Novo, M., Perez-Porro, A., Vahtera, V., Gonzalez, V., Kawauchi, G. & Giribet, G. (2012): Comparative description of ten transcriptomes of newly sequenced invertebrates and efficiency estimation of genomic sampling in non-model taxa. *Frontiers in Zoology* 9: 33.

Roeding, F., Borner, J., Kube, M., Klages, S., Reinhardt, R. & Burmester, T. (2009): A 454 sequencing approach for large scale phylogenomic analysis of the common emperor scorpion (Pandinus imperator). *Molecular Phylogenetics and Evolution* 53: 826–834.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Roeding, F., Hagner-Holler, S., Ruhberg, H., Ebersberger, I., von, Haeseler, A., Kube, M., Reinhardt, R. & Burmester, T. (2007): EST sequencing of Onychophora and phylogenomic analysis of Metazoa. *Molecular Phylogenetics and Evolution* 45: 942–951.

de Rosa, R., Grenier, J.K., Andreeva, T., Cook, C.E., Adoutte, A., Akam, M., Carroll, S.B. & Balavoine, G. (1999): Hox genes in brachiopods and priapulids and protostome evolution. *Nature* 399: 772–776.

Rota, E. (1998): Morphology and adaptations of *Parergodrilus* Reisinger and *Hrabeiella* Pizl & Chalupsky, two enigmatic soil-dwelling annelids. *Italian Journal of Zoology* 65: 75–84.

Rota, E. & Lupetti, P. (1996): An ultrastructural investigation of *Hrabeiella* Pizl and Chalupsky (Annelida). I. Chaetae and body wall organization. *Hydrobiologia* 334: 229–239.

Rota, E. & Lupetti, P. (1997): An ultrastructural investigation of *Hrabeiella* Pizl and Chalupsky, 1984 (Annelida). II. The spermatozoon. *Tissue Cell* 29: 603–609.

Rota, E., Martin, P. & Erséus, C. (2001): Soil-dwelling polychaetes: enigmatic as ever? Some hints on their phylogenetic relationships as suggested by a maximum parsimony analysis of 18S rRNA gene sequences. *Contributions to Zoology* 70: 127–138.

Rouse, G.W. (1999): Trochophore concepts: ciliary bands and the evolution of larvae in spiralian Metazoa. *Biological Journal of the Linnean Society* 66: 411–464.

Rouse, G.W. (2000): Bias? What bias? The evolution of downstream larval-feeding in animals. *Zoologica Scripta* 29: 213–236.

Rouse, G.W. (2006): Annelid sperm and spermiogenesis. In: Rouse, G.W. & Pleijel, F. (eds.) *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Inc., Enfield, New Hampshire: 45–76.

Rouse, G.W. & Fauchald, K. (1995): The articulation of annelids. *Zoologica Scripta* 24: 269–301.

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

Rouse, G.W., Goffredi, S.K. & Vrijenhoek, R.C. (2004): *Osedax*: Bone-Eating Marine Worms with Dwarf Males. *Science* 305: 668–671.

Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, New York: 1–354.

Rouse, G.W. & Pleijel, F. (2003): Problems in polychaete systematics. *Hydrobiologia* 496: 175–189.

Rouse, G.W. & Pleijel, F. (2006): *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield, NH, Jersey, Plymouth.

Rouse, G.W. & Pleijel, F. (2007): Annelida. *Zootaxa* 1668: 245–264.

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

Rousset, V., Rouse, G.W., Siddall, M.E., Tillier, A. & Pleijel, F. (2004): The phylogenetic position of Siboglinidae (Annelida) inferred from 18S rRNA, 28S rRNA and morphological data. *Cladistics* 20: 518–533.

Ruiz-Trillo, I., Paps, J., Loukota, M., Ribera, C., Jondelius, U., Baguñà, J. & Riutort, M. (2002): A phylogenetic analysis of myosin heavy chain type II sequences corroborates that Acoela and Nemertodermatida are basal bilaterians. *Proceedings of the National Academy of Sciences of the United States of America* 99: 1124611251.

Ruppert, E.E., Fox, R.S. & Barnes, R.D. (2004): *Invertebrate Zoology – A Functional Evolutionary Approach*. Brooks/Cole – Thomson Learning, Belmont, CA.

Salensky, W. (1907): Morphogenetische Studien an Würmern. II. Über den Bau der Archianneliden nebst Bemerkungen über den Bau einiger Organe des *Saccocirrus papillocercus* Bobr. III. Über die Metamorphose des *Polygordius*. IV. Zur Theorie des Mesoderm. *Mémoires de l'Academie Impériale des Sciences de St. Pétersbourg* 19: 103–451.

von Salvini-Plawen, L. (2000): What is convergent/homoplastic in Pogonophora? *Journal of Zoological Systematic and Evolutionary Research* 38: 133–147.

Savigny, J.C. (1822): Système des annelides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les caractères tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Espèces. Description de l'Egypte. Histoire. *Naturelle, Paris* 1: 1–128.

Sawyer, R.T. (1984): Arthropodization in the Hirudinea: evidence for a phylogenetic link with insects and other Uniramia? *Zoological Journal of the Linnean Society* 80: 303–322.

Sawyer, R.T. (1986): *Leech Biology and Behaviour*. Clarendon Press, Oxford.

Scheltema, A.H. (1993): Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *Biological Bulletin* 184: 57–78.

Schimkewitsch, W. (1895): Zur Kenntniss des Baues und Entwicklung des *Dinophilus* vom Weissem Meere. *Zeitschrift fuer Wissenschaftliche Zoologie* 59: 46–79.

Schmidt, O. (1848): Neue Beiträge zur Naturgeschichte der Würmer gesammelt auf einer Reise nach den Färör im Frühjahr 1848. F. Mauke, Jena.

Schmidt-Rhaesa, A. (2006): Perplexities concerning the Ecdysozoa: a reply to Pilato *et al*. *Zoologischer Anzeiger – A Journal of Comparative Zoology* 244: 205–208.

Schmidt-Rhaesa, A. (2007): *The Evolution of Organ Systems*. Oxford University Press, Oxford: 385.

Schmidt-Rhaesa, A., Bartolomaeus, T., Lemburg, C., Ehlers, U. & Garey, J.R. (1998): The position of the Arthropoda in the phylogenetic system. *Journal of Morphology* 238: 263–285.

Schmidt-Rhaesa, A. & Rothe, B.H. (2006): Postembryonic development of dorsoventral and longitudinal musculature in *Pycnophyes kielensis* (Kinorhyncha, Homalorhagida). *Integrative and Comparative Biology* 46: 144–150.

Scholtz, G. (1997): Cleavage, germ band formation and head segmentation: the ground pattern of the Euarthropoda. In: Fortey, R.A. & Thomas, R.H. (eds.) *Arthropod Relationships*. Chapman & Hall, London: 317–332.

Scholtz, G. (2002): The Articulata hypothesis – or what is a segment? *Organisms, Diversity and Evolution* 2: 197–215.

Scholtz, G. (2003): Is the taxon Articulata obsolete? Arguments in favour of a close relationship between annelids and arthropods. In: Legakis, A., Sfenthourakis, S., Polymeni, R. & Thessalou-Legaki, M. (eds.) *The New Panorama of Animal Evolution*. Proceedings of the 18th International Congress of Zoology. PENSOFT Publisher, Sofia, Moskau: 489–501.

Schulze, A., Cutler, E. & Giribet, G. (2005): Reconstructing the phylogeny of the Sipuncula. *Hydrobiologia* 535–536: 277–296.

Schulze, A., Cutler, E.B. & Giribet, G. (2007): Phylogeny of sipunculan worms: a combined analysis of four gene regions and morphology. *Molecular Phylogenetics and Evolution* 42: 171–192.

Schwalm, F.E. (1997): Arthropods: the insects. In: Gilbert, S.F. & Raunio, A.M. (eds.) *Embryology: Constructing the Organism*. Sinauer Associates, Sunderland: 259–278.

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Sedgwick, A. (1898): *A Student's Textbook of Zoology. Protozoa to Chaetognatha*. Vol. 1. Swan Sonnenschein, London.

Sempere, L.F., Martinez, P., Cole, C., Baguna, J. & Peterson, K.J. (2007): Phylogenetic distribution of microRNAs supports the basal position of acoel flatworms and the polyphyly of Platyhelminthes. *Evolution & Development* 9: 409–415.

Shearer, C. (1910): On the anatomy of *Histriobdella homari*. *Quarterly Journal of Microscopical Science* 55: 287–359.

Shen, X., Ma, X., Ren, J. & Zhao, F. (2009): A close phylogenetic relationship between Sipuncula and Annelida evidenced from the complete mitochondrial genome sequence of *Phascolosoma esculenta*. *BMC Genomics* 10: 136.

Simmons, M.P., Pickett, K.M. & Miya, M. (2004): How meaningful are Bayesian support values? *Molecular Biology and Evolution* 21: 188–199.

Sørensen, M.V., Funch, P., Willerslev, E., Hansen, A.J. & Olesen, J. (2000): On the phylogeny of the metazoa in the light of Cycliophora and Micrognathozoa. *Zoologischer Anzeiger* 239: 297–318.

Southward, E.C. (1988): Development of the gut and segmentation of newly settled stages of Ridgeia (Verstimentifera): implications for relationship between Vestimentifera and Pogomophora. *Journal of the Marine Biological Association of the UK* 68: 465–487.

Southward, E.C. (1993): Pogonophora. In: Harrison, F.W. & Rice, M.E. (eds.) *Microscopic Anatomy of Invertebrates, vol. 12 Onychophora, Chilopoda and Lesser Protostomata*. Wiley-Liss, New York: 327–369.

Southward, E.C. (1999): Development of Perviata and Vestimentifera (Pogonophora). *Hydrobiologia* 402: 185–202.

Sperling, E.A., Peterson, K.J. & Pisani, D. (2009a): Phylogenetic-Signal dissection of nuclear housekeeping genes supports the paraphyly of sponges and the monophyly of Eumetazoa. *Molecular Biology and Evolution* 26: 2261–2274.

Sperling, E.A., Vinther, J., Moy, V.N., Wheeler, B.M., Sémon, M., Briggs, D.E.G. & Peterson, K.J. (2009b): MicroRNAs resolve an apparent conflict between annelid systematics and their fossil record. *Proceedings of the Royal Society B: Biological Sciences* 276: 4315–4322.

Stephen, A.C. & Edmonds, S.J. (1972): *The Phyla Sipuncula and Echiura*. British Museum (Natural History), London.

Stephenson, L. (1930): *The Oligochaeta*. Clarendon Press, Oxford.

Storch, V. (1968): Zur vergleichenden Anatomie der segmentalen Muskelsysteme und zur verwandtschaft der Polychaeten-Familien. *Zeitschrift für Morphologie der Tiere* 63: 251–342.

Storch, V. (1984): Echiura and Sipuncula. In: Bereiter-Hahn, J., Matoltsy, A.G. & Richards, K.S. (eds.) *Biology of the Integument. 1. Invertebrates*. Springer-Verlag, Berlin: 368–375.

Struck, T.H. (2006): Progenetic species in polychaetes (Annelida) and problems assessing their phylogenetic affiliation. *Integrative and Comparative Biology* 46: 558–568.

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

Struck, T.H. (2013): The impact of paralogy on phylogenomic studies – a case study on annelid relationships. *PLoS ONE* 8: e62892.

Struck, T.H. & Fisse, F. (2008): Phylogenetic position of Nemertea derived from phylogenomic data. *Molecular Biology and Evolution* 25: 728–736.

Struck, T.H., Golombek, A., Weigert, A., Franke Franziska, A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Struck, T.H., Halanych, K.M. & Purschke, G. (2005): Dinophilidae (Annelida) is most likely not a progenetic Eunicida: evidence from 18S and 28S rDNA. *Molecular Phylogenetics and Evolution* 37: 619–623.

Struck, T.H., Hessling, R. & Purschke, G. (2002a): The phylogenetic position of the Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of the "Polychaeta", based on molecular data from 18SrDNA sequences. *Journal of Zoological Systematics and Evolutionary Research* 40: 155–163.

Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

Struck, T.H. & Purschke, G. (2005): The sister group relationship of Aeolosomatidae and Potamodrilidae (Annelida: "Polychaeta") – a molecular phylogenetic approach based on 18S rDNA and Cytochrome Oxidase I. *Zoologischer Anzeiger* 243: 281–293.

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

Struck, T.H., Westheide, W. & Purschke, G. (2002b): Progenesis in Eunicida ("Polychaeta," Annelida) – separate evolutionary events? Evidence from molecular data. *Molecular Phylogenetics and Evolution* 25: 190–199.

Struck, T.H., Wey-Fabrizius, A.R., Golombek, A., Hering, L., Weigert, A., Bleidorn, C., Klebow, S., Iakovenko, N., Hausdorf, B., Petersen, M., Kück, P., Herlyn, H. & Hankeln, T. (2014): Platyzoan paraphyly based on phylogenomic data supports a non-coelomate ancestry of Spiralia. *Molecular Biology and Evolution* 31: 1833–1849.

Suzuki, Y., Glazko, G.V. & Nei, M. (2002): Overcredibility of molecular phylogenies obtained by Bayesian phylogenetics. *PNAS* 99: 16138–16143.

Svesnikov, V.A. (1958): The morphology of certain eunicemorph (Polychaeta) larvae (in Russian). *Doklady Akademii Nauk SSSR* 121: 695–697.

Telford, M.J., Wise, M.J. & Gowri-Shankar, V. (2005): Consideration of RNA secondary structure significantly improves likelihood-based estimates of phylogeny: examples from the Bilateria. *Molecular Biology and Evolution* 22: 1129–1136.

Tiegs, O.W. (1947): The development and affinities of the Pauropoda, based on a study of *Pauropus silvaticus*. *Quarterly Journal of Microscopical Science* 88: 165–267 (Part I), 275–336 (Part II).

Timm, T. (1981): On the origin and evolution of aquatic Oligochaeta. *Eesti NSV eaduste Akadeemia Toimetised Biologia Seeria* 30: 174–181.

Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535–536: 199–225.

Tzetlin, A. & Purschke, G. (2006): Fine structure of the pharyngeal apparatus of the pelagosphera larva in *Phascolosoma agassizii*

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

(Sipuncula) and its phylogenetic significance. *Zoomorphology* 125: 109–117.

Tzetlin, A.B. & Filippova, A.V. (2005): Muscular system in polychaetes (Annelida). *Hydrobiologia* 535–536: 113–126.

Ulrich, W. (1950): Über die systematische Stellung einer neuen Tierklasse (Pogonofora K.E. Johansson), den Begriff der Archicoelomaten und die Einteilung der Bilaterien. *Sonderbericht der deutschen Akademie der Wissenschaft Mathematisch-naturwissenschaftliche Klasse* 11: 1–25.

Urry, L.A., Cain, M.L., Wasserman, S.A., Minorsky, P.V. & Reece, J.B. (2017): *Campbell Biology.* 11th ed. Pearson Education, Inc., New York.

Uschako, P.V. (1933): Eine neue Form aus der Familie Sabellidae (Polychaeta). *Zoologischer Anzeiger* 104: 205–208.

Uschakov, P.V. (1955): *Polychaeta of the Far Eastern Seas of the U.S.S.R.* Izdatel'stvo Akademii Nauk SSSR, Moscow.

Vallès, Y. & Boore, J.L. (2006): Lophotrochozoan mitochondrial genomes. *Integrative Comparative Biology* 46: 544–557.

Van de Peer, Y., Baldauf, S.L., Doolittle, W.F. & Meyer, A. (2000): An updated and comprehensive rRNA phylogeny of (crown) eukaryotes based on rate-calibrated evolutionary distances. *Journal of Molecular Evolution* 51: 565–576.

Van der Land, J. & Nørrevang, A. (1975): The systematic position of *Lamellibrachia* (Annelida, Vestimentifera). *Zeitschrift für zoologische Systematik and Evolutionsforschung Sonderheft* 1975: 86–101.

Wägele, J.W., Erikson, T., Lockhart, P.J. & Misof, B. (1999): The Ecdysozoa: artifact or monophylum? *Journal of Zoological Systematics and Evolutionary Research* 37: 211–223.

Wägele, J.W. & Misof, B. (2001): On quality of evidence in phylogeny reconstruction: a reply to Zrzavý's defence of the 'Ecdysozoa' hypothesis.' *Journal of Zoological Systematics & Evolutionary Research* 39: 165–176.

Wanninger, A. & Haszprunar, G. (2002): Chiton myogenesis: perspectives for the development and evolution of larval and adult muscle systems in molluscs. *Journal of Morphology* 251: 103–113.

Webb, M. (1964a): The posterior extremity of *Siboglinum fiordicum* (Pogonophora). *Sarsia* 15: 33–36.

Webb, M. (1964b): A rediscription of *Siboglinum ekmani* Jägersten (Pogonophora). *Sarsia* 15: 37–47.

Webb, M. (1969): *Lamellibrachia barhami*, gen. nov. sp. nov. (Pogonophora), from the northeast Pacific. *Bulletin of Marine Science* 19: 18–47.

Weigert A., Bleidorn C. (2016): Current status of annelid phylogeny. *Organisms Diversity & Evolution*: 1–18.

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

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Weldon, W.F.R. (1886): On *Dinophilus gigas*. *Quarterly Journal of Microscopical Science* 27: 109–121.

Westheide, W. (1971a): *Apharyngtus punicus* nov. gen. nov. spec., ein aberranter Archiannelide aus dem Mesopsammal der tunesischen Mittelmeerküste. *Mikrofauna des Meeresbodens* 6.

Westheide, W. (1971b): Interstitial Polychaeta (excluding Archiannelida). *Smithsonian Contribution to Zoology* 76: 57–70.

Westheide, W. (1984): The concept of reproduction in polychaetes with small body size: adaptations in interstitial species. In: Pfannenstiel, H-D. & Fischer, A. (eds.) *Polychaete Reproduction*. Fortschritte der Zoologie, Stuttgart: 265–287.

Westheide, W. (1985a): The systematic position of the Dinophildae and the archiannelid problem. In: Morris, S.C., George, J.D., Gibson, R. & Platt, H.M. (eds.) *The Origins and Relationships of Lower Invertebrates*. The Systematics Association, Oxford: 310–326.

Westheide, W. (1985b): Ultrastructure of the Protonephridia in the dorvilleid polychaete *Apodotrocha progenerans* (Annelida). *Zoologica Scripta* 14: 273–278.

Westheide, W. (1987): Progenesis as a principle in meiofauna evolution. *Journal of Natural History* 21: 843–854.

Westheide, W. (1990): *Polychaetes: Interstitial families*. Universal Book Services, Oegstgeest.

Westheide, W. (1996): Annelida. In: Westheide, W. & Rieger, R.M. (eds.) *Spezielle Zoologie – Erster Teil: Einzeller und Wirbellose Tiere*. Gustav Fischer Verlag, Stuttgart, Jena, New York: 353–410.

Westheide, W. (1997): The direction of evolution within the Polychaeta. *Journal of Natural History* 31: 1–15.

Westheide, W. (2007): Annelida. In: Westheide, W. & Rieger, R.M. (eds.) *Spezielle Zoologie – Erster Teil: Einzeller und Wirbellose Tiere*. 2nd ed. Gustav Fischer Verlag, Stuttgart, Jena, New York: 374–437.

Westheide, W., McHugh, D., Purschke, G. & Rouse, G. (1999): Systematization of the Annelida: different approaches. *Hydrobiologia* 402: 291–307.

Westheide, W. & Purschke, G. (1996): *Leptonerilla diplocirrata*, a new genus and species of interstitial polychaetes from the island of Hainan, south China (Nerillidae). *Proceedings of the Biological Society of Washington* 109: 586–590.

Westheide, W. & Rieger, G. (2013): *Spezielle Zoologie – Erster Teil: Einzeller und Wirbellose Tiere. 3*. Auflage. Springer-Verlag, Berlin Heidelberg.

Westheide, W. & Rieger, R.M. (1996): *Spezielle Zoologie – Erster Teil: Einzeller und Wirbellose Tiere*. Gustav Fischer Verlag, Stuttgart, Jena, New York.

Westheide, W. & Riser, N.W. (1983): Morphology and phylogenetic relationships of the neotenic interstitial polychaete *Apodotrocha progenerans* n.gen.,n.sp. (Annelida). *Zoomorphology* 103: 67–87.

Wheeler, B.M., Heimberg, A.M., Moy, V.N., Sperling, E.A., Holstein, T.W., Heber, S. & Peterson, K.J. (2009): The deep evolution of metazoan microRNAs. *Evolution & Development* 11: 50–68.

Winnepenninckx, B., Van de Peer, Y. & Backeljau, T. (1998): Metazoa relationships on the basis of 18S rRNA sequences: a few years later.... *American Zoologist* 38: 888–906.

Witek, A., Herlyn, H., Ebersberger, I., Mark Welch, D.B. & Hankeln, T. (2009): Support for the monophyletic origin of Gnathifera from phylogenomics. *Molecular Phylogenetics and Evolution* 53: 1037–1041.

Witek, A., Herlyn, H., Meyer, A., Boell, L., Bucher, G. & Hankeln, T. (2008): EST based phylogenomics of Syndermata questions monophyly of Eurotatoria. *BMC Evolutionary Biology* 8: 345.

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Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). *Hydrobiologia* 535–536: 319–340.

Worsaae, K., Nygren, A., Rouse, G., Giribet, G., Persson, J., Sundberg, P. & Pleijel F. (2005): Phylogenetic position of Nerillidae and *Aberranta* (Polychaeta, Annelida), analysed by direct optimization of combined molecular and morphological data. *Zoologica Scripta* 34: 313–328.

Worsaae, K. & Rouse, G.W. (2008): Is *Diurodrilus* an annelid? *Journal of Morphology* 269: 1426–1455.

Wu, Z., Shen, X., Sun, M.A., Ren, J., Wang, Y., Huang, Y. & Liu, B. (2009): Phylogenetic analyses of complete mitochondrial genome of *Urechis unicinctus* (Echiura) support that echiurans are derived annelids. *Molecular Phylogenetics and Evolution* 52: 558–562.

Young, C.M., Vásquez, E., Metaxas, A. & Tyler, P.A. (1996): Embryology of vestimentiferan tube worms from deep-sea methane/sulfide seeps. *Nature* 381: 514–516.

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

Zhong, M., Struck, T.H. & Halanych, K.M. (2008): Phylogenetic information from three mitochondrial genomes of Terebelliformia (Annelida) worms and duplication of the methionine tRNA. *genomes* 416: 11–21.

Zrzavy, J. (2001): Ecdysozoa versus Articulata: clades, artifacts, prejudices. *Journal of Zoological Systematics and Evolutionary Research* 39: 159–163.

Zrzavy, J. (2003): Gastrotricha and metazoan phylogeny. *Zoologica Scripta* 32: 61–81.

Zrzavy, J., Hypsa, V. & Tietz, D.F. (2001): Myzostomida are not annelids: molecular and morphological support for a clade of animals with anterior sperm flagella. *Cladistics* 17: 170–198.

Zrzavy, J., Mihulka, S., Kepka, P., Bezdek, A. & Tietz, D. (1998): Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. *Cladistics* 14: 249–285.

Zrzavy, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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# 3 The Annelid Fossil Record

## 3.1 Introduction

As the last common ancestor of annelids lacked hard parts that are readily fossilized, such as calcareous tubes (Ippolitov *et al.* 2014) or hardened, sclerotized jaws (Hints and Eriksson 2007), much of our knowledge of early annelid evolution is derived from sites of exceptional preservation, or Lagerstätten. This record is patchy and incomplete as annelids decay rapidly (Briggs and Kear 1993) and very specific processes, including rapid burial and entombment, decay suppression, and tissue replacement by minerals, are required in order for annelids to fossilize (Briggs and Kear 1993, Parry *et al.* 2018). Nevertheless, soft-bodied annelid fossils are found in rocks from a suite of marine environments and are preserved in a variety of ways, including three-dimensional (3D) pyritization (Farrell and Briggs 2007) and phosphatization (Parry *et al.* 2015a) entombment in iron carbonate concretions in marginal marine settings (Thompson 1979) and carbonaceous compression in fine grained siliciclastic rocks (Conway Morris 1979). Such deposits are unevenly distributed in time (Fig. 3.1).

The oldest annelids appeared at the same time as most other bilaterian phyla in the early Cambrian in deposits in China and Greenland (Fig. 3.2 A, B), which are approximately 520 million years old (Conway Morris and Peel 2008, Liu *et al.* 2015), with slightly younger examples known from the middle Cambrian Burgess Shale (Fig. 3.2 C, D). These fossil taxa are clearly polychaetes, possessing well-developed parapodia, homonomous segmentation, and chaetae. Other taxa whose affinities are more obscure have also been linked with annelids, such as *Wiwaxia corrugata* from the Burgess Shale (Conway Morris 1985), and there has been an intense debate about how early trochozoans are related to each other and to extant phyla (Fig. 3.2 E, F) (Conway Morris and Peel 1995, Eibye-Jacobsen 2004, Vinther *et al.* 2017, Zhao *et al.* 2017). The origin of annelids and the characters that define Annelida as a phylum have been featured heavily in these discussions (Eibye-Jacobsen 2004). The most diverse Cambrian annelid fauna is known from the middle Cambrian Burgess Shale (Fig. 3.2 C, D) (Conway Morris 1979).

Although sites preserving annelids were fairly common in the Cambrian (Fig. 3.1), sites preserving whole-body fossil polychaetes become much rarer from the Ordovician onward (Fig. 3.1). Diverse annelid faunas are rare in the fossil record, but notable examples include those from the Devonian Hunsrück Slate (Fig. 3.3 B, C) (Briggs and Bartels 2010), Carboniferous Mazon Creek (Fig. 3.3 E–H) (Thompson 1979), and the Late Cretaceous Hakel and Hjoula lithographic limestones (Fig. 3 I–K) (Bracchi and Alessandrello 2005, Parry *et al.* 2015a). Many occurrences of whole bodies of fossil polychaetes are limited to single taxa, often known from few, or single, specimens from a given locality, such as *Arkonips topororum* from the Devonian of Ontario (Fig. 3.3 D) (Farrell and Briggs 2007).

The record of exceptionally preserved annelid fossils is punctuated by the appearance of features that more readily survive fossilization in particular clades (Fig. 3.1). During the Ordovician, there was a major radiation of eunicidans (Figs. 3.4 A–E and 3.5), the jaws of which are found abundantly as microfossils from acid digested residues of marine rocks (Hints and Eriksson 2007). Machaeridians (Withers 1926, Adrain 1992) (Fig. 3.6), an extinct group of epibenthic and infaunal armored annelid worms, also originated during this period (Vinther *et al.* 2008). Both of these groups contained high-level taxa (family and above) that are now extinct, revealing hidden morphological disparity in ancient annelids not present in the extant diversity.

Sedentary polychaetes were well represented by fossil tubes from the mid to late Paleozoic onward, and the evolutionary history of Serpulidae (Fig. 3.7), in particular, is well illustrated by the fossil record (Ippolitov *et al.* 2014). Fossils of taxa with agglutinated tubes are reported less frequently and their taxonomic affinities are known with less certainty. Fossils more readily comparable to living families are known, such as a pectinariid-like tube from the Cretaceous (Vinn and Luque 2013) and even potential oweniids from the Pliocene (Uchman *et al.* 2017). The fossil record of non-tube-dwelling sedentary annelid body fossils is highly incomplete, with a single occurrence of Flabelligeridae (Fig. 3.3 H) in the Carboniferous (Hay 2002). Although clitellates have effectively no preservation potential as body fossils, they nonetheless do have a fossil record, both in the form of leech cocoons (Bomfleur *et al.* 2012) from the Triassic onward (Manum *et al.* 1991) and potential earthworm burrows (Retallack 1976).

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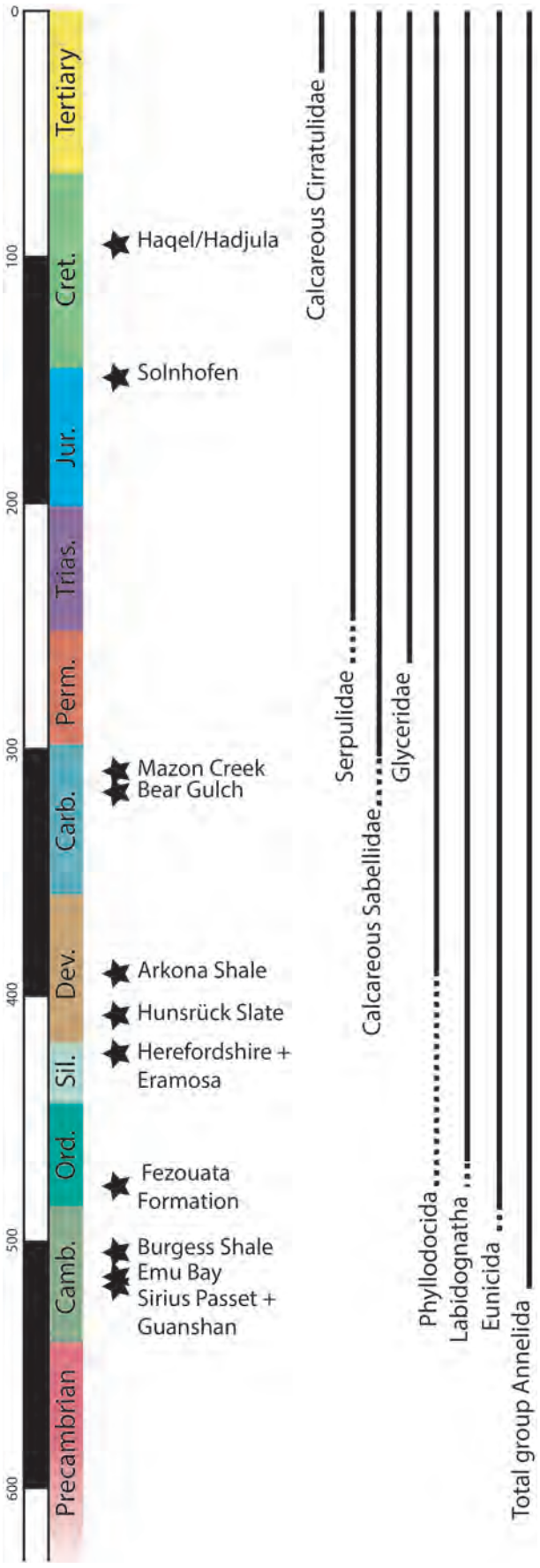


**Fig. 3.1:** Statigraphic distribution of fossil sites preserving exceptionally preserved annelid fossils and ranges of taxa that preserve frequently. See text for discussion.

# 3.2 Soft-bodied annelid fossils

## 3.2.1 The oldest annelids

Numerous fossil taxa from the Precambrian (before 541 million years ago) have historically been compared with annelids, but their phylogenetic affinities are highly controversial. This includes the iconic soft-bodied Ediacaran organism *Dickinsonia* (see Wade 1972), which is currently interpreted only as a total group eumetazoan or putative bilaterian (Sperling and Vinther 2010, Hoekzema *et al.* 2017). The oldest fossil evidence for bilaterians is in the form of trace fossils, such as ancient scratch traces called *Kimberichnus* (see Gehling *et al.* 2014). These ichnofossils are attributed to the stem group mollusc *Kimberella*, which is at least as old as 555 Ma (Martin *et al.* 2000). Younger examples of trace fossils made by vermiform animals occur at, or close to, the Ediacaran Cambrian boundary but are more likely to have been made by ecdysozoans rather than spiralian worms such as annelids (Vannier *et al.* 2010, Parry *et al.* 2017). Diverse trace fossils occurred in the Fortunian (~541–529 Ma) (Mángano and Buatois 2014), including traces often attributed to annelids, such as *Nereites*, but these trace fossils could have been made by other phyla, including arthropods (Martin and Rindsberg 2007).

The oldest unequivocal annelids occurred as whole-body carbonaceous compression fossils in Burgess Shale–type deposits from the early and middle Cambrian (Fig. 3.2 A–D). The oldest of these are from the early Cambrian (approximately 520 million years ago), which are two taxa from Sirius Passet of North Greenland (Fig. 3.2 A, B) (Conway Morris and Peel 2008, Vinther *et al.* 2011) and one taxon from the Guanshan biota of Yunnan Province, China (Liu *et al.* 2015). The annelids from the Middle Cambrian (~505 Ma) Burgess Shale (Fig. 3.2 C, D) have been featured most prominently in discussions of early annelid evolution (Conway Morris 1979, Conway Morris and Peel 1995, Eibye-Jacobsen 2004, Parry *et al.* 2015b) and are known from six taxa from the Walcott Quarry locality (Conway Morris 1979), as well as the more recently discovered Marble Canyon (Nanglu and Caron 2018). This record is supplemented by the "small carbonaceous fossils" (SCFs), which are organic remains of recalcitrant parts of a diverse suite of organisms, including priapulid spines, molluscan radulae, and trochozoan chaetae

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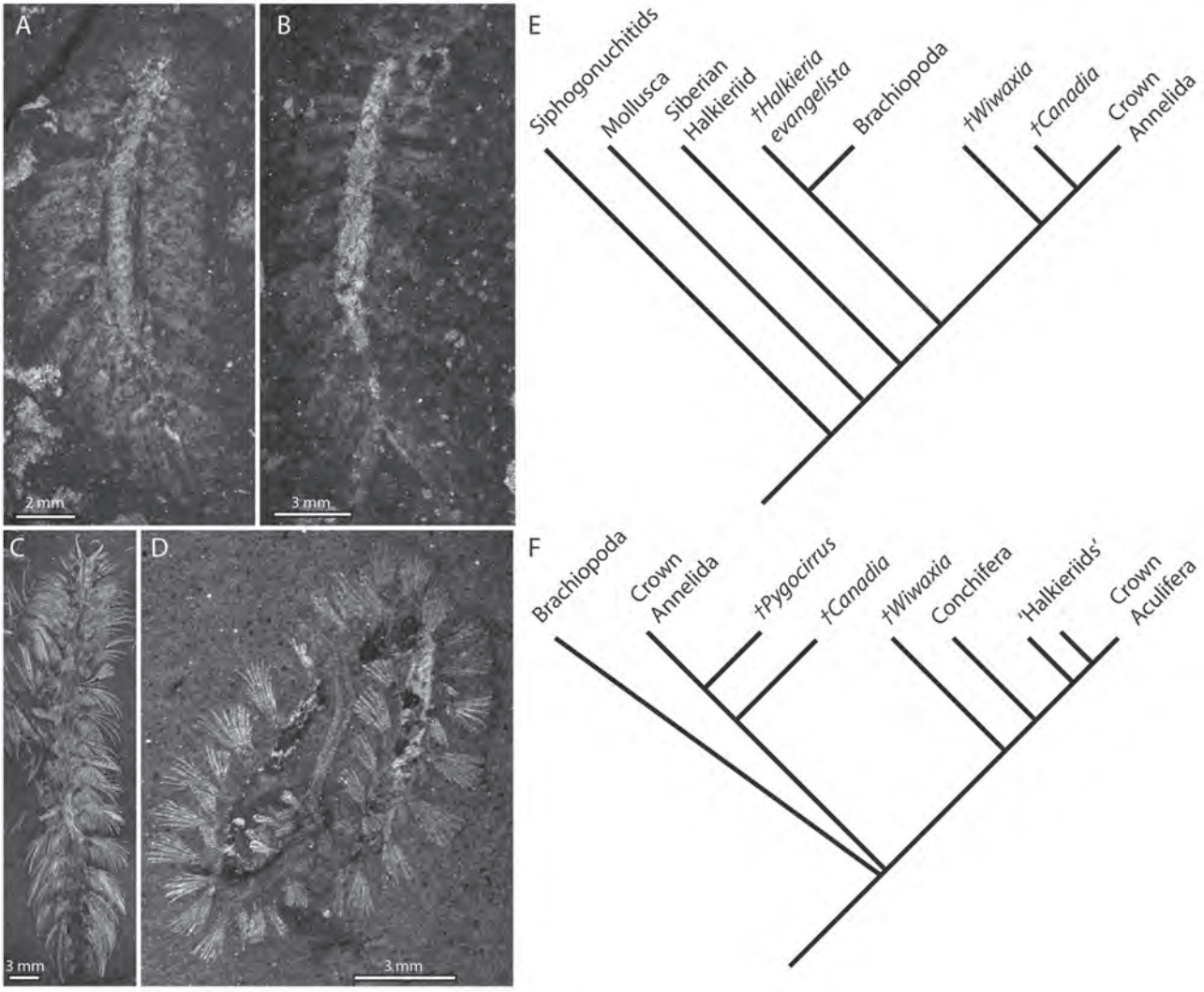


**Fig. 3.2:** Cambrian annelid fossils and phylogenetic hypotheses of Cambrian trochozoans. A, *Phragmochaeta canicularis,* MGUH31365. B, *Pygocirrus butyricampum*. A and B, from the early Cambrian, Sirius Passet, North Greenland. C, *Canadia spinosa,* USNM83929c. D, *Burgessochaeta setigera* USNM198705. C, D, from the middle Cambrian Walcott Quarry locality of the Burgess Shale, British Columbia. E and F, End member hypotheses of relationships of Cambrian trochozoans to extant and fossil annelids. E, Hypothesis of Conway Morris and Peel (1995). F, Hypothesis following phylogenetic analyses in Parry *et al.* (2016) and Vinther *et al.* (2017).

(Butterfield and Harvey 2012). Annelid chaetae are apparently rare components of these fossil assemblages, having been described in only one study on the early Cambrian of Baltica, which postdate the annelid body fossils from Sirius Passet and Guanshan (Slater *et al.* 2017). The reason for this rarity is not clear given that *Wiwaxia* chaetae are commonly recovered as SCFs (and presumably have similar preservation potential) and annelid chaetae have been successfully isolated from Burgess Shale macrofossils (Butterfield 1990).

Three Cambrian taxa have taken center stage in the discussion of the origin of trochozoans and consequently the early evolution of annelids: *Wiwaxia corrugata*, *Halkieria evangelista*, and *Canadia spinosa*. Debate has primarily focused on the origin of chaetae and biomineralized sclerites, shells and valves, radulae, and segmentation (Conway Morris and Peel 1995, Eibye-Jacobsen 2004, Butterfield 2006, Vinther *et al.* 2017). Of these three taxa, only *C. spinosa* is unambiguously a polychaete, possessing differentiated and well-developed noto- and neurochaetae, prominent parapodial lobes, and a pair of palps (Fig. 3.2 C) (Conway Morris 1979, Eibye-Jacobsen 2004). *Canadia* displays some interesting and unique character combinations, such as inter-ramal gills that are similar to molluscan ctenidia in gross morphology (Conway Morris 1979), along with flattened notochaetae that are superficially similar to those of extant Chrysopetalidae and the scaleworm *Palmyra* (Butterfield 1990, Eibye-Jacobsen 2004).

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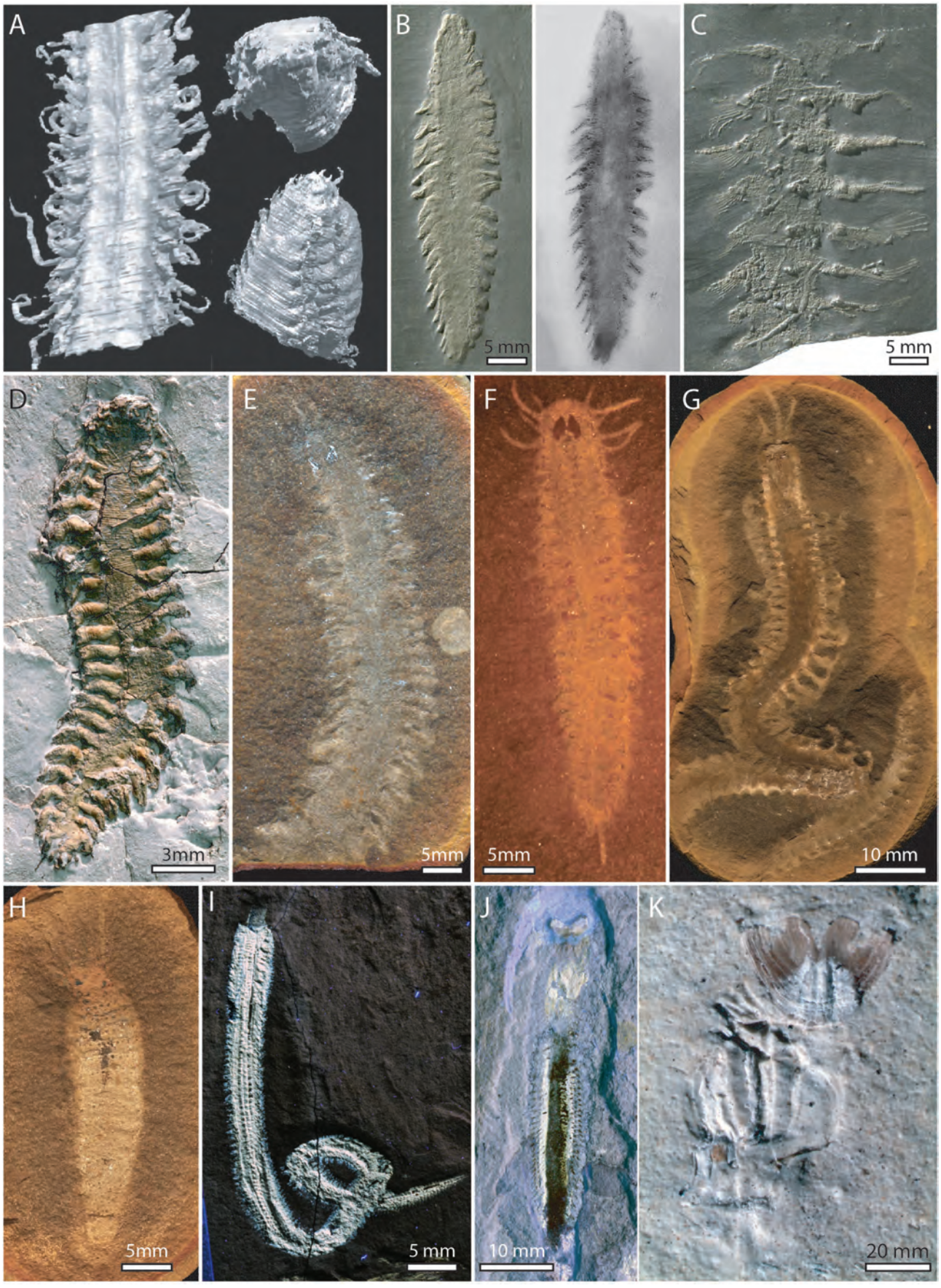


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*Wiwaxa* is an early to middle Cambrian animal with a dorsal covering of flattened chaetae, paired spines, and a radula-like feeding organ with a median tooth (Conway Morris 1985, Eibye-Jacobsen 2004, Smith 2012). Although *Wiwaxia* is present in several Burgess Shale–type localities, its true geographic and stratigraphic range is revealed by the SCF record (Slater *et al.* 2017). *Wiwaxia* has been interpreted as a polychaete previously and was placed explicitly in the Phyllodocida (along with *Canadia*) by Butterfield (1990) or in the annelid stem group by Conway Morris and Peel (1995). Placing *Wiwaxia* in the crown or stem group of annelids has nontrivial implications for the hypotheses of character evolution leading to and within annelids. For instance, if *Wiwaxia* is a stem group annelid, then annelids may have possessed a radula-like feeding organ early in their history, which was subsequently lost prior to the origin of the crown group, as in the hypothesis of Conway Morris and Peel (1995) (Fig. 3.2 E). The presence of chaetae has been the primary evidence linking *Wiwaxia* to annelids, as the sclerites of *Wiwaxia* possess dense tubular striations indicative of microvillar secretion (Butterfield 1990). However, chaetae are plesiomorphies of a more inclusive clade within Spiralia, as they are present also in brachiopods and molluscs (Lüter 2000, Schiemann *et al.* 2017), as well as bryozoans (Gordon 1975). Furthermore, *Wiwaxia* shows no signs of true segmentation, only serial repetition (Eibye-Jacobsen 2004), which is not unique to annelids as serialized dorsal chaetal bundles occur in the larvae of some extant (Nielsen 1991) and probably also in extinct (Zhang *et al.* 2018) brachiopods.

Halkieriids and related taxa have a tumultuous history regarding their phylogenetic position, having previously been placed in the stem lineages (and common stem lineages) of brachiopods, molluscs, and annelids (Conway Morris and Peel 1995, Vinther and Nielsen 2005, Conway Morris and Caron 2007, Vinther 2009, Vinther *et al.* 2017, Zhao *et al.* 2017) (Fig. 3.2 E, F). Halkieriids possess either one (anterior) or two (anterior and posterior) shells and a dorsoventrally flattened body that is covered in calcarous sclerites (Conway Morris and Peel 1995). These sclerites are arranged in distinct zones, much like those of extant chitons (Vinther and Nielsen 2005). In the hypothesis of Conway Morris and Peel (1995), brachiopods, molluscs, and annelids evolved from a creeping *Halkieria*-like ancestor with a covering of biomineralized sclerites that are homologous with annelid chaetae. However, the discovery of specimens from the early Ordovician of Morocco preserving polystichous radulae with hundreds of tooth rows confirmed that halkieriids are in fact crown group molluscs (Vinther *et al.* 2017). Phylogenetic analyses place halkieriids in the stem group of Aculifera (chitons and aplacophorans) and *Wiwaxia* in the molluscan stem, and so these fossil taxa are only obliquely related to the origin of annelids (Fig. 3.2 F) (Vinther *et al.* 2017).

The unequivocal polychaete taxa from the Cambrian have broadly similar and fairly generalized polychaete body plans and share a number of characters with each other to the exclusion of most extant taxa. They are all approximately homonomously segmented, with the only body regionalization currently recognized shown in the gills of *Canadia*, which commence at chaetiger 4 (Conway Morris 1979). A pair of head appendages, which are best interpreted as palps based on their varying aspect ratios and presumably contractile nature (Eibye-Jacobsen 2004), are present in several taxa where the head is known, including *C. spinosa* (Fig. 3.2 C), *Burgessochaeta setigera* (Fig 3.2 B), *Kootenayscolex barbarensis*, *Pygocirrus butyricampum*, and *Guanshanchaeta felicia* (see Eibye-Jacobsen 2004, Liu *et al.* 2015, Parry *et al.* 2015b, Nanglu and Caron 2018). The head morphology of *Insolicorypha psygma* and *Stephenoscolex argutus* from the Burgess Shale is currently unknown as these taxa are known from few and incomplete specimens (Eibye-Jacobsen 2004). *Peronochaeta dubia* may possess a pair of stubby head appendages, but these are present in only one specimen (Conway Morris 1979). A short median antenna is known in *Kootenayscolex* (see Nanglu and Caron 2018), but unlike the palps,

◂ **Fig. 3.3:** Selected polychaete body fossils known from Lagerstätten deposits. A, *Kenostrychus clementsi,* an aciculate polychaete from the Silurian Herefordshire Biota, images produced by / through serial grinding of fossil specimens, OUM C.29544 (top right), OUM C.29543 (images courtesy of Mark Sutton). B, *Bundenbachochaeta eschenbachensis*, holotype, DBM:HS 717, photograph at left, image at right. C, *Scopyrites magnus* NM: PWL 2009/6, fragment of trunk. B and C, From the Devonian Hunsrück Slate, Germany. Hunsrück photographs and X radiographs courtesy of Derek E.G. Briggs, taken by Georg Oleschinski. From Briggs and Bartels (2010). D, *Arkonips topororum,* a Devonian phyllodocidan from the Arkona Shale, UMMP 73795. Image courtesy of Derek E.G. Briggs. From Farrell and Briggs (2007). E, *Dryptoscolex matthiesae* ROM48542. F, *Fossundecima konecniorum* ROM47990. G, *Esconites zelus* ROM47521. H, *Mazopherusa prinosi.* E–H, Carboniferous (Pennsylvanian) Mazon Creek, Illinois. Images from Parry *et al.* (2016). I, *Rollinschaeta myoplena*, AN 15078, photographed under ultraviolet (UV) light to highlight phosphatized muscle tissue which fluoresces white. From Parry *et al.* (2015). J, *Eunicites joinvillei* preserving ventral longitudinal muscles in calcium phosphate, AN 15062, photographed under UV light to highlight phosphatized longitudinal muscle bands. K, jaw apparatus of Lumbrineridae sp. Note the preservation of fine details of the cutting plates of the mandibles, AN 15080. I–K, Upper Cretaceous (Cenomanian), Lebanon.

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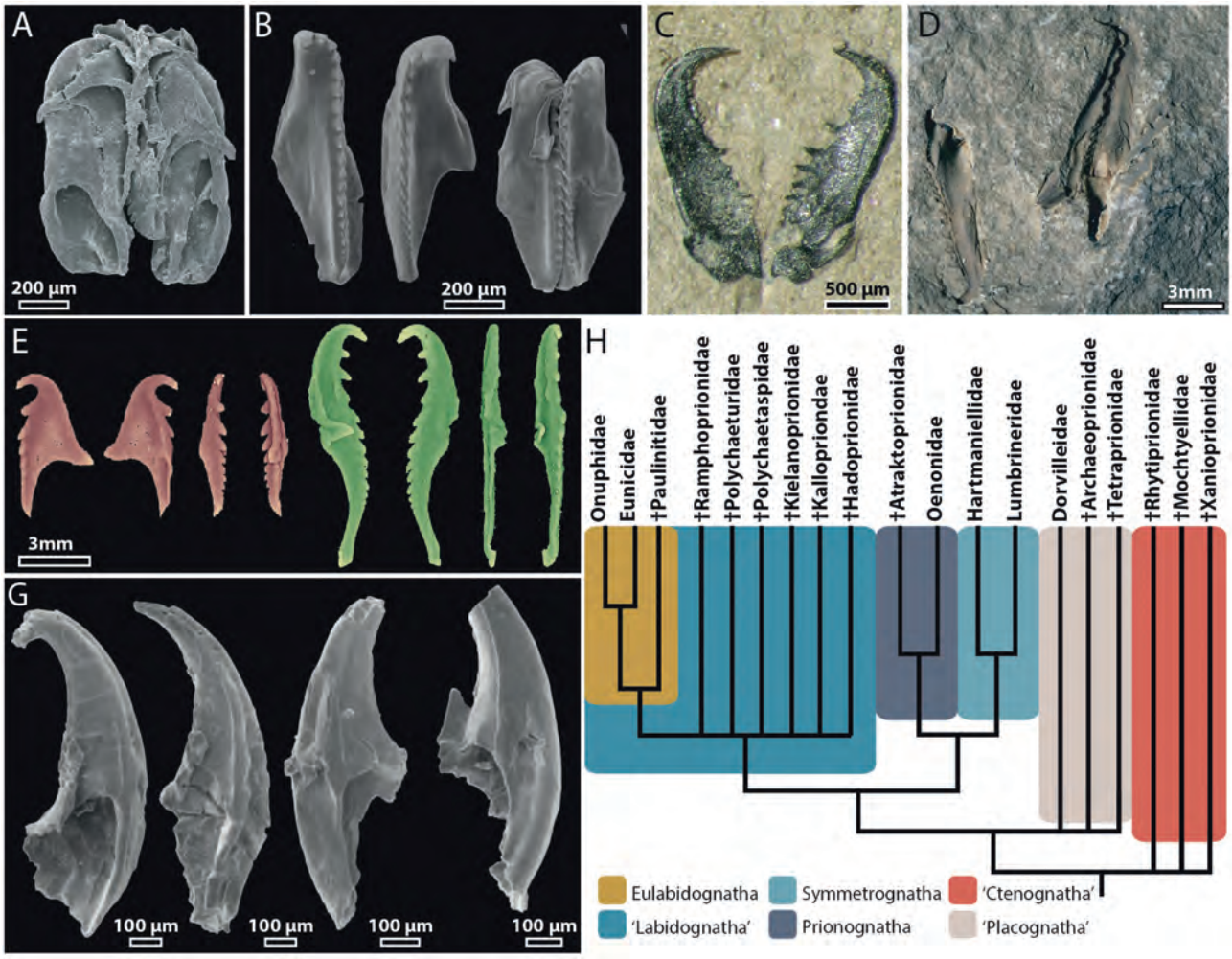


**Fig. 3.4:** Fossil polychaete jaw apparatuses, scolecodonts, and relationship of jaw-bearing eunicidans. A, Scanning electron microscopy (SEM) micrograph of a virtually complete (carriers are missing) dorsal maxillary jaw apparatus of the paulinitid *Hindenites parkheadensis* from the Silurian Eramosa Lagerstätte, Ontario, Canada. Note that the maxillae are hollow (ROM 62852). From Eriksson and Bitter (2015). B, SEM micrograph of the left MI (OSU 48452), right MI (OSU 48453), and partial maxillary apparatus (OSU 48463) of the polychaetaspid *Oenonites* sp. from the Cincinnatian (Upper Ordovician) of the USA; all specimens in dorsal view. Note the "basal plate" fitting into the bight of the right first maxilla (MI) in the apparatus. From Bergman (1998). C, Light microscope photograph of bedding plane specimens of the paulinitid *Paulinites paranaensis* from the Devonian Ponta Grossa Formation of Paraná, Brazil. The cluster consists of a right and left MI (note also the basal plate preserved in situ in posterior portion of right MI) and vague impressions of the posteriormost carriers, dorsal view, LO 11164t. From Eriksson *et al.* (2011). D, Light microscope photograph of bedding plane cluster of the giant putative labidognath species *Websteroprion armstrongi* (ROM63122) from the Devonian Kwataboahegan Formation, Ontario, Canada. Individual jaws are preserved in dorso-ventral view as negative molds (except for small black pieces of original jaw wall, e.g., posteriormost tip of right MI; lighting makes the specimens appear in positive relief in the photograph). From Eriksson *et al.* (2017). E, Reconstruction from computed tomographic scan (with artificial coloring) of the anterior maxillae of *W. armstrongi*, originally concealed within slab ROM 63120. Red element is the right MII (posteriormost tip might be missing) in dorsal, ventral, left lateral, and right lateral view; green element is the laterally strongly compressed left MII in left lateral, right lateral, ventral, and dorsal view. From Eriksson *et al.* (2017). G, SEM micrographs of scolecodonts of the phyllodocidan *Glycera* sp. from the Danian (early Paleogene) of Sweden; specimen numbers, from left to right, LO 9173, LO 9174, LO 9175, and LO 9172. From Bergman and Eriksson (2003). H, Tentative cladogram summarizing possible phylogenetic relationships of eunicidans. Modified from Paxton (2009).

the homology of this median antenna with structures in extant annelids is obscure. It may represent an autapomorphy of *Kootenayscolex* (see Nanglu and Caron 2018) as median antennae may have evolved multiple times in annelids, given that they are present in aciculates, as well as Nerillidae and some Spionidae and Paraonidae (Rouse and Pleijel 2001). These taxa are scattered throughout the annelid tree of life based on both morphological and molecular data (Struck *et al.* 2015, Parry *et al.* 2016). However, the innervation of the median antenna in

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| TYPE OF MAXILLARY APPARATUS | | | | | |
|---|---|---|---|---|---|
| **Placognatha** | **Ctenognatha*** | **Labidognatha** | **Eulabidognatha** | **Symmetrognatha** | **Prionognatha** |
| | *Ctenognatha herein includes the Xenognatha. | | | | |
| **CHARACTERISTICS** | | | | | |
| Symmetrical to asymmetrical; posterior elements plate-like; 2 anterior rows of denticles; carriers lacking. | Symmetrical to subsymmetrical; posterior elements plate-like; 4 or more rows of numerous minute denticles; carries lacking. | Asymmetrical; posterior elements dentate; conical to plate-like; MIr reduced (basal plate); 5 pairs of elements in 2 rows; short to moderately long carriers. | Asymmetrical; posterior elements dentate to forceps-like; conical; surrounded in front by 2 semi-circles of anterior elements; MIr very reduced/fused; 5-6 pairs of elements; short carriers. | Symmetrical; posterior elements dentate to forceps-like; conical; 2-4 pairs of elements in two rows; short to moderately long carriers. | Asymmetrical; posterior elements dentate; conical to plate-like; MIr reduced (basal plate); 5 pairs of elements in 2 rows; long carriers. |
| **AGE (STRATIGRAPHIC RANGE)** | | | | | |
| ?Late Cambrian to Permian | ?Late Cambrian to the present | Mid Ordovician to the Cretaceous | Late Ordovician to the present | Early Ordovician to the present | Mid Ordovician to the present |
| **FOSSIL FAMILIES** | | | | | |
| Mochtyellidae<br>Rhytiprionidae<br>Xanioprionidae | ?Archaeoprinidae<br>Dorvilleidae<br>?Iphitimidae<br>Tetraprionidae | Hadoprionidae<br>Kalloprionidae<br>Kielanoprionidae<br>Polychaetaspidae<br>Polychaeturidae<br>Ramphoprionidae | Paulinitidae | Conjugaspidae<br>Hartmaniellidae<br>Symmetroprionidae | Atraktoprionidae<br>Skalenoprionidae |
| **EXTANT FAMILIES** | | | | | |
| X | Dorvilleidae<br>?Iphitimidae | X | Eunicidae<br>Onuphidae | Hartmaniellidae<br>Lumbrineridae | Oenonidae<br>?Histriobdellidae |

**Fig. 3.5:** Different types of eunicidan maxillary jaw apparatus architectures (modified from Paxton 2009). Placognath type; *Mochtyella polonica*. Ctenognath type; *Tetraprion pozaryskae*. Labidognath type; *Ramphoprion elongatus*. Eulabidognath type; *Kettnerites (Aeolus) sisyphi klasaardensis*. Symmetrognath type; *Symmetroprion spatiosus*. Prionognath type; *Oenone fulgida*. All jaw apparatus illustrations are modified from Kielan-Jaworowska (1966), except *K.* (*A.*) *s. klasaardensis*, after Bergman (1989), and *O. fulgida*, after Glasby *et al.* (2000). Xenognath apparatuses are included in Ctenognatha, following Paxton (2009).

distantly related taxa is effectively identical (Orrhage and Müller 2005), and so if the median antenna has a deep origin, then it must have been lost numerous times independently.

With the exception of *Peronochaeta*, Cambrian taxa have prominent parapodia lobes, which are covered by very elongate chaetae that are often similar in morphology in each ramus (Conway Morris 1979, Eibye-Jacobsen 2004, Parry *et al.* 2015b). These chaetae are often posteriorly directed and cover the dorsum occurring either in fascicles (e.g., *Phragmochaeta*) or transverse rows of paleae (e.g., *Canadia*). These dorsal chaetae are thought to have provided a protective function (Westheide 1997, Parry *et al.* 2015b). In *Burgessochaeta* and *Pygocirrus*, the notopodia and neuropodia both project laterally (Conway Morris 1979, Vinther *et al.* 2011, Parry *et al.* 2015b). *Peronochaeta*

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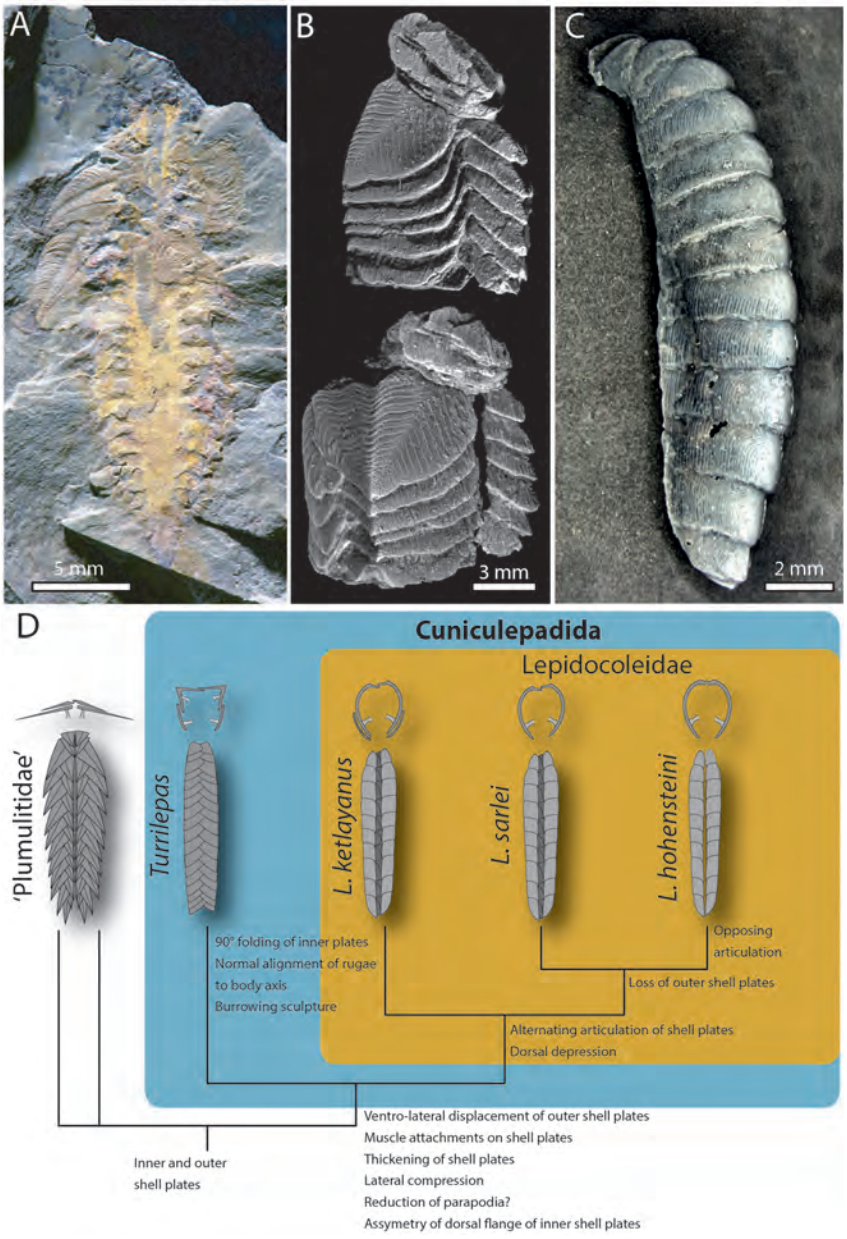


**Fig. 3.6:** Machaeridian body fossils and evolution. A, *Plumulites bengtsoni* (Plumulitidae) showing preservation of soft tissue, Tremadocian, Fezouata Shale, Morocco, YPM IP221134. B, *Turrilepas wrightiana* (Turrilepadidae), Silurian, Hemse marl, Gotland, Sweden, Naturhistoriska Riksmuseet 3852, incomplete specimen in different views. C, *Lepidocoleus sarlei* (Lepidocoleidae), Middle Silurian, Wenlock, Rochester Shale, New York, USA, YPM IP227508. D, Phylogeny and body plan evolution of machaeridian families and genera. Topology and character evolution follows discussion in Vinther and Briggs (2009) and Parry *et al.* (2014).

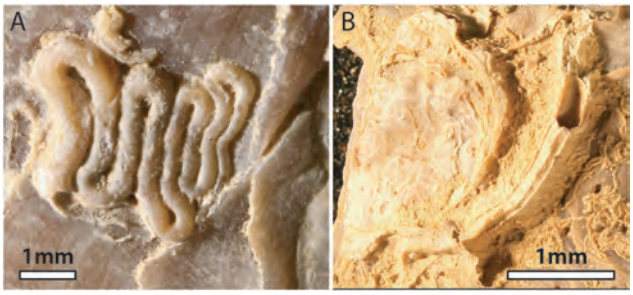


**Fig. 3.7:** Fossils of calcareous tubeworms of Serpulidae and Sabellidae. A, *Glomerula serpentina,* a calcareous sabellid tube encrusting the shell of the bivalve *Gryphaea mucronata*, YPM IP 537624. B, *Mucroserpula tricarinata*, a serpulid tube also encrusting the shell of a specimen of *Gryphaea mucronata,* YPM IP 537720. Both specimens from Early Cretaceous, Washita Group, Del Rio Formation, photographs by Jessica Utrup.

is unique among Cambrian taxa in possessing stout hooked chaetae, which may indicate a lifestyle different from that of the other Cambrian taxa (Conway Morris 1979). The parapodia of *Peronochaeta* are also thought to be uniramous, a condition also not seen in any other Cambrian polychaete (Conway Morris 1979).

*Pygocirrus* is notable among Cambrian polychaetes in the possession of pygidial cirri, although possibly

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also present in *Guanshanchaeta* (see Liu *et al.* 2015), a character that is a synapomorphy of the annelid crown group (Eibye-Jacobsen 2004, Vinther *et al.* 2011, Parry *et al.* 2016). Consequently, *Pygocirrus* is likely the Cambrian polychaete most closely related to extant annelids among Cambrian polychaetes (Fig. 3.2 F) based on current evidence and phylogenetic analysis (Vinther *et al.* 2011, Parry *et al.* 2016).

The morphology of the head of the Cambrian taxa has been the source of some controversy (Parry *et al.* 2015b, Nanglu and Caron 2018), but it has long been recognized that the typical prostomium-peristomium head complex characteristic of extant annelids is not well expressed in Cambrian forms (Budd and Jensen 2000). There are parapodia and chaetae closely associated with the palps and mouth in *Canadia*, *Burgessochaeta*, and *Kootenayscolex* (see Parry *et al.* 2015b, Nanglu and Caron 2018), which has led to hypotheses suggesting a chaetigerous origin of the entire head (Parry *et al.* 2015b), peristomium, and mouth region (Nanglu and Caron 2018) or total absence of the peristomium (Budd and Jensen 2000). Distinguishing which (if any) of these hypotheses are correct is difficult, especially if the peristomium is limited to only the lips around the mouth and therefore not visible dorsally in the fossil taxa, as recovered in some ancestral state reconstructions for the last common ancestor of annelids (Struck *et al.* 2015). Nevertheless, the head of many Cambrian stem group annelids is poorly delineated from the trunk, suggesting that differentiation of the annelid head phylogenetically postdated the origin of biramous parapodia and a segmented body plan (Parry *et al.* 2015b, Nanglu and Caron 2018).

Presently, all Cambrian polychaetes are recovered either as a paraphyletic grade of stem group annelids (*Phragmochaeta*, *Canadia, Kootenayscolex,* and *Burgessochaeta*) or in a polytomy with the annelid crown group (*Guanshanchaeta* and *Pygocirrus*) (Parry *et al.* 2016, Nanglu and Caron 2018) (Fig. 3.2 F). The Burgess Shale taxa *Peronochaeta, Insolicorypha,* and *Stephenoscolex* have not yet been included in a phylogenetic analysis due to their incompleteness, particularly regarding the anterior and posterior regions (Eibye-Jacobsen 2004). As they are recovered in the annelid stem group, polychaetes from the Cambrian are important for unraveling the sequence of character evolution that led to the origin of the annelid crown group and also for inferring the characters that might be annelid plesiomorphies. These annelid fossils suggest that prominent parapodial lobes equipped with only capillary chaetae (and without aciculae/supporting chaetae), paired sensory palps, a bipartite head, and a single pair of pygidial cirri are plesiomorphic for the annelid crown group (Eibye-Jacobsen 2004, Vinther *et al.* 2011, Eibye-Jacobsen and Vinther 2012, Parry *et al.* 2014, 2015b, 2016). This suite of characters is mostly in agreement with ancestral state reconstructions based on phylogenomic trees (Weigert *et al.* 2014), with some notable differences. For example, in the ancestral state reconstructions of Struck *et al.* (2011), the annelid ancestor was reconstructed with parapodia of uncertain morphology, but possessing aciculae and a head with grooved palps, which is in conflict with hypotheses derived from fossils (Eibye-Jacobsen and Vinther 2012). However, with an improved taxonomic sample, Weigert *et al.* (2014) reconstructed a hypothesized ancestral annelid much more concordant with the fossil record, lacking aciculae and parapodial cirri, but unable to distinguish if the palps of the annelid crown ancestor were sensory or grooved. Also, the ancestral state reconstructions of both Struck *et al.* (2011) and Weigert *et al.* (2014) do not suggest the presence of pygidial cirri in the annelid ancestor. If the phylogenetic hypotheses that are commonly recovered from phylogenomic trees are in fact correct, then such discrepancies between the fossil record and these ancestral state reconstructions could potentially be accounted for by convergent evolution of sessile lifestyles in Magelonidae, Oweniidae, and Chaetopteridae (and consequent loss or modification of characters correlated with a sessile lifestyle) or independent evolution of grooved palps in several families (Parry *et al.* 2016). Another possibility entertained is that some of the early diverging taxa could be drawn to the base of the annelid tree due to a systematic error (Eibye-Jacobsen and Vinther 2012). The presence of protective chaetae in the taxa that form the deepest divergences in the annelid stem group suggests that protective notochaetae are primitive for annelids (Parry *et al.* 2016) but may have been lost prior to the diversification of the crown group, given their absence in crownward forms such as *Pygocirrus* (see Vinther *et al.* 2011, Parry *et al.* 2015b).

Sipunculan worms have also been reported from the early Cambrian Maotianshan Shales (Huang *et al.* 2004), as well as an additional undescribed putative sipunculan from a Burgess Shale locality (Caron *et al.* 2010), revealing that the sipunculan body plan has an ancient origin. Two taxa are described from the Maotianshan Shales, *Archaeogolfingia caudata* and *Cambrosipunculus tentaculatus*, which are identified as members of total group Sipuncula by the preservation of U-shaped guts. *Cambrosipunculus* preserves circumoral tentacles, hooks that occur both scattered and in rings, approximately 10 perioral tentacles, and papillae of the trunk. *Archaeogolfingia* possesses a thin caudal appendage. Although these taxa are broadly

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morphologically similar to golfingiids (Huang *et al.* 2004), they lack the coiled gut morphology that characterizes most extant members of Sipuncula (Huang *et al.* 2004), and phylogenetic analyses recover these taxa as stem group sipunculans (Parry *et al.* 2016), suggesting that coiling of the gut arose later. Analyses of morphological (Parry *et al.* 2016) and miRNA (Sperling *et al.* 2009) data exclude sipunculans from annelids, where they are found as the annelid sister group. They are found nested within annelids but close to the crown node in phylogenomic analyses (Struck *et al.* 2011, Weigert *et al.* 2014). Consequently, these early sipunculans would represent the oldest crown group annelids if a placement within annelids is correct, as no fossil polychaetes from the Cambrian can be assigned to any extant annelid subtaxon based on current evidence (Parry *et al.* 2016).

### 3.2.2 Soft-bodied annelid fossils beyond the Cambrian

Exceptionally preserved fossils of polychaetes are less frequently preserved in the Phanerozoic after the Cambrian. Several deposits that do preserve whole-body annelid fossils contain low diversity and are often restricted to single taxa, such as the 3D preserved polychaete *Kenostrychus clementsi* from the Silurian Herefordshire Lagerstätte (Fig. 3.3 A), which may represent an early phyllodocidan (Sutton *et al.* 2001) or amphinomidan (Parry *et al.* 2016). Other notable examples of early Palaeozoic annelids include *Plumulites bengtsoni* (Fig. 3.6 A), a machaeridian preserving soft parts from the Early Ordovician Fezouata Formation (Vinther *et al.* 2008), spectacularly well-preserved specimens of *Myoscolex*-like forms and aphroditid-like polychaetes with phosphatized muscle tissue from the middle Silurian Eramosa Lagerstätte (Bitter *et al.* 2007), and *Arkonips topororum* (Fig. 3.3 D), an early phyllodocidan with tentacular cirri from the Middle Devonian Arkona Shale of Ontario. Following the Burgess Shale–type biotas, there are no diverse faunas preserving soft-bodied polychaetes until the Devonian (Emsian) Hunsrück slate (Fig. 3.3 B, C) (Briggs and Bartels 2010). Although the Hunsrück Slate preserves multiple polychaete genera, they are not sufficiently well preserved to be placed with confidence in a phylogeny and have not been included in more recent analyses, but may represent early aciculates (Briggs and Bartels 2010). The older Silurian Eramosa Formation may also contain a substantial diversity of soft-bodied polychaetes, but the taxa from this locality await detailed description and their annelid affinities need to be confirmed (Bitter *et al.* 2007).

The late Carboniferous Mazon Creek preserves numerous taxa (Fig. 3.3 E–H) that are strikingly similar to extant orders and families (Thompson and Johnson 1977, Thompson 1979, Fitzhugh *et al.* 1997, Hay 2002). Although some of these fossils have previously been assigned to extant families, they may only preserve character combinations that are diagnostic of suprafamilial groups and their precise phylogenetic affinities require closer investigation. For example, *Fossundecima* (Fig. 3.3 F) was previously considered a member of Nereididae (Fitzhugh *et al.* 1997) but may belong to the stem lineage of a clade of nereidiform phyllodocidans with lateral jaws, such as Nereididae and Hesionidae (Parry *et al.* 2016). While placing the taxa from Mazon Creek into the extant families with which they share most similarities is tempting, many of these similarities may be plesiomorphies of more inclusive clades, and so the true phylogenetic position of these taxa requires reassessment in cladistic analyses (Parry *et al.* 2016). Nevertheless, Mazon Creek fossils provide strong evidence that the major divergences within Phyllodocida are at least Carboniferous in age, with glyceriforms, aphroditaceans, and nereidiforms represented in the fauna (Thompson 1979, Fitzhugh *et al.* 1997). The Mazon Creek fauna also includes the only fossil flabelligerid (Fig. 3.3 H), which preserves details of the chaetal basket and trunk papillae (Hay 2002), indicating that cirratuliforms had also diversified by at least the Carboniferous.

The slightly older Bear Gulch plattenkalk preserves a similar, although less diverse, fauna of polychaetes, which is likewise dominated by jaw bearing, errant taxa. This includes the genus *Astreptoscolex*, a nephtyid-like polychaete, which occurs in both deposits (Schram 1979, Thompson 1979). Goniadids are known from both deposits, but the older *Carbosesostris* from Bear Gulch is more similar to extant Goniadidae. The jaw apparatus of *Carbosesostris* contains both micrognaths and a pair of macrognaths (Schram 1979), whereas only micrognaths are present in *Pieckonia* from Mazon Creek (Thompson 1979), which is a condition that is known in the extant species *Goniada amacrognatha* (see Böggemann and Eibye-Jacobsen 2002, Böggemann 2006).

Polychaete body fossils from the Mesozoic have received relatively little attention recently, and the annelid affinities of some historical claims require reinvestigation. For example, in the Late Jurassic Solnhofen Limestone, there were approximately 15 genera of described "worms," but the annelid affinity of some of these has been questioned and they may not even represent body fossils (Barthel *et al.* 1990). The affinities of polychaetes from the Late Cretaceous Haqel and Hadjula lithographic limestones (Fig. 3.3 I–K) are more secure, however, as they are

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primarily based on the morphology of jaws (Bracchi and Alessandrello 2005). This deposit includes many genera of Eunicida, including large species of Eunicidae (Fig. 3.3 J) (Bracchi and Alessandrello 2005). The eunicidan fossils in the Cretaceous sites in Lebanon are unusual in that the calcareous components of the jaws are preserved (Fig. 3.3 K), including fine details of the mandibles, such as growth lines, in taxa belonging to Lumbrineridae and Eunicidae (Fig. 3.3 I) (Wilson *et al.* 2016). These features are usually dissolved and disaggregated following death and do not commonly survive even as subfossils in recent sediments (Colbath 1988).

Other than eunicidans, the Haqel and Hadjula Lagerstätten also contain some phyllodocidans, such as aphroditaceans and the goniadid *Ferragutia cenomania* (see Bracchi and Alessandrello 2005). Unlike the Palaeozoic goniadids, *Ferragutia* possesses the sclerotized chevron elements in the pharynx (Bracchi and Alessandrello 2005). A single specimen of *F. cenomania* and a specimen of *Eunicites* (Fig. 3.3 K) preserve some evidence of the original musculature (Bracchi and Alessandrello 2005, Wilson *et al.* 2016), which is replicated by calcium phosphate. *Rollinschaeta myoplena* (Fig. 3.3 I), a fossil amphinomid, preserves extensive details of myoanatomy by early replacement by calcium phosphate, including segmentally arranged ventral circular muscles, a pair of ventral longitudinal muscles, and two pairs of dorsal longitudinal muscles, a condition that is thought to be restricted to Amphinomidae among extant taxa (Parry *et al.* 2015a)

## 3.3 Machaeridians

Machaeridians are an enigmatic group of armored polychaete worms with a fossil record from the Early Ordovician (Vinther *et al.* 2008) to the Permian (Hoare *et al.* 1996). They possess a unique calcitic dorsal armor (Fig. 3.6) of imbricating inner and outer shell plates that cover the dorsum (e.g., Plumulitidae; Fig. 3.6 A) or enclose the body (e.g., Turrilepadidae [Fig. 3.6 B] and Lepidocoleidae [Fig. 3.6 C]). Previously, machaeridians were a paleontological mystery, having been compared to echinoderms, barnacles, molluscs, and annelids (Withers 1926, Bengtson 1978, Jell 1979, Dzik 1986). The discovery of a specimen described as *Plumulites bengtsoni* from the Early Ordovician (Tremadocian) Fezouata Formation, Morocco (Vinther *et al.* 2008), demonstrated that machaeridians possessed serially repeated bundles of chaetae born on prominent biramous parapodia, confirming their identity as total group annelids (Fig. 3.6 A). It has been proposed that machaeridians are members of the annelid crown group (Vinther and Rudkin 2010) and can specifically be allied with scaleworms (Aphroditiformia). Evidence for this relationship includes a proposed homology of the shell plates with the elytrae of scaleworms, which are probably modified dorsal cirri (Glasby *et al.* 2008). The alternation pattern seen in the inner and outer shell plates is comparable with the alternating dorsal cirrus pattern seen in numerous families of Phyllodocida (Glasby *et al.* 2008), the more inclusive clade to which Aphroditiformia belongs. A position within the stem or crown of Aphroditiformia would greatly reduce the length of the Phyllodocidan ghost lineage, which otherwise extends to the latest Cambrian or Early Ordovician, given the appearance of euncidans, the phyllodocidan sister group (Struck *et al.* 2015, Parry *et al.* 2016), at this time (Fig. 3.1).

It has alternatively been proposed that machaeridians could be stem-group (rather than crown-group) annelids (Caron 2008), and resolution of macheridians nested in the annelid crown group was contingent on whether or not the homology of shell plates with dorsal cirri and elytrae was coded in a cladistic analyses (Vinther *et al.* 2008). However, referring machaeridians to the annelid stem group based on their possession of unique apomorphies (Caron 2008) is problematic, as assignment to a stem group should be justified by the presence of only a subset of the characters that define a given clade (Vinther and Rudkin 2010). Nevertheless, discovery of further specimens preserving soft tissues is necessary to resolve the precise phylogenetic position of machaeridians among annelids.

Machaeridians are typically studied as compression fossils (e.g., Vinther *et al.* 2008) or from isolated shell plates, particularly when silicified and extracted from rocks by acid maceration (e.g., Adrain *et al.* 1991). Computed tomography scanning can be a useful tool to extract further information from machaeridian fossils, exemplified by disarticulated specimens preserved as molds where little detail is visible from the bedding plane (Gügel *et al.* 2017) or in pyritized examples where the shell plates obscure soft tissues (Högström *et al.* 2009). Machaeridians are divided into three families, the Plumulitidae (Fig. 3.6 A), the Turrilepadidae (Fig. 3.6 B), and the Lepidocoleidae (Fig. 3.6 C). The machaeridian scleritome is typically composed of two sclerite series, the outer and inner shell plates. Machaeridian shell plates consist of two mineralized layers: an inner densely packed layer and a granulated surface layer (Bengtson 1978). This configuration has been observed in the Turrilepadidae and Lepidocoleidae (Bengtson 1978), as well as in the Plumulitidae (Vinther *et al.* 2008). The outer shell layer bears the prominent concentric rugae, which develop parallel to more

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fine growth lines and represent discrete growth intervals where additional plate material is added (Adrain *et al.* 1991). The inner layer possesses a fine, granular texture and bears an inner groove (Adrain *et al.* 1991, Vinther and Rudkin 2010), which has an unknown relationship with the attachment of soft tissues. The fine marginal spines occurring on the nonaccreting margin of the plates of turrilepadids and certain plumulitids (Adrain *et al.* 1991, Vinther *et al.* 2008) are probably also formed from the inner, rather than outer, plate layer as they are out of phase with both the growth lines and rugae.

Both inner and outer plates are present in all Plumulitidae and Turrilepadidae, but the outer sclerite series is retained only in some lepidocoleid taxa, such as *Lepidocoleus ketlayanus*. The presence of the outer shell plate series lepidocoleids is interpreted as a machaeridian plesiomorphy, and the loss of the outer plates is interpreted as an apomorphy of some members of Lepidocoleidae (Parry *et al.* 2014) (Fig. 3.6 E). This distinction is not currently reflected in the taxonomy of lepidocoleids, which are mostly assigned to the genus *Lepidocoleus*, and the family is likely in need of revision.

Morphologically distinct anterior plates have been described for plumulitids (Jell 1979, Vinther and Rudkin 2010) and turrilepadids (Adrain *et al.* 1991), but not for lepidocoleids. In turrilepadids and plumulitids, the anterior shell plates occur on two anterior segments. Two pairs of anterior plates have been described in detail for *Plumulites richorum* and *Plumulites canadensis* (see Vinther and Rudkin 2010), as well as the plate of the second segment in *Plumulites* cf. *taffaenensis* (see Vinther and Rudkin 2010). Based on the topology advocated by Vinther and Briggs (2009) and Parry *et al.* (2014), the absence of modified plates in the anterior region in lepidocoleids may also be apomorphic.

Turrilepadids and lepidocoleids have been proposed to form a clade (Cuniculepadida) to the exclusion of plumulitids in a preliminary cladistic analysis (Vinther *et al.* 2008) based on the ventro-lateral displacement of their shell plates, the presence of discrete muscle attachments, and lateral compression of the body, which is enclosed inside the scleritome (Parry *et al.* 2014) (Fig. 3.6 E). This enclosed scleritome configuration has been implicated as an adaptation to burrowing and an infaunal lifestyle (Vinther and Briggs 2009), which may have occurred in tandem with the reduction of the parapodial lobes in these families (Högström *et al.* 2009), a common trend among annelids that have transitioned from an epibenthic to infaunal mode of life (Westheide 1997).

The plumulitids, in contrast, have shell plates that are wholly dorsal and lack the muscular attachment present in the other families (Fig. 3.6 A). Given that the machaeridian-type scleritome is an autapomorphy of the group and that an epibenthic ancestor with well-developed parapodia is the likely plesiomorphic state for annelids as a whole (Westheide 1997, Eibye-Jacobsen 2004, Vinther *et al.* 2011, Eibye-Jacobsen and Vinther 2012, Parry *et al.* 2016), identifying a synapomorphy that supports the monophyly of Plumulitidae is difficult. The characters shared by species of *Plumulites* may in fact be machaeridian plesiomorphies, and therefore, Plumulitidae may be paraphyletic (Parry *et al.* 2014). Although the machaeridians are clearly monophyletic, united by their unique biserial scleritome (Vinther and Rudkin 2010), some of the currently recognized genera and families may be paraphyletic, and a comprehensive cladistic analysis of the group is necessary to assess the validity of the currently named machaeridian taxa.

## 3.4 Fossil jaw-bearing polychaetes

Among extant polychaetes, jaws are produced by all families in Eunicida, some families of Phyllodocida, and a few small species of Ampharetidae (Tzetlin and Purschke 2005). As they are more resistant to decay than other tissues (Briggs and Kear 1993), the sclerotized jaw elements of polychaetes are commonly preserved as microscopic fossils (Fig 3.4 A–G), which are known as scolecodonts. The preservation potential of different jaw types is controlled not only by their decay resistance (Briggs and Kear 1993) but also by their resistance to other taphonomic and subsequent diagenetic processes, which occur as sediments are transformed into rocks. By comparing the frequency with which jaws of different groups of polychaetes were recovered from recent sediments with predictions based on the population densities of those same groups, Colbath (1988) demonstrated that Glyceridae, Arabellidae (=Oenonidae), and Dorvilleidae have a high fossilization potential, whereas Onuphidae, Eunicidae, and Lumbrineridae were less likely to fossilize due to disaggregation of the mineral components of the jaws following degradation of the more weakly sclerotized cuticle. Although nereidid jaws have a high resistance to short-term decay, these jaws slowly degrade in sediments during diagenesis and only persist as subfossils (Colbath 1988). Older fossil jaws previously assigned to the Nereididae actually belong to different families such as Goniadidae and the extinct Paulinitidae (Szaniawski 1974). Currently, there is no known fossil record for the jaws of Nereididae or the closely related Nephtyidae (Szaniawski 1974) outside of

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Lagerstätten like Mazon Creek (Thompson 1979, Fitzhugh *et al*. 1997), which is likely driven by a difference in chemical composition between the jaws of these families and those of eunicidans and Goniadidae (Szaniawski 1974, Colbath 1988). The jaws of ampharetids have not been recognized as fossils, and if they do fossilize, then it is likely that they will be difficult to assign to the Ampharetidae with confidence given their lack of diagnostic features and rarity among extant taxa. The jaws of leeches have also not been described as fossils.

Eunicidan jaws are among the most numerous and most frequently preserved annelid fossils and can readily be recovered from marine rocks via acid maceration (Kielan-Jaworowska 1966, Bergman 1989, Hints and Eriksson 2007). Thus, rocks comprising ancient sea-floor sediments that are barren of macroscopic polychaete fossils can still contain scolecodonts in great abundance and diversity (up to several thousand specimens per kilogram of rock in productive lithologies). This also means that these microscopic remains might be the only evidence available for once thriving faunas, and therefore, they contribute greatly to our understanding of the evolutionary history, temporal, and geographic distribution of annelids. Eunicidan pharyngeal apparatuses may also be preserved as bedding plane assemblages (Fig. 3.4 A, C, D) (Eriksson and Bitter 2015), sometimes without original jaw material, where the fossils are preserved as molds (Fig. 3.4 D) (Eriksson *et al*. 2017). Eunicidan jaws are considerably more complex architecturally than those of other polychaetes, generally consisting of a pair of massive ventral mandibles and numerous hollow dorsal maxillae, which are numbered from the posterior to the anterior, and accessory elements (Fig. 3.5) (Paxton 2009). The pairwise maxillae vary in number, and the relative size between families and the apparatus can either be symmetrical or be asymmetrical (Paxton 2009). Six distinct jaw architectures are recognized (Fig. 3.5), but these architectures do not necessarily correspond to monophyletic groups, and taxa possessing two of these types, the placognath and ctenognath apparatus, are wholly extinct (Fig. 3.5) (Paxton 2009). Paxton (2009) defined six distinct types of jaw apparatuses: the placognath, ctenognath (including "xenognath"), prionognath, symmetrognath, labidognath, and eulabidognath type (Fig. 3.5). Taxa with labidognath jaws traditionally have included the extant families Onuphidae and Eunicidae and consist of jaws with dissimilar elements one each side, with the most posterior two pairs of maxillae surrounded by a semicircle of smaller elements. In Eunicidae and Onuphidae and Lumbrineridae, the first maxillary (MI) element (just anterior of the carriers) is forceps like and the elements of the left and the right side are linked at the base by ridges that form a locking hinge-like structure (Paxton 2009). Although the lumbrinerids show a condition similar to the Eunicidae and Onuphidae, the locking hinge structures and forceps-like jaws are not homologous. In Eunicidae and Onuphidae, the right outer "ridge" is actually a maxillary element (homologous with the MI of other eunicid jaws), which is referred to as the basal plate (bp) in the paleontological literature (Paxton 2009). Therefore, although eunicids + onuphids and lumbrinerids both possess forceps like MI, the elements forming the forceps themselves are not homologous between the two groups, as the forceps consist of three (maxillary) elements (the right two of which have fused; that is, the MI and bp) in the Onuphidae and Eunicidae, but only two elements (left and right MI) in the Lumbrineridae. The gradual reduction of the right MI (bp) and its eventual fusion to the right second maxilla (MII) in fossil labidognaths is documented in the fossil record, with end members exemplified by *Andiprion paxtonae,* where the right MI (or bp) is only slightly smaller than the left MI, and members of the Paulinitidae, such as *Kettnerites*, where the right MI forms the articulation structure of the right MII (or that the bp is fused with the right MI) (Hints *et al*. 2017). Taxa where the smaller right MI (bp) has fused are now referred to as the Eulabidognatha, which contains the extant labidognaths and the fossil family Paulinitidae (Figs. 3.4 H and 5) (Paxton 2009, Hints *et al*. 2017). Lumbrineridae were formerly considered part of the Labidognatha, but the similarities between this family and labidognaths are the result of convergence (Paxton 2009), and they differ also in the fact that the right and left jaw elements are symmetrical. Consequently, Paxton (2009) referred the Lumbrineridae (and Hartmaniellidae) to a new taxon, the Symmetrognatha. Lumbrinerids have a low fossilization potential (Colbath 1988), but Hartmaniellidae are known as fossils from the Carboniferous to Cretaceous (Szaniawski and Imajima 1996). Prionognath jaws are known among extant families from the Oenonidae, which are defined as jaws with approximately similar elements, arranged in parallel rows. Like labidognaths, prionognaths also have a right MI (bp) that is reduced in size relative to the left MI (Paxton 2009).

In ctenognath jaws, the elements are symmetrical to subsymmetrical, with posterior plate-like elements and four or more rows of small denticles and are found in extant polychaetes in the Dorvilleidae (Paxton 2009). Placognath jaws are similar in morphology to ctenognath jaws, possessing symmetrical to asymmetrical maxillae, plate-like posterior elements, and two anterior rows of denticles. The placognath jaws are known only from fossil taxa and, together with the ctenognath jaws, are the oldest known

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from the fossil record (Hints and Eriksson 2007). Dorvilleidae (the extant placognaths) are currently recovered as the sister group of all other extant Eunicida (Fig. 3.4 H) based on both morphological (Parry *et al.* 2016) and molecular (Struck *et al.* 2015) data, which, together with the ancient first appearance of the ctenognath apparatus, suggests that this jaw morphology is plesiomorphic for Eunicida. The placognath-type apparatus may belong to members of the eunicidan stem group, as in the topology suggested by Paxton (2009) that is most congruent with current understanding of eunicidan phylogeny (Fig. 3.4 H). Likewise, some ctenognath fossil taxa may represent stem eunicidans, a stem group of the nondorvilleid eunicidans or stem group dorvilleids, rather than all belonging to a clade that contains extant Dorvilleidae. There is currently no cladistic analysis of eunicidans incorporating scolecodont fossils, but a cladogram summarizing possible relationships (mostly following the hypothesis of Paxton 2009) is provided in Fig. 4 H. As the sequence of character evolution leading to the extant families and due to the imprecise phylogenetic placement of the fossil taxa, identifying the oldest crown group Eunicida is difficult. Consequently, the oldest fossils that can be confidently assigned to the eunicidan crown are the Polychaetaspidae (Labidognatha), as regardless of the precise relationships of other fossil taxa, the labidognath condition is clearly apomorphic (Paxton 2009, Hints *et al.* 2017). This suggests that crown group Eunicida is at least Middle Ordovician in age but is likely to be older (Fig. 3.1).

As the majority of jaws are recovered as isolated elements (e.g., Fig. 3.4 B, D, E) (rather than complete apparatuses or clusters), historical work on scolecodonts resulted in the erection of many form taxa, with individual names applied to elements belonging to the same animal (Eriksson and Bergman 1998). This situation was further complicated when Lange (1947) described many articulated scolecodont apparatuses without linking this work to previously erected form taxa based on isolated elements. As a result, there were two taxonomic systems for polychaete jaws in simultaneous use, one based on real biological entities and another of form taxa. For example, *Kettnereites invisibilis* (see Eller 1940) was originally described as five genera and eight species (Bergman 1991). Although form taxonomy persisted for much of the twentieth century, more recent work has aimed to focus on reconstructing and naming complete apparatuses and integrating apparatus-based and single-element-based taxa when possible (see Eriksson and Bergman 1998). Where the elements are fused or where apparatuses and elements are preserved on bedding planes, not all taxonomically important features may necessarily be easily visible, and so study of isolated elements in addition to articulated examples is important for reconstructing the morphology of individual elements as well as the relative proportions of maxillae. Although the use of 3D computed tomography has become widespread in paleontology (Rahman *et al.* 2012), this technique has only recently been applied to scolecodonts (Fig. 3.4 E), where it is especially useful when the specimens are preserved only as molds and so cannot be extracted via acid maceration (Eriksson *et al.* 2017).

The scolecodont fossil record has proven to be a useful resource for understanding the evolution of jaw morphology and diversity within Eunicida. In particular, the fossil record demonstrates that eunicidan diversity was greater in the past, with the seven extant families contrasted with the 15–20 known from the fossil record (Hints and Eriksson 2007, Paxton 2009). The oldest scolecodont fossils are documented from the latest Cambrian (Furongian, 497–485.4 Ma) (Williams *et al.* 1999) from a single occurrence in Newfoundland, but eunicidans did not become abundant and diverse until the Middle Ordovician (Hints and Eriksson 2007). Unfortunately, the Cambrian specimens have since been lost (Hints and Eriksson 2007), and the occurrence of scolecodonts elsewhere during this time period is yet to be confirmed. Most scolecodont research has been focused on the lower Paleozoic rock record, and therefore, the Ordovician through Devonian jaw-bearing polychaetes are most well known (e.g., Eriksson *et al.* 2004, 2013, Hints and Eriksson 2007, Tonarovà *et al.* 2016), whereas the remainder of the Phanerozoic is more patchy and in need of more in-depth investigations. As well as revealing extinct diversity, diversification events (Hints and Eriksson 2007), palaeobiogeographic distribution (origination and migration), patterns (Eriksson *et al.* 2013), and character evolution (Paxton 2009, Paxton and Eriksson 2012, Hints *et al.* 2017), the scolecodont fossil record also reveals convergence between extinct and extant taxa. For example, the recently described labidognath *Websteroprion armstrongi* (Fig. 3.4 D, E) from the Devonian of Ontario attained a body size in excess of 1 m, which is unique in the fossil record and comparable to extant giant eunicidans, but it is only distantly related to the extant onuphids and eunicids (Eriksson *et al.* 2017).

Phyllodocidan jaws first occur as part of whole-body fossils in the Carboniferous, representing a number of families (Schram 1979, Thompson 1979) but are more rarely described as isolated jaws from acid digested rocks compared with eunicidans. Jaws of Glyceridae (Fig. 3.4 G) are the only phyllodocidan scolecodonts that are common in the rock record, first appearing in the late Palaeozoic (Fig. 3.1) and frequently in the Mesozoic (Szaniawski 1974, Nakrem *et al.* 2001). The macrognaths of Goniadidae have

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been described as isolated fossils from the Triassic and Creteaceous (Szaniawski 1974), but this family first occurs as body fossils in much older rocks in the Mississippian (early Carboniferous) (Schram 1979, Böggemann 2006).

## 3.5 Tube worms

Secretion of an external dwelling tube is a common trait among polychaetes, which has evolved in both sedentary and errant clades independently. The materials used to construct these tubes and the manner of secretion vary widely between taxa from organic materials like chitin and proteins (Merz 2015) agglutination of sediment grains and shell material (e.g., some Onuphidae and Oweniidae; Uchman *et al.* 2017) and calcium carbonate (e.g., Serpulidae; Ippolitov *et al.* 2014, Merz 2015). Use of chitin in tube building is taxonomically widespread as it is present in vestimentiferans (Ravaux *et al.* 2000), oweniids, and spionids (Guggolz *et al.* 2015) but is not present in chaetopterids as is often assumed (Georgieva *et al.* 2017).

Polychaete tubes perform a variety of functions, ranging from providing protection from predators and hostile environments to elevation and support to assist in feeding (Merz 2015). Although tube building enhances the preservation potential of a given taxon, agglutinated and mud/mucous tubes are comparatively rare in the fossil record, which is dominated by tubes constructed of calcium carbonate (Ippolitov *et al.* 2014). Among extant annelids, Serpulidae are the dominant builders of calcareous tubes, which otherwise occurs in only a single genus in both Cirratulidae and Sabellidae (see Ippolitov *et al.* 2014).

The use of similar tube building materials and construction methods in distantly related taxa makes identifying fossil tubes even to family level challenging, and fossil tubes are often assigned affinities to extant annelid families based on extremely limited evidence. In some cases, tubes that likely belong to other phyla have been assigned to various annelid groups, obscuring the true evolutionary history of extant families, often making them appear far older (Taylor and Vinn 2006, Vinn and Mutvei 2009, Vinn and Zaton 2012). Detailed analysis of ultrastructure is often necessary to confidently assign fossil to their correct branches in the tree of life, particularly in very ancient examples (Vinn and Zaton 2012).

Macroscopic fossils of tubular organisms first appeared in the Ediacaran period, but the systematic placement of these fossils is controversial, and those that can be placed in extant animal clades with the highest confidence are total group cnidarians (Vinn and Zaton 2012, Cunningham *et al.* 2017). *Cloudina* is one of the oldest plausible animal fossils to secrete a mineralized skeleton and has historically been compared with serpulid polychaetes (Glaessner 1976, Vinn and Zaton 2012). However, the granular tube microstructure and gross morphology suggest that *Cloudina* is not closely related to any calcareous tube-building polychaetes (e.g., Serpulidae, Cirratulidae, and Sabellidae) (Vinn and Zaton 2012), and the lack of a flattened attachment surface contrasts with most serpulid genera, with the exception of *Ditrupa* (see Ten Hove and Smith 1990, Vinn and Zaton 2012). Furthermore, the presence of closed tube bases and daughter tubes with approximately equal diameter following asexual reproduction is a character consistent more with a cnidarian, rather with than annelid affinity (Vinn and Zaton 2012).

*Sabellidites cambriensis* is another late Ediacaran fossil that has been assigned to Annelida, more specifically to Siboglinidae (Moczydłowska *et al.* 2014). The assignment of this Neoproterozoic fossil to Siboglinidae has been challenged, however, and fossils that can confidently be assigned to siboglinids are only as old as the Jurassic (Georgieva *et al.* 2017). Furthermore, siboglinids are deeply nested within annelids based on morphology and molecular data (Rouse and Fauchald 1997, Struck *et al.* 2011, Parry *et al.* 2016), and so an annelid affinity for *S. cambriensis* would necessitate at least a Neoproterozoic age for the annelid crown group, which is not supported by the occurrence of only stem group annelids in the Cambrian (Parry *et al.* 2014) nor by molecular clock analyses (Erwin *et al.* 2011).

During the Palaeozoic, there are many other groups of tubular organisms, some of which have historically been considered fossil annelids. This includes taxa that have been assigned to Serpulidae but are now recognized as Palaeozoic imposters (Vinn and Mutvei 2009). These "pseudoserpulid" (Ippolitov *et al.* 2014) taxa include the microconchids and cornulitids, which first appeared in the Ordovician and have been compared to serpulids based on their calcareous, tubular shells. Detailed analysis of the ultrastructure of these taxa reveals similarities with lophophorates, such as shell microstructure (Taylor and Vinn 2006, Vinn and Mutvei 2009, Taylor *et al.* 2010). The most strikingly serpulid–like characteristics of such fossils are small spiral worm tubes that are similar in gross morphology to extant spirorbins, which occurred from the Ordovician to Jurassic (Taylor and Vinn 2006). Analysis of the tube ultrastructure of Devonian – Triassic *Spirorbis* fossils revealed key differences between these ancient tubes and true serpulids. These characters include closed tube bases (in contrast to serpulids, where the tube origin is open), the absence of chevron-shaped

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growth increments, and the presence of a lamellar microstructure and pores, neither of which is present in recent *Spirorbis* nor other serpulids (Taylor and Vinn 2006). Tubes that can confidently be assigned to spirobin serpulids did not appear until the Cretaceous, and the older specimens are now included in the Microconchida (Taylor and Vinn 2006), a group that is currently interpreted as an extinct group of lophophorates, possibly stem-group phoronids (Taylor *et al.* 2010). The misidentification of these Palaeozoic tubes as serpulids resulted in a range extension for this group of hundreds of millions of years, which would have nontrivial implications for macroevolutionary studies of annelids, such as use of the serpulid fossil record for molecular clock calibration.

The oldest calcareous tube fossils that can be assigned to annelids belong to the Sabellid genus *Glomerula* (an example of Cretaceous age is shown in Fig. 3.7 A), which occurs from the late Carboniferous (Hoare *et al.* 2002, Ippolitov *et al.* 2014). The fossil record of true serpulids extends at least to the early Mesozoic, with possible occurrences in the Permian (Ippolitov *et al.* 2014, Sanfilippo *et al.* 2016). Serpulids became broadly distributed by the Late Triassic, a time period in which they also began to construct reefs (Braga and Lopez-Lopez 1989). The fossil record and diversification of serpulids were reviewed extensively by Ippolitov *et al.* (2014), and an example of fossil serpulid is shown in Fig. 3.7 B. Calcareous cirratulid tubes were also known as fossils from the late Oligocene onward and were identified by a microstructure that is distinct from that of sabellidans (Fischer *et al.* 2000), and so all of the calcareous tube building groups of extant polychaetes are known from the fossil record (Fig. 3.1), which is a testament to the high preservation potential of these structures.

Worm tubes from fossilized hydrothermal vent communities are found in rocks at least as old as the Silurian or possibly the late Ordovician (Georgieva *et al.* 2017). Although their paleoenvironmental occurrence invites an obvious comparison with extant siboglinids, identifying these tubes to any taxonomic level is extremely difficult (Georgieva *et al.* 2017). Nevertheless, tubes that have less ambiguous siboglinid affinities are at least Mesozoic in age (Georgieva *et al.* 2017), and borings on plesiosaur and sea turtle bones that are comparable with modern *Osedax* borings have been found in the Late Cretaceous (Danise and Higgs 2015). Both of these discoveries suggest that Siboglinidae had diversified by at least the Mesozoic.

The fossil record of agglutinated tubes is sparse, and identification of agglutinated tubes is hampered by a lack of diagnostic characters. In an extreme example, the families Oweniidae, Onuphidae, and Terebellidae have all been implicated as tracemakers of the fossil *Diopatrichnus* (Uchman *et al.* 2017), which are families that bracket the extant diversity of annelids. This fossil is currently interpreted as having been constructed by Oweniidae (see Uchman *et al.* 2017). Nevertheless, some fossil agglutinated tubes can be more easily attributed to extant families, such as an agglutinated tube assigned to the Pectinariidae from the Late Cretaceous (Santonian, ~84 Ma) by Vinn and Luque (2013).

## 3.6 The clitellate fossil record

The origin of clitellates is obscure from a paleontological point of view, as the majority of clitellates live in freshwater or terrestrial environments and so have an extremely limited preservation potential. Clitellate fossils are known, however, but their record is limited to fossil cocoons, which occurred in palynological samples from the Middle Triassic onward (Manum *et al.* 1991) and to rare reports of burrows of earthworms, the oldest of which are also of Triassic age (Retallack 1976). Although leech cocoons are of limited taxonomic value (and, thus, their fossils mostly have limited potential to inform the timing of cladogenesis within leeches), these cocoons sometimes have inclusions in the cocoon wall that preserve fossils of other organisms, occasionally in great detail. Such fossils have included a nematode with the gut, cuticle, and chaetae preserved (Manum *et al.* 1994) and a ciliate that is similar to the extant "bell animal" *Vorticella* (see Bomfleur *et al.* 2012). A remarkable example has been described from the early Eocene (~50 Ma) that preserves various inclusions interpreted as fossilized spermatozoans. These inclusions are 18 µm long by approximately 600 nm wide, with a conspicuous helical "drill bit" structure (see Bomfleur *et al.* 2015). This helical structure is closely comparable to the acrosome of *Branchiobdella*, which are the longest known in nature (Ferraguti and Erséus 1999, Bomfleur *et al.* 2015). Curiously, extant branchiobdellans are limited in geographic range to the northern hemisphere, but these fossil cocoons occur in Antarctica, and so their correct identification implies either a large contraction or shift in branchiobdellan biogeography (Bomfleur *et al.* 2015).

## 3.7 References

Adrain, J.M. (1992): Machaeridian Classification. *Alcheringa* 16: 15–32.

Adrain, J.M., Chatterton, B.D.E. & Cocks, L.R.M. (1991): A new species of machaeridian from the Silurian of Podolia, USSR, with a review of the Turrilepadidae. *Palaeontology* 34: 637–651.

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Barthel, K.W., Swinburne, N.H.M. & Conway Morris, S. (1990): *Solnhofen* (CUP Archive). Cambridge University Press, Cambridge.

Bengtson, S. (1978): The Machaeridia – a square peg in a pentagonal hole. *Thalassia Jugoslavica* 12: 1–10.

Bergman, C.F. (1989): Silurian paulinitid polychaetes from Gotland. *Fossils and Strata* 25: 1–128.

Bergman, C.F. (1991): Revision of some Silurian paulinitid scolecodonts from Western New York. *Journal of Paleontology* 65: 248–254.

Bergman, C.F. (1998): Reversal in some fossil polychaete jaws. *Journal of Paleontology* 72: 632–638.

Bergman, C.F. & Eriksson, M.E. (2003): Scolecodonts from the Upper Danian (Paleocene) of Skåne, Sweden. *GFF* 125: 163–167.

Bitter, P.H. von, Purnell, M.A., Tetreault, D.K. & Stott, C.A. (2007): Eramosa Lagerstätte–exceptionally preserved soft-bodied biotas with shallow-marine shelly and bioturbating organisms (Silurian, Ontario, Canada). *Geology* 35: 879–882.

Böggemann, M. (2006): Worms that might be 300 million years old. *Marine Biology Research* 2(2): 130–135.

Böggemann, M. & Eibye-Jacobsen, D. (2002): The Glyceridae and Goniadidae (Annelida: Polychaeta) of the BIOSHELF Project, Andaman Sea, Thailand. *Phuket Marine Biological Center, Special Publication* 24: 149–196.

Bomfleur, B., Kerp, H., Taylor, T.N., Moestrup, O. & Taylor, E.L. (2012): Triassic leech cocoon from Antarctica contains fossil bell animal. *Proceedings of the National Academy of Sciences of the United States of America* 109: 20971–20974.

Bomfleur, B., Mörs, T., Ferraguti, M., Reguero, M.A. & McLoughlin, S. (2015): Fossilized spermatozoa preserved in a 50-yr-old annelid cocoon from Antarctica. *Biology Letters* 11: 20150431.

Bracchi, G. & Alessandrello, A. (2005): Paleodiversity of the Free-Living Polychaetes (Annelida, Polychaeta) and Description of New Taxa from the Upper Cretaceous Lagerstätten of Haqel, Hadjula and Al-Namoura (Lebanon). *Memoires Società italiana di scienze naturali, Museo di storia naturale Milano* 32: 1–64.

Braga, J.C. & Lopez-Lopez, J.R. (1989): Serpulid Bioconstructions at the Triassic-Liassic Boundary in Southern Spain. *Facies* 21: 1–9.

Briggs, D.E.G. & Bartels, C. (2010): Annelids from the lower Devonian Hunsrück Slate (lower Emsian, Rhenish Massif, Germany). *Palaeontology* 53: 215–232.

Briggs, D.E.G. & Kear, A.J. (1993): Decay and preservation of polychaetes; taphonomic thresholds in soft-bodied organisms. *Paleobiology* 19: 107–135.

Budd, G. E. & Jensen, S. (2000): A critical reappraisal of the fossil record of the Bilaterian phyla. *Biological Reviews of the Cambridge Philosophical Society* 75: 253–95.

Butterfield, N.J. (1990): A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology* 16: 287–303.

Butterfield, N.J. (2006): Hooking some stem-group "worms": fossil lophotrochozoans in the Burgess Shale. *BioEssays* 28: 1161–1166.

Butterfield, N.J. & Harvey, T.H.P. (2012): Small carbonaceous fossils (Scfs): a new measure of early Paleozoic paleobiology. *Geology* 40: 71–74.

Caron, J.-B. (2008): Palaeontology: ancient worms in armour. *Nature* 451: 133–34.

Caron, J.-B., Gaines, R.R., Mángano, M.G., Streng, M. & Daley, A.C. (2010): A new Burgess Shale-type assemblage from the "thin" Stephen formation of the Southern Canadian Rockies. *Geology* 38: 811–14.

Colbath, K.G. (1988): Taphonomy of recent polychaete jaws from Florida and Belize. *Micropaleontology* 34: 83–89.

Conway Morris, S. (1979): Middle Cambrian polychaetes from the Burgess Shale of British Columbia, *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences* 285: 227–74.

Conway Morris, S. (1985): The middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and ogygopsis shale, British Columbia, Canada. *Phil. Trans. R. Soc. Lond. B* 307: 507–82.

Conway Morris, S. & Caron, J-B. (2007): Halwaxiids and the early evolution of the Lophotrochozoans. *Science* 315: 1255–58.

Conway Morris, S. & Peel, J.S. (1995): Articulated halkieriids from the lower Cambrian of North Greenland and their role in early protostome evolution. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 347: 305–58.

Conway Morris, S. & Peel, J.S. (2008): The earliest annelids: lower Cambrian polychaetes from the Sirius Passet Lagerstatte, Peary Land, North Greenland. *Acta Palaeontologica Polonica* 53: 135–46.

Cunningham, J.A., Liu, A.G., Bengtson, S. & Donoghue, P.C.J. (2017): The origin of animals: can molecular clocks and the fossil record be reconciled? *Bioessays* 39: 1–12.

Danise, S. & Higgs, N.D. (2015): Bone-eating osedax worms lived on Mesozoic marine reptile deadfalls. *Biology Letters* 11: 20150072.

Dzik, J. (1986): Turrilepadida and other Machaeridia. *Problematic Fossil Taxa* 5: 116–34.

Eibye-Jacobsen, D. (2004): A reevaluation of *Wiwaxia* and the polychaetes of the Burgess Shale. *Lethaia* 37: 317–35.

Eibye-Jacobsen, D. & Vinther, J. (2012): Reconstructing the ancestral annelid. *Journal of Zoological Systematics and Evolutionary Research* 50: 85–87.

Eller, E.R. (1940): New Silurian scolecodonts from the Albion Beds of the Niagara Gorge, New York. *Annals of the Carnegie Museum* 28: 9–46.

Eriksson, M.E. & Bergman, C.F. (1998): Scolecodont systematics exemplified by the polychaete *Hadoprion cervicornis* (Hinde, 1879). *Journal of Paleontology* 72: 477–85.

Eriksson, M.E., Bergman, C.F. & Jeppsson, L. (2004): Silurian scolecodonts. *Review of Palaeobotany and Palynology*, *131*(3–4), pp. 269–300.

Eriksson, M.E., & Bitter, P.H. von (2015): Jaw-bearing polychaetes of the Silurian Eramosa Lagerstätte, Ontario, Canada. *Journal of Paleontology* 89: 222–35.

Eriksson, M.E., Grahn, Y., Bosetti, E. & Vega, C.S. (2011): Chapter 4: Malvinokaffric realm polychaetes from the Devonian Ponta Grossa formation, Paraná Basin (southern Brazil), with a discussion and re-evaluation of the species described by Lange. *In* Bosetti, E.P., Grahn, Y. and Melo, J.H.G. (eds.): *Essays in Honour of Federico Waldemar Lange – Pioneer of Brazilian Micropaleontology*, p. 118–150. Petrobras, Editora Interciência Ltda., Brazilian Paleontological Society. Also in Portuguese in the same volume.

Eriksson, M.E., Hints, O., Paxton, H. & Tonarová, P. (2013): Ordovician and Silurian polychaete diversity and biogeography. *Geological Society. London, Memoirs*, 38(1), pp. 265–272.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Eriksson, M.E, Parry, L.A. & Rudkin, D.M. (2017): Earth's oldest 'Bobbit worm' – gigantism in a Devonian eunicidan polychaete. *Scientific Reports* 7: 43061.

Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D. & Peterson, K.J. (2011): The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* 334: 1091–97.

Farrell, U.C. & Briggs, D.E.G. (2007): A pyritized polychaete from the Devonian of Ontario. *Proceedings of the Royal Society B-Biological Sciences* 274: 499–504.

Ferraguti, M. & Erséus, C. (1999): Sperm types and their use for a phylogenetic analysis of aquatic clitellates. *Hydrobiologia* 402: 225–37.

Fischer, R., Pernet, B. & Reitner, J. (2000): Organomineralization of cirratulid annelid tubes – fossil and recent examples. *Facies* 42: 35.

Fitzhugh, K., Sroka, S., Kruty, M.D., Henderson, A.A. & Hay, A.A. (1997): Polychaete worms. *Richardson's Guide to the Fossil Fauna of Mazon Creek*: 64–83.

Gehling, J.G., Runnegar, B.N. & Droser, M.L. (2014): Scratch traces of large Ediacara bilaterian animals. *Journal of Paleontology* 88: 284–98.

Georgieva, M.N., Little, C.T.S., Watson, J.S., Sephton, M.A., Ball, A.D. & Glover, A.G. (2017): Identification of fossil worm tubes from phanerozoic hydrothermal vents and cold seeps. *Journal of Systematic Palaeontology*: 1–43.

Glaessner, M.F. (1976): Early Phanerozoic annelid worms and their geological and biological significance. *Journal of the Geological Society* 132: 259–75.

Glasby, C.J., Glasby, S.P. & Pleijel, F. (2008): Worms by number. *Proceedings of the Royal Society B: Biological Sciences* 275: 2071–76.

Glasby, C.J., Hutchings, P.A., Fauchald, K., Paxton, H., Rouse, G.W., Watson Russell, C. & Wilson, R.S. (2000): Class polychaeta. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (eds.), *Polychaetes & Allies: The Southern Synthesis*. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing: Melbourne xii, pp. 1–296.

Gordon, D.P. (1975): The resemblance of bryozoan gizzard teeth to annelid-like setae. *Acta zoologica* 56: 283–89.

Gügel, B., De Baets, K., Jerjen, I., Schuetz, P. & Klug, C. (2017): A new subdisarticulated machaeridian from the Middle Devonian of China: insights into taphonomy and taxonomy using x-ray microtomography and 3D-analysis. *Acta Palaeontologica Polonica* 62: 237–47.

Guggolz, T., Henne, S., Politi, Y., Schütz, R., Mašić, A., Müller, C.H.G. & Meißner, K. (2015): Histochemical evidence of B-chitin in parapodial glandular organs and tubes of Spiophanes (Annelida, Sedentaria: Spionidae): and first studies on selected Annelida. *Journal of Morphology* 276: 1433–47.

Hay, A.A. (2002): Flabelligerida from the Francis Creek shale of Illinois. *Journal of Paleontology* 76: 764–66.

Hints, O. & Eriksson, M.E (2007): Diversification and biogeography of scolecodont-bearing polychaetes in the Ordovician. *Palaeogeography Palaeoclimatology Palaeoecology* 245: 95–114.

Hints, O., Tonarová, P., Eriksson, M.E., Rubinstein, C.V. & Puente, G.S. (2017): Early middle Ordovician scolecodonts from North-Western Argentina and the emergence of labidognath polychaete jaw apparatuses. *Palaeontology* 60: 583–93.

Hoare, R.D., Mapes, R.H. & Yancey, T.E. (2002): Structure, taxonomy, and epifauna of Pennsylvanian rostroconchs (Mollusca). *Journal of Paleontology* 76: 1–30.

Hoare, R.D., Mapes, R.H., Yancey, T.E. & Nestell, M.K. (1996): Late Paleozoic turrilepadid machaeridians from North America. *Acta Palaeontologica Polonica* 41: 127–45.

Hoekzema, R.S., Brasier, M.D., Dunn, F.S. & Liu, A.G. (2017): Quantitative study of developmental biology confirms *Dickinsonia* as a metazoan. *Proc. R. Soc. B* 284: 20171348.

Högström, A.E.S., Briggs, D.E.G. & Bartels, C. (2009): A pyritized lepidocoleid machaeridian (Annelida) from the lower Devonian Hunsrück Slate, Germany. *Proceedings of the Royal Society B: Biological Sciences* 276: 1981–86.

Huang, D. Y., Chen, J.Y., Vannier, J. & Salinas, J.I.S. (2004): Early Cambrian sipunculan worms from Southwest China. *Proceedings of the Royal Society B-Biological Sciences* 271: 1671–76.

Ippolitov, A. Vinn, O., Kupriyanova, E. & Jäger, M. (2014): *Written in Stone: History of Serpulid Polychaetes through Time*. Vol. 71 (*Memoirs of Museum Victoria*).

Jell, P.A. (1979): Plumulites and the machaeridian problem. *Alcheringa* 3: 253–59.

Kielan-Jaworowska, Z. (1966): Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. *Palaeontologia Polonica* 16: 1–152.

Lange, F.W. (1947): Anelideos Poliquetos Dos Folhelhos Devonianos Do Paraná. *Bulletins of American Paleontology* 33: 5–103.

Liu, J., Ou, Q., Han, J., Li, J., Wu, Y., Jiao, G. & He, T. (2015): Lower Cambrian polychaete from China sheds light on early annelid evolution. *The Science of Nature* 102: 1–7.

Lüter, C. (2000): Ultrastructure of larval and adult setae of Brachiopoda. *Zoologischer Anzeiger* 239: 75–90.

Mángano, M.G. & Buatois, L.A. (2014): Decoupling of body-plan diversification and ecological structuring during the Ediacaran-Cambrian transition: evolutionary and geobiological feedbacks. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140038.

Manum, S.B., Bose, M.N. & Sawyer, R.T. (1991): Clitellate cocoons in freshwater deposits since the Triassic. *Zoologica Scripta*, 20(4), pp. 347–366.

Manum, S.B., Bose, M.N., Sayer, R.T. & Boström, S. (1994): A nematode (*Captivonema cretacea* gen. et sp. n.) preserved in a clitellate cocoon wall from the Early Cretaceous. *Zoologica Scripta*, 23(1), pp. 27–31.

Martin, A.J. & Rindsberg, A.K. (2007): Arthropod tracemakers of nereites? Neoichnological observations of juvenile limulids and their paleoichnological applications in *Trace Fossils* (Elsevier): 478–91.

Martin, M.W., Grazhdankin, D.V., Bowring, S.A., Evans, D.A.D., Fedonkin, M.A. & Kirschvink, J.L. (2000): Age of Neoproterozoic bilatarian body and trace fossils, White Sea, Russia: implications for Metazoan evolution. *Science* 288: 841–45.

Merz, R.A. (2015): Textures and traction: how tube-dwelling polychaetes get a leg up. *Invertebrate Biology* 134: 61–77.

Moczydłowska, M., Westall, F. & Foucher, F. (2014): Microstructure and biogeochemistry of the organically preserved Ediacaran metazoan *Sabellidites*. *Journal of Paleontology* 88: 224–39.

Nakrem, H.A., Szaniawski, H. & Mork, A. (2001): Permian-Triassic scolecodonts and conodonts from the Svalis Dome, Central Barents Sea, Norway. *Acta Palaeontologica Polonica* 46: 69–86.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Nanglu, K. & Caron, J-B. (2018): A new Burgess Shale polychaete and the origin of the annelid head revisited. *Current Biology* 28: 319–26. e1.

Nielsen, C. (1991): The development of the brachiopod *Crania (Neocrania) Anomala* (of Müller) and its phylogenetic significance. *Acta Zoologica* 72: 7–28.

Orrhage, L. & Müller, M.C.M. (2005): Morphology of the nervous system of polychaeta (Annelida) in *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa* (Springer): 79–111.

Parry, L.A., Boggiani, P.C., Condon, D.J., Garwood, R.J., Leme, J.D.M., McIlroy, D., Brasier, M.D., Trindade, R., Campanha, G.A., Pacheco, M.L. & Diniz, C.Q. (2017): Ichnological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. *Nature Ecology & Evolution* 1: 1455.

Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D. & Vinther, J. (2016): The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society B* 283: 20161378.

Parry, L.A., Smithwick, F., Nordén, K.K., Saitta, E.T., Lozano-Fernandez, J., Tanner, A.R., Caron, J.B., Edgecombe, G.D., Briggs, D.E. & Vinther, J. (2018): Soft-bodied fossils are not simply rotten carcasses – toward a holistic understanding of exceptional fossil preservation, *BioEssays* 40.

Parry, L., Tanner, A. & Vinther, J. (2014): The origin of annelids. *Palaeontology* 57: 1091–103.

Parry, L., Vinther, J. & Edgecombe, G.D. (2015b): Cambrian stem-group annelids and a metameric origin of the annelid head. *Biology Letters* 11: 20150763.

Parry, L.A., Wilson, P., Sykes, D., Edgecombe, G.D. & Vinther, J. (2015a): A new fireworm (Amphinomidae) from the Cretaceous of Lebanon identified from three-dimensionally preserved myoanatomy. *BMC Evolutionary Biology* 15: 256.

Paxton, H. (2009): Phylogeny of Eunicida (Annelida) based on morphology of jaws. *Zoosymposia* 2: 241–64.

Paxton, H. & Eriksson, M.E. (2012): Ghosts from the past – ancestral features reflected in the jaw ontogeny of the polychaetous annelids *Marphysa fauchaldi* (Eunicidae) and *Diopatra aciculata* (Onuphidae). *GFF* 134: 309–16.

Rahman, I.A., Adcock, K. & Garwood, R.J. (2012): Virtual fossils: a new resource for science communication in paleontology, *Evolution: Education and Outreach* 5: 635–41.

Ravaux, J., Chamoy, L. & Shillito, B. (2000): Synthesis and maturation processes in the exoskeleton of the vent worm *Riftia pachyptila*. *Marine Biology* 136: 505–12.

Retallack, G.J. (1976): Triassic palaeosols in the Upper Narrabeen Group of New South Wales. Part I: features of the palaeosols, *Journal of the Geological Society of Australia* 23: 383–99.

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

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

Sanfilippo, R., *et al.* (2016): A new tubeworm of possible serpulid affinity from the permian of Sicily. *Acta Palaeontologica Polonica* 61: 621–26.

Schiemann, S.M., *et al.* (2017): Clustered brachiopod Hox genes are not expressed collinearly and are associated with lophotrochozoan novelties. *Proceedings of the National Academy of Sciences*: 201614501.

Schram, F.R. (1979): Worms of the Mississippian Bear Gulch limestone of Central Montana, USA. *Transactions of the San Diego Society of Natural History* 19: 107–20.

Slater, B.J., Harvey, T.H.P., Guilbaud, R. & Butterfield, N.J. (2017): A cryptic record of Burgess Shale-type diversity from the early Cambrian of Baltica. *Palaeontology* 60: 117–40.

Smith, M.R. (2012): Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences*: rspb20121577.

Sperling, E.A. & Vinther, J. (2010): A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolution & development* 12: 201–09.

Sperling, E.A., Vinther, J., Moy, V. M., Wheeler, B. M., Semon, M., Briggs, D. E. G. & Peterson, K. J. (2009): MicroRNAs resolve an apparent conflict between annelid systematics and their fossil record. *Integrative and Comparative Biology* 276: 4315–22.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–99.

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–U113.

Sutton, M.D., Briggs, D.E.G., Siveter, D.J. & Siveter, D.J. (2001): A three-dimensionally preserved fossil polychaete worm from the silurian of Herefordshire, England. *Proceedings of the Royal Society B: Biological Sciences*: 2355–63.

Szaniawski, H. (1974): Some Mesozoic scolecodonts congeneric with recent forms. *Acta Palaeontologica Polonica* 19: 179–99.

Szaniawski, H. & Imajima, M. (1996): Hartmaniellidae–living fossils among polychaetes. *Acta Palaeontologica Polonica* 41: 111–25.

Taylor, P.D. & Vinn, O. (2006): Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications. *Journal of the Geological Society* 163: 225–28.

Taylor, P.D., Vinn, O. & Wilson, M.A. (2010): Evolution of biomineralisation in lophophorates'. *Special Papers in Palaeontology* 84: 317–33.

Ten Hove, H.A. & Smith, R.S. (1990): A re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a discussion of the genus. *Records of the Australian Museum* 42: 101–18.

Thompson, I. (1979): Errant polychaetes (Annelida) from the Pennsylvanian Essex Fauna of Northern Illinois. *Palaeontographica Abteilung A* 163: 169–99.

Thompson, I. & Johnson, R.G. (1977): *New Fossil Polychaete from Essex, Illinois* (Field Museum of Natural History).

Tzetlin, A. & Purschke, G.(2005): Pharynx and intestine in *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa* (Springer): 199–225.

Tonarová, P., Hints, O., Königshof, P., Suttner, T.J., Kido, E., Da Silva, A.C. & Pas, D. (2016). A Middle Devonian jawed polychaete fauna from the type Eifel area, western Germany, and its biogeographical and evolutionary affinities. *Papers in Palaeontology,* 2(2): 295–310.

Uchman, A., Quintino, V., Rodrigues, A.M., Johnson, M.E., Melo, C.S., Cordeiro, R., Ramalho, R.S. & Ávila, S.P. (2017): The trace fossil *Diopatrichnus santamariensis* Nov. Isp. – a shell armored

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tube from Pliocene sediments of Santa Maria Island. Azores (Ne Atlantic Ocean), *Geobios* 50: 459–69.
Vannier, J., Calandra, I., Gaillard, C. & Żylińska, A. (2010): Priapulid worms: pioneer horizontal burrowers at the Precambrian-Cambrian boundary. *Geology* 38: 711–14.
Vinn, O. & Luque, J. (2013): First record of a Pectinariid-like (Polychaeta, Annelida) agglutinated worm tube from the Late Cretaceous of Colombia. *Cretaceous Research* 41: 107–10.
Vinn, O. & Mutvei, H. (2009): Calcareous tubeworms of the Phanerozoic. *Estonian Journal of Earth Sciences* 58: 286–96.
Vinn, O. & Zaton, M. (2012): Inconsistencies in proposed annelid affinities of Early biomineralized organism *Cloudina* (Ediacaran): structural and ontogenetic evidences, *Carnets de Géologie [Note-books on Geology], Brest, Article* 3: 39–47.
Vinther, J. (2009): The canal system in sclerites of lower Cambrian sinosachites (Halkieriidae: Sachitida): significance for the molluscan affinities of the sachitids. *Palaeontology* 52: 689–712.
Vinther, J. & D.E.G. Briggs (2009): Machaeridian locomotion. *Lethaia* 42: 357–64.
Vinther, J., Eibye-Jacobsen, D. & Harper, D.A. (2011): An early Cambrian stem polychaete with pygidial cirri. *Biology Letters* 7: 929–32.
Vinther, J. & Nielsen, C. (2005): The Early Cambrian *Halkieria* is a mollusc. *Zoologica Scripta* 34: 81–89.
Vinther, J., Parry, L., Briggs, D.E. & Van Roy, P. (2017): Ancestral morphology of molluscs revealed by a new Ordovician stem Aculiferan. *Nature 542:*472:474
Vinther, J. & Rudkin, D. (2010): The first articulated specimen of *Plumulites canadensis* (Woodward, 1989) from The upper Ordovician of Ontario, with a review of the anterior region of Plumulitidae (Annelida: Machaeridia). *Palaeontology* 53: 327–34.
Vinther, J., Van Roy, P. & Briggs, D.E. (2008): Machaeridians are Palaeozoic armoured annelids. *Nature* 451: 185–88.
Wade, M. (1972): *Dickinsonia*: polychaete worms from the Late Precambrian Ediacara fauna, South Australia. *Memoirs of the Queensland Museum* 16: 171–90.
Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–401.
Westheide, W. (1997): The direction of evolution within the polychaeta. *Journal of Natural History* 31: 1–15.
Williams, S.H., Nowlan, G.S., Barnes, C.R. & Batten, R.S.R. (1999): The ledge section at Cow Head, Western Newfoundland as a Gssp candidate for the lower boundary of the second stage of the Ordovician system: new data and discussion of the Graptolite, Conodont and Chitinozoan assemblages, *A report to the IUGS/ICS Subcommission on Ordovician stratigraphy*: 1–30.
Wilson, P., Parry, L.A., Vinther, J. & Edgecombe, G.D. (2016): Unveiling biases in soft-tissue phosphatization: extensive preservation of musculature in the Cretaceous (Cenomanian) polychaete *Rollinschaeta myoplena* (Annelida: Amphinomidae). *Palaeontology* 59: 463–79.
Withers, T.H. (1926): *Catalogue of the Machaeridia (Turrilepas and Its Allies) in the Department of Geology* (order of the Trustees).
Zhang, Z., Zhang, Z., Popov, L.E., Holmer, L.E. & Zhang, Z. (2018): Earliest ontogeny of early Cambrian acrotretoid brachiopods – first evidence for metamorphosis and its implications. *BMC Evolutionary Biology* 18: 42.
Zhao, F., Smith, M.R., Yin, Z., Zeng, H., Li, G. & Zhu, M. (2017): *Orthrozanclus elongata* n. sp. and the significance of sclerite-covered taxa for early trochozoan evolution. *Scientific Reports* 7: 16232.

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# Part 2: **Systematic**

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# 4 Palaeoannelida

María Capa, Julio Parapar and Pat Hutchings

## 4.1 Oweniidae Rioja, 1917

### Introduction

Oweniidae is a small group of polychaetes that comprises four genera (*Owenia* Delle Chiaje, 1844, *Myriochele* Malmgren, 1867, *Galathowenia* Kirkegaard, 1959, and *Myriowenia* Hartman, 1960) (Figs. 4.1.1 and 4.1.2) and around 60 species (Capa *et al.* 2012), with a relatively simple external morphology. Members of *Owenia* can reach up to 10 cm in length, but most species measure between 20 and 30 mm and can live for about four years (Ménard *et al.* 1989). They are associated with soft bottoms and can form patchy but dense populations. They are often common in continental shelves but not exclusive to these environments, and some species are restricted to shallow depths or deep-sea habitats (e.g., Kirkegaard 1956, Fiege *et al.* 2000).

Oweniids present unusual annelid features that support its monophyly. These are the mitraria larva, presence of monociliated epidermal cells, absence of a cuticle, particular arrangement of neuropodial hooks or uncini in patches, presence of specialized parapodial glands, and reduction of the nephridia, except for a single pair in the sixth segment (Wilson 1932, Thorson 1946, Liwanow and Porfirjewa 1967, Gardiner 1978, Gardiner and Rieger 1980, Nilsen and Holthe 1985, Smith *et al.* 1987, Meyer and Bartolomaeus 1996, Westheide 1997, Hausen 2005a, Smart and Dassow 2009, Capa *et al.* 2012).

Phylogenetic relationships within the family have recently been addressed based on morphology (Sene-Silva 2002, Capa *et al.* 2012), and four of the traditional oweniid genera were recovered as monophyletic after some synonymizations and nomenclatural changes (Capa *et al.* 2012). Before these revisions and for the last 30 years, Oweniidae was considered to consist of five genera, including also *Myrioglobula* Hartman, 1967, recently synonymized with *Myriochele* (see Capa *et al.* 2012). Main oweniid taxonomic contributions include regional studies from different geographic areas (Hartman 1969, Blake and Dean 1973, Blake 1984, 2000, Milligan 1984, Nilsen and Holthe 1985, Imajima and Morita 1987, Hartmann-Schröder and Rosenfeldt 1989, 1991, Martín 1989, Cantone di Pietro 1998, Parapar 2001, 2003a, 2006, Ford and Hutchings 2005, Villalobos-Guerrero 2009, Capa *et al.* 2012). Several oweniid species have been considered as cosmopolitan or widely distributed due to apparent morphological similarity along their distribution range. Modern techniques, including scanning electron microscopy and DNA sequencing, have allowed the recognition of discrete and distinct entities within these taxa, permitting in some cases their description as new species (Dauvin and Thiébaut 1994, Blake 2000, Koh and Bhaud 2001, 2003, Koh *et al.* 2003, Parapar 2003a, 2006, Ford and Hutchings 2005, Jolly *et al.* 2006, Martín *et al.* 2006, Capa *et al.* 2012).

The position of the oweniids in the annelid tree, however, has been convoluted. Some hypotheses suggest a close relationship of Oweniidae and Siboglinidae as derived annelids (e.g., Liwanow and Porfirjewa 1967, Meyer and Bartolomaeus 1996, Rouse and Fauchald 1997, Eeckhaut *et al.* 2000, Rousset *et al.* 2004, Struck *et al.* 2007, Capa *et al.* 2011), whereas others (including recent phylogenomic analyses) point to a basal position among Annelida (Bubko 1973, Rieger 1976, 1988, Smith *et al.* 1987, Minichev and Bubko 1992, Westheide 1997, Struck *et al.* 2008, 2015, Zrzavý *et al.* 2009, Capa *et al.* 2012, Weigert *et al.* 2014, Andrade *et al.* 2015, Helm *et al.* 2018).

### Morphology

#### External morphology

Oweniids are, in general, elongated, cylindrical, and fairly rigid annelids (Blake 2000, Rouse 2001), but some variability of body form is present in the family. Species of *Myriochele* have a cigar-shaped body with both ends tapering, whereas *Owenia* has a truncated anterior end. *Galathowenia* and *Myriowenia* have long and slender bodies, which often appear contorted after fixation.

**Prostomium and Peristomium.** The head consists of a fused prostomium and peristomium (Nilsen and Holthe 1985, Smart and Dassow 2009), and its shape exhibits considerable variation within the family. Its anterior end may be truncated (*Galathowenia*) (Figs. 4.1.1 A and 4.1.2 A, B), rounded (*Myriochele*) (Figs. 4.1.1 B and 4.1.2 C), rounded with a pair of grooved tentacles (*Myriowenia*) (Figs. 4.1.1 C and 4.1.2 D, E), or multilobed and forming a tentacular crown (*Owenia*) (Figs. 4.1.1 D and 4.1.2 F, G). The nature and function of anterior appendages are, in most cases, unknown, and it is not clear if they are homologous between members of the family or with similar structures found in other polychaetes. Berkeley (1949) and Sene-Silva (2002) suggest that the tentacular crown of *Owenia* represents modified lips and therefore is of peristomial origin, whereas others believe

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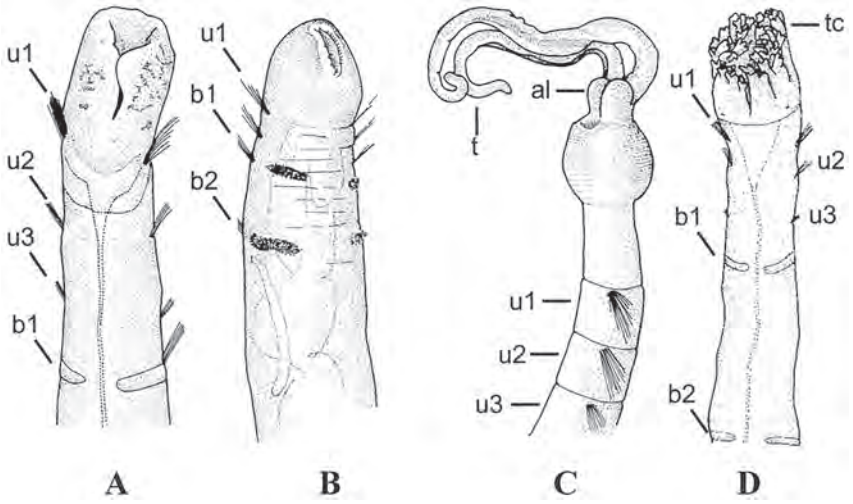


**Fig. 4.1.1:** Stylized drawings of the anterior region of some representative species of Oweniidae genera. A, *Galathowenia oculata* showing three uniramous chaetigers (u1–u3) and first biramous chaetiger (b1). B, *Myriochele heeri* showing two uniramous chaetigers (u1–u2) and first two biramous chaetigers (b1–b2). C, *Myriowenia californiensis* showing anterior lobes (al), tentacles (t), and first three uniramous chaetigers (u1–u3). D, *Owenia australis* Ford & Hutchings, 2005 showing tentacular crown (tc), three uniramous chaetigers (u1–u3), and first two biramous chaetigers (b1–b2). From Capa *et al.* (2012), modified after the following: A, Imajima and Morita (1987: 95, Fig. 6); B, Blake (2000: 112, Fig. 5.5); C, Hartman (1960: 209, Fig. 16.5); D, Hartmann-Schröder (1996: 477).

the crown to be of prostomial origin (Rouse and Fauchald 1997, Rouse 2001). Similarly, the anterior appendages of *Myriowenia* have been considered as palps and homologous to those present in Spionida, Terebellida, and Sabellida (Orrhage 1964, 1978, 1980, Sene-Silva 2002), but this is not universally accepted (Capa *et al.* 2012). The anterior low lobes characteristic of *Myriowenia* (Fig. 4.1.1 C) are of unknown origin but have been regarded as labial lobes of peristomial origin (Sene-Silva 2002) or as prostomial structures and, therefore, of prostomial origin (Hartman and Bernard 1960, Hartman 1969, Blake 2000).

**Epidermis and cuticle.** Oweniids lack a cuticle. Instead, they possess a fine and loose fibrillar matrix around the epithelial microvilli (Gardiner 1978, Storch 1988). The epithelium of the tentacular crown of *Owenia* (Gardiner 1978) and *Myriowenia* (Westheide 1997) exhibits an unusual feature. It is dominated by unspecialized epidermis, monociliated cells, instead of multiciliary epidermal cells present in *Myriochele* (Westheide 1997) and most other annelids (Gardiner 1978, Hausen 2005a). These unspecialized monociliated cells are more similar to those found in the epithelia of lophophorates and basal deuterostomes than to the epithelia of other polychaetes (Gardiner 1978). In *Owenia,* monociliated epidermal cells coexist with biciliated cells, scattered or clumped monociliated mucous cells, and nonciliated cells (Gardiner 1978). The mucous cells are present on both the oral and aboral surfaces of the tentacles.

Some oweniids have a button-hole mouth with shallow lips arranged either obliquely or terminally around it (*Myriochele* and *Myriowenia*) (Figs. 4.1.1 B, C, 4.1.3 D–G, and 4.1.4 C, D), whereas others have a cleft continuing posteriorly from the mouth, forming two large lips on its sides that show considerable variation in shape (*Galathowenia*) (Figs. 4.1.1 A and 4.1.3 A–C) (see Capa *et al.* 2012). Some species bear a collar, an epithelial fold between the head and the first segment (Imajima and Morita 1987, Hartmann-Schröder and Rosenfeldt 1989, Dauvin and Thiébaut 1994, Blake 2000, Parapar 2006) (Fig. 4.1.4 A). This is a different structure to what has been termed a cephalic groove that is also an epithelial fold formed when the head contracts into the anterior segments (Gibbs 1971) (Fig. 4.1.4 B) or to the breakage groove, or constriction zone between the head and the first chaetiger, and related to asexual reproduction (Aguirrezabalaga *et al.* 2000, Parapar 2001, 2003a, Capa *et al.* 2012) (Figs. 4.1.3 A, 4.1.4 C, D, 4.1.11 A, B, and 4.1.12 D).

**Parapodia and segments.** Segments are often not distinguishable externally if an intersegmental constriction is not conspicuous. The trunk is divided into two distinct regions based on the presence of uniramous or biramous parapodia. These regions have been traditionally known as thorax and abdomen (e.g., Nilsen and Holthe 1985, Blake 2000), although some authors discourage the use of these terms (e.g., Parapar 2003a,b, Capa *et al.* 2012). In general, adults of *Owenia* and *Myriowenia* have bodies with up to 50–60 segments, whereas species of *Galathowenia* and *Myriochele* have less than 30 segments (Capa *et al.* 2012). The number of uniramous segments in the anterior region is

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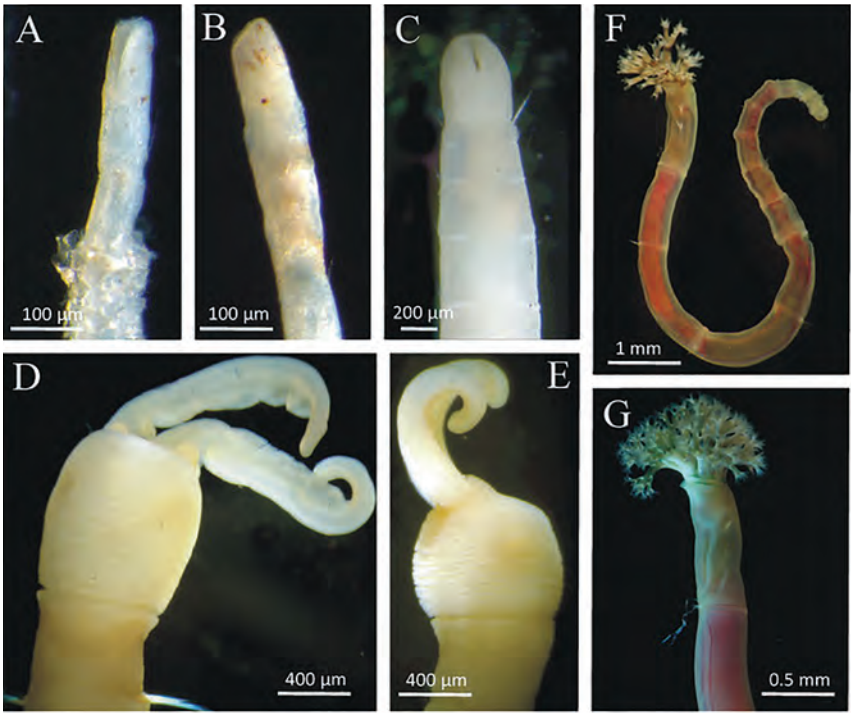


**Fig. 4.1.2**: Micrographs of the anterior region of some representative species of Oweniidae genera. A and B, Ventrolateral and lateral views of *Galathowenia annae* Capa, Parapar & Hutchings, 2012, respectively. C, Ventral view of *Myriochele australiensis* Capa, Parapar & Hutchings, 2012. D and E, Dorsal and lateral views of *Myriowenia* sp., respectively. F and G, General view and anterior end of *Owenia sp*. A–E from Capa *et al* (2012); F and G originals, by Greg Rouse.

three in *Galathowenia* (two in a few species) (Fig. 4.1.3 A, B), one to three in *Myriochele* (Fig. 4.1.3 E, F), and three in *Owenia* (Fig. 4.1.4 A) and *Myriowenia* (Fig. 4.1.4 C, D). The number of biramous segments in the posterior region shows intraspecific variation in most cases, as segments are added with age, although some species seem to have a more constant number of body segments (Parapar 2006). Biramous segments are unequal in length, and those from the midbody region are distinctly longer compared to those situated more posteriorly. Segments become progressively shorter toward the pygidium, and this is most evident in *Galathowenia*, *Myriowenia*, and most species of *Myriochele* (e.g., Parapar 2003a,b, Capa *et al.* 2012).

Oweniids possess longitudinal grooves on the dorsal, ventral, and lateral body surfaces (Fig. 4.1.9 B–D) that are either ciliated or nonciliated (Capa *et al.* 2012). While the lateral grooves are ciliated (Fig. 4.1.9 B, C), the dorsal groove appears to lack cilia (Fig. 4.1.9 D), and the ventral groove seems to be glandular and different from the other grooves (Parapar 2003c).

**Chaetae.** Members of this family have reduced parapodia that lack dorsal and ventral cirri, branchiae, or epidermal papillae. Notochaetae emerge directly from the body wall, whereas neurochaetae emerge from low glandular transverse tori (Hutchings 2000). *Galathowenia* (Fig. 4.1.5 A), *Myriowenia*, and *Owenia* (Fig. 4.1.5 E) bear only one type of tapering capillary notochaeta that is similar in structure on all segments. These chaetae are smooth proximally and distally show the characteristic structure of the cortex that resembles small imbricated scales (Fig. 4.1.5 F, G) (Ford and Hutchings 2005, Capa *et al.* 2012).

In *Myriochele*, these capillaries coexist with others called acicular chaetae, at least in some segments (Fig. 4.1.5 B, C) (Nilsen and Holthe 1985, Imajima and Morita 1987, Parapar 2001, 2003a, 2006, Capa *et al.* 2012). Acicular chaetae are shorter and smooth, and their tips are more abrupt (Fig. 4.1.5 C). Although the first anterior chaetiger from which they are present is a specific diagnostic feature, intraspecific variability has been reported in a few species (Capa *et al.* 2012).

Neurochaetae are long-handled dentate hooks or uncini, which have two teeth homologous to the capitium of the hooks of other annelids. The chaetal rostrum is lacking in all species of Oweniidae (Meyer and Bartolomaeus 1996, Bartolomaeus 1998 [contrary to Nilsen and Holthe's 1985 interpretation], and discussed by Hausen 2005b). Uncini are arranged in multiple modified transverse rows (Hausen 2005b) called uncinal patches (Fig. 4.1.6 A, B). Numbers of uncini in a single torus can reach 7,600 in *Owenia*, indicating a total of 150,000 to 450,000 hooks in an entire animal (Watson 1901). This large number of hooks is related to the burrowing habits of the worm and ensures that removal of the animal from its tube is very difficult (Watson 1901). In anterior segments, the uncinal patches extend from the dorsolateral to the ventral side of the body, and toward the caudal end, they are smaller and restricted ventrolaterally. The handle

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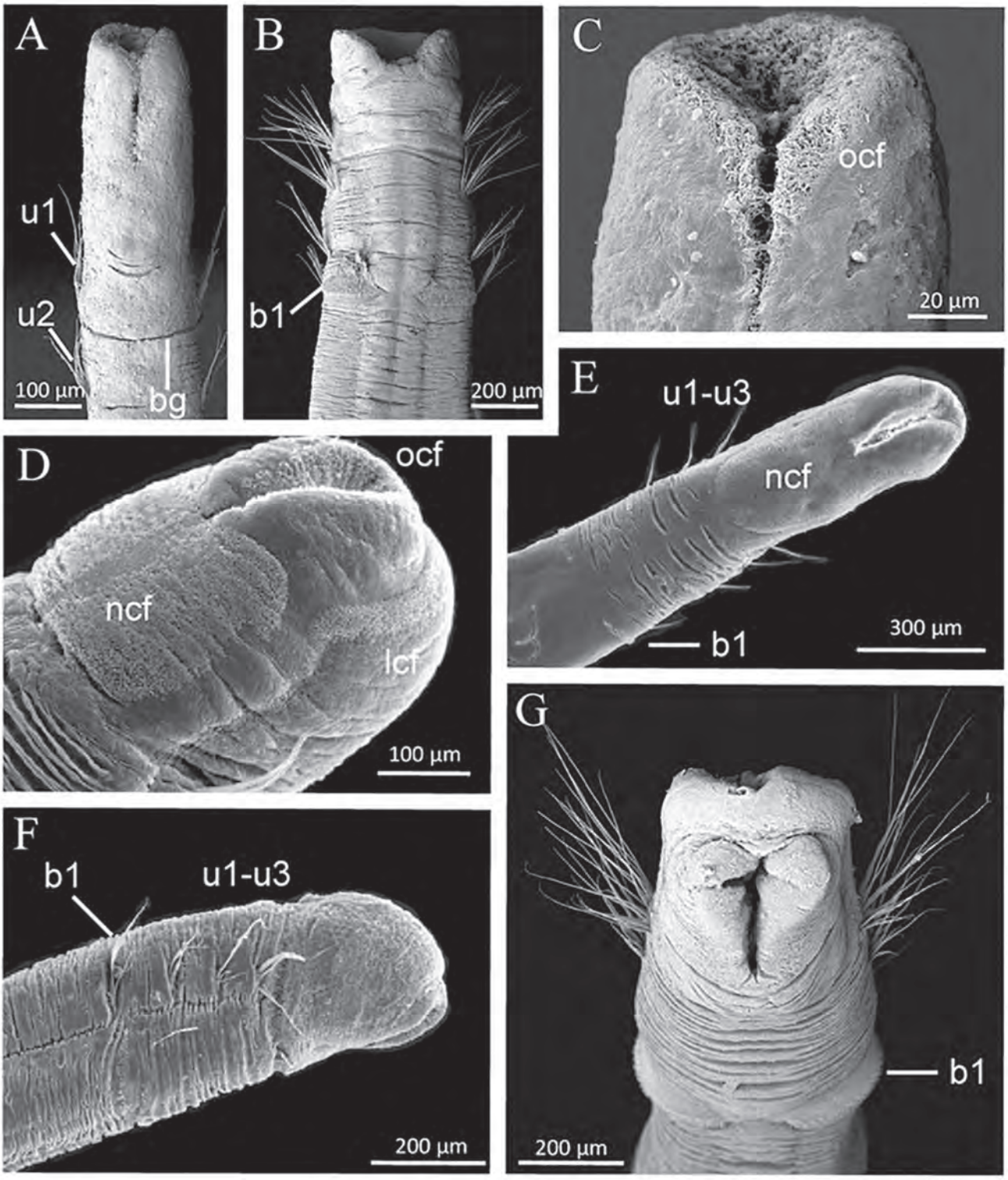


**Fig. 4.1.3:** SEM of the anterior end of *Galathowenia* and *Myriochele*. A, Ventral view of *Galathowenia quelis* Capa, Parapar & Hutchings, 2012 showing first two uniramous chaetigers (u1 and u2) and the breakage groove (bg) between u1 and u2. B, Ventral view of *Galathowenia arafurensis* Capa, Parapar & Hutchings, 2012 showing first biramous chaetiger (b1). C, Ventral view of *G. quelis* showing oral ciliary field (ocf). D, Ventrolateral view of *Myriochele heeri* Malmgren, 1867 showing lateral ciliary field (lcf), neck ciliary field (ncf), and oral ciliary field (ocf). E, Ventral view of *Myriochele olgae* Blake, 2000 showing neck ciliary field and three thoracic uniramous chaetigers (u1–u3). F, Lateral view of *M. heeri* showing thoracic uniramous chaetigers (u1–u3) and first biramous chaetigers (b1). G, Ventro-anterior view of *Myriochele heruensis* showing first biramous chaetiger (b1). A–C and G after Capa *et al.* (2012); D–F after Parapar (2006).

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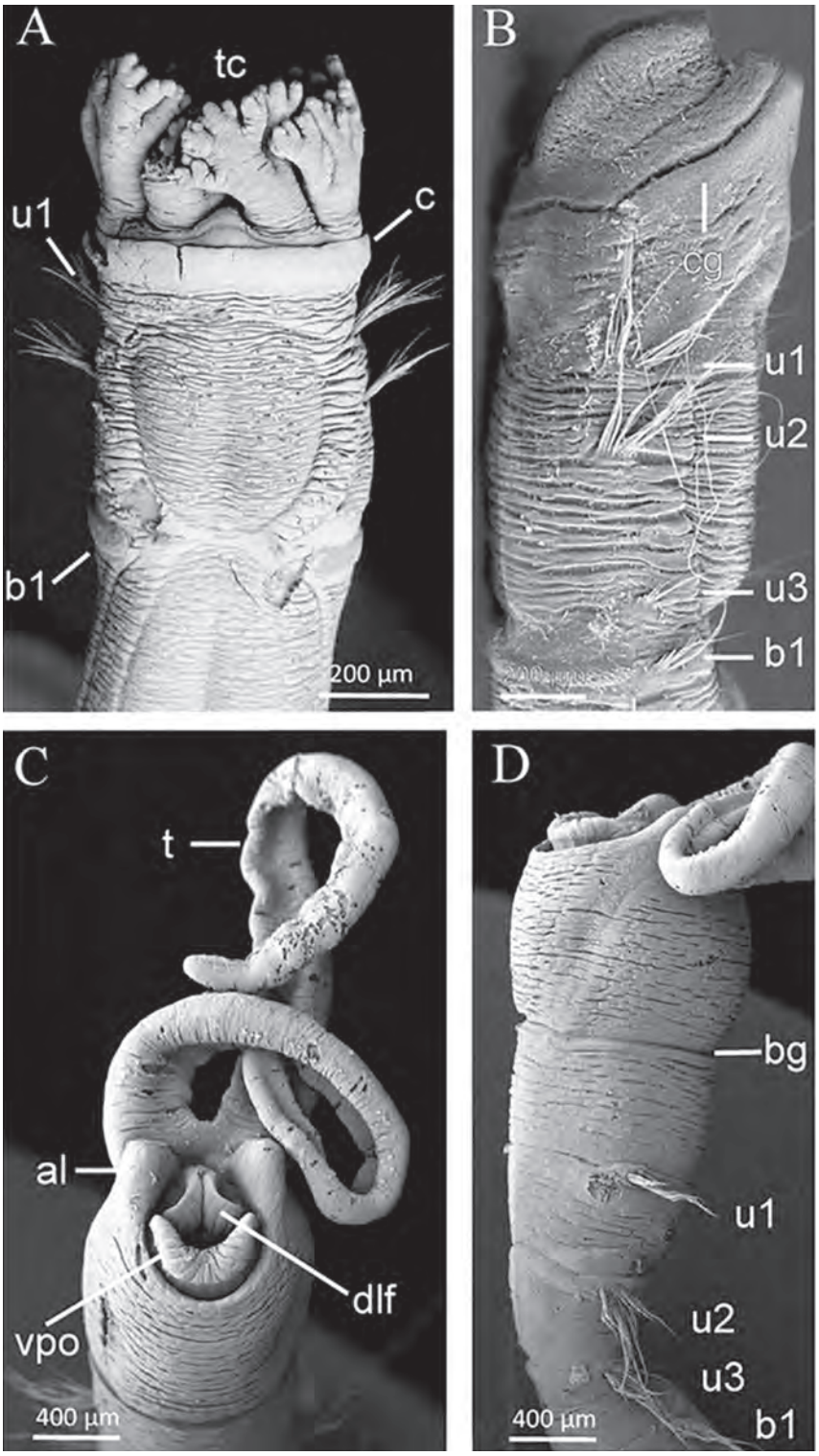


**Fig. 4.1.4:** SEM of anterior end of several genera of Oweniidae. A, Dorsal view of *Owenia mirrawa* Ford & Hutchings, 2005 showing tentacular crown (tc), collar (c), first uniramous chaetiger (u1), and first biramous chaetiger (b1). B, Lateral view of *Myriochele heruensis* showing cephalic groove (cg), three uniramous chaetigers (u1–u3), and first biramous chaetiger (b1). C, Frontal view of *Myriowenia sp*. showing anterior lobes (al), dorsolateral folds (dlf), tentacles (t), and ventral pharyngeal organ (vpo). D, Lateral view of *Myriowenia sp*. showing the breakage groove (bg) between head and u1, three uniramous chaetigers (u1–u3), and first biramous chaetiger (b1). A original; B–D after Capa *et al.* (2012).

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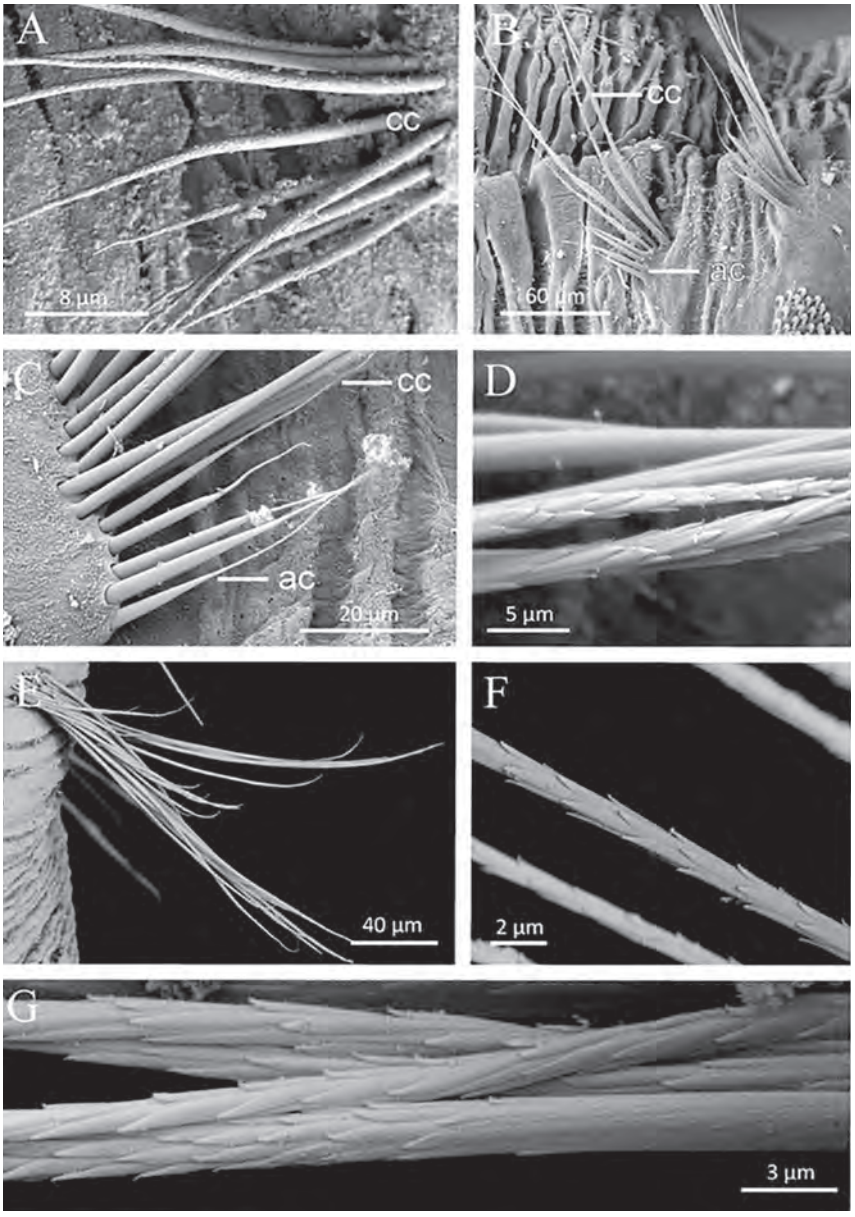


**Fig. 4.1.5:** SEM of notochaetae of some representative species of Oweniidae genera. A, Capillary chaetae (cc) of *Galathowenia quelis*. B, Notochaetal bundle of chaetigers 2 and 3 of *Myriochele heruensis* showing both capillary chaetae (cc) and acicular chaetae (ac). C, Notopodial chaetae of *M. heruensis* showing both capillary and acicular chaetae. D, Detail of scales covering capillary chaetae of *Myriochele australiensis*. E, Notochaetal bundle of *Owenia mirrawa*. F, Detail of scales covering capillary chaetae of *Owenia bassensis* Ford & Hutchings 2005. G, Detail of scales covering capillary chaetae of *Owenia australis*. A–G original.

of the uncini, also known as a shaft or manubrium, can either be straight as in species of *Myriowenia* (see Hartman 1965) or bent as in other oweniids (Imajima and Morita 1987, Capa *et al.* 2012). The uncinal breast or subrostrum is considered as absent (Capa *et al.* 2012, but see other interpretations, e.g., Rousset *et al.* 2004). Uncini are typically provided with two teeth. In *Galathowenia*, teeth are arranged in an oblique row (Fig. 4.1.6 C, D), whereas in *Myriochele* (Figs. 4.1.6 E, F and 4.1.7 A) and *Myriowenia* (Fig. 4.1.7 B–D), they are arranged one on top of the other, and in *Owenia*, they are arranged side by side (Fig. 4.1.7 E, F). Nevertheless, some exceptions to this pattern are known (e.g., *Myriochele heruensis* Gibbs, 1971). Both teeth are similar in size, except in *Myriowenia*, where the proximal tooth is larger than the distal tooth.

Oweniids exhibit a particular pattern of production of uncini. The formative site in each uncinal patch in adult oweniids is located dorsally along its posterior edge (Meyer and Bartolomaeus 1996), and it is only in this posterior-dorsal edge of the uncinal patch where developing hooks, which have not yet pierced the cuticle, are observed. Chaetogenesis is a rather discontinuous process in older animals and has been studied in detail in juveniles of *Owenia* by Meyer and Bartolomaeus (1996). Each follicle of a fully differentiated hook of *Owenia* consists of one basal chaetoblast, one or several follicle cells, and a number of epidermal cells that surround the hook

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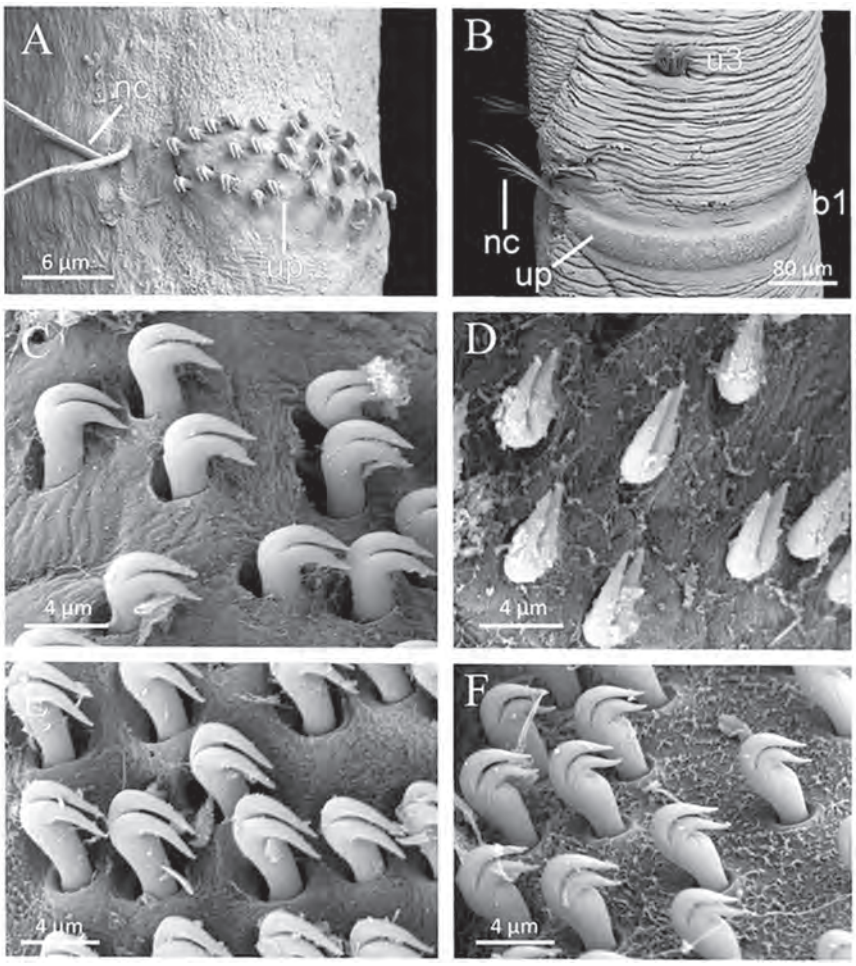


**Fig. 4.1.6:** SEM of neuropodia and uncini of some representative species of Oweniidae genera. A, First biramous chaetiger of *Galathowenia annae* showing notopodial chaetae (nc) and neuropodial uncinal patch (up). B, Third uniramous chaetiger (u3) and first biramous chaetiger (b1) of *Owenia mirrawa* showing notopodial chaetae (nc) and neuropodial uncinal patch (up) of the latter. C, Uncini of first biramous unciniger of *Galathowenia quelis*, lateral view. D, Same in top view. E, Uncini of first biramous unciniger of *Myriochele heruensis*, latero-frontal view. F, Uncini of first biramous unciniger of *Myriochele australiensis*, latero-frontal view. A and C–F after Capa *et al.* (2012); B original.

apically. Clusters of extracellular matrix are interspersed between the epidermal and follicle cells and play a critical role in the stabilization of the multiple rows of hooks (Meyer and Bartolomaeus 1996). Degenerating chaetae have been observed at the opposite (antero-ventral) end of the uncinal patch (Meyer and Bartolomaeus 1996).

Two segmentally arranged structures of unknown function were found in two oweniid species by Capa *et al.* (2012): parapodial flaps in the anterior biramous chaetigers of *Galathowenia* sp. (Fig. 4.1.9 E) and parapodial tubular projections, which originate from lateral pores in some midbody segments of *Myriowenia* sp. (Fig. 4.1.9 F). The composition and function of these structures are unknown and deserve a more in-depth investigation. Some believe that they may be related to thread glands (e.g., Watson 1901).

**Pygidium.** The shape of the pygidium shows intrageneric variability (Parapar 2003c). It can be a simple rim or with two or more lobes, but in general terms, it is simple or bilobed in *Myriochele* (Fig. 4.1.8 A–C), bilobed or multilobed in *Galathowenia* (Fig. 4.1.8 D, E), and pointed in *Owenia* (Fig. 4.1.8 F). The pygidium with two long terminal cirri described for *Myriowenia gosnoldi* (Hartman, 1965) needs further investigation. It is probable that these cirri are artifacts, potentially related to the regeneration process after breakage (Capa *et al.* 2012).

### Anatomy

**Pharynx.** A ventral pharyngeal organ and a pair of dorsolateral ciliary folds are found inside the mouth in some oweniids. The ventral pharyngeal organ in some oweniids has been described as having a bulb organ that protrudes slightly from the mouth (Purschke and Tzetlin 1996, Tzetlin and Purschke 2005) (Figs. 4.1.4 C and 4.1.9 A). This structure may have confused some authors who described it as a proboscis (e.g., Blake 2000). Species of *Owenia*, *Myriochele* and *Myriowenia* have been described or illustrated as having a ventral pharyngeal organ (Watson 1901, Wilson 1932, Dales 1957, Blake 1984, Nilsen and Holthe 1985, Hartmann-Schröder 1996, Parapar 2006). Similarly, protrusible ciliary folds on the dorsolateral walls of the foregut were observed in *Galathowenia*, *Myriochele*, and *Myriowenia* (Purschke and Tzetlin 1996, Parapar 2006, Capa *et al.* 2012) (Fig. 4.14 C).

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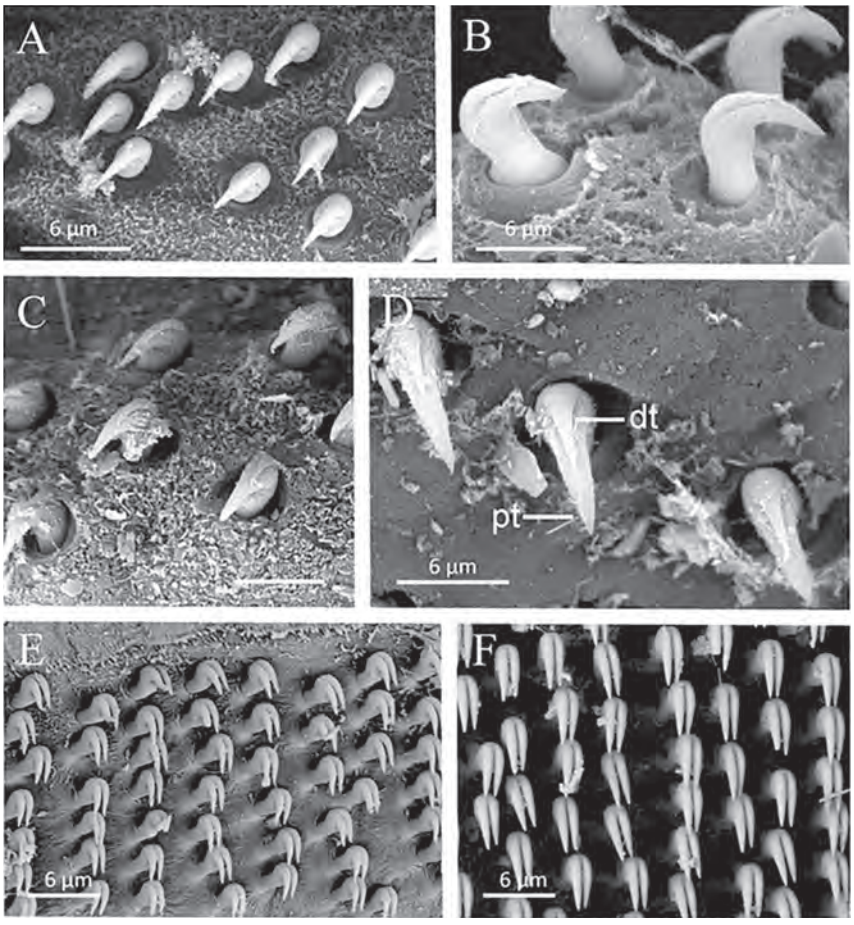


**Fig. 4.1.7:** SEM of the uncini of some representative species of Oweniidae genera. A, Uncini of *Myriochele australiensis*, top view. B, Uncini of chaetiger 8, *Myriowenia* sp., lateral view. C and D, Same, top view, showing vertical arrangement of teeth with distal tooth (dt) smaller than proximal tooth (pt). E, Uncini of *Owenia australis*, top-lateral view. F, Uncini of *Owenia bassensis*, top view, showing parallel arrangement of teeth. A–D after Capa *et al.* (2012); E–F originals.

**Digestive system:** The gut of oweniids is composed of three regions: foregut (esophagus and stomach), midgut (intestine), and hindgut (rectum), which can be easily distinguished histologically (Dales 1957, Tzetlin and Purschke 2005). The buccal region and the esophagus are lined ciliated epithelial cells interspersed with glandular cells that secrete digestive enzymes (Dales 1957). The stomach has thick and involuted walls that contain numerous glandular epithelial cells of two different types (Dales 1957). Glandular cells are lacking in the intestine, where absorption occurs. The rectum is thin walled and less convoluted, with no absorption occurring in this area. Rather, the rectum is responsible for the collection of sand grains and other non-digestible particles and the formation of discrete pellets that are defecated intermittently by the animal reversing in its tube (Dales 1957). Movement of material through the gut is accomplished by gut musculature, although this is poorly developed in some areas, as well as by contraction of the body wall muscles acting via the coelomic fluid.

**Musculature.** Longitudinal muscles in members of the Oweniidae are grouped into bundles that gradually decrease in thickness, from 10–20 cells in the anterior region to a single cell in the posterior region (Gardiner and Rieger 1980). Circular musculature is absent in the group (Tzetlin and Filippova 2005). A layer of monociliated peritoneal cells covers the muscle cells and forms the coelomic lining of the body wall, except near the ventral and dorsal mesenteries, where longitudinal muscle fibers form the lining (Gardiner and Rieger 1980, Fransen 1988). These monociliated cells are similar to those found in the tentacles but possess shorter cilia (Gardiner and Rieger 1980). In the case of traumatic breakage, muscle cells of *Owenia fusiformis* Delle Chiaje, 1844 dedifferentiate and become muscle cells again in the regenerated tissue (Fontés *et al.* 1983).

**Nervous system.** The nervous system of oweniids is largely intraepidermal with a well-developed nerve plexus, including a large number of peripheral nerves, but segmental ganglia are lacking (Bubko and Minichev 1972, Coulon and Bessone 1979). The ventral nerve cord has an extension into the hindgut, which again is atypical for polychaetes (Gardiner 1978).

**Sensory organs.** Nuchal organs have not been observed (Rullier 1951), but further investigations are needed before

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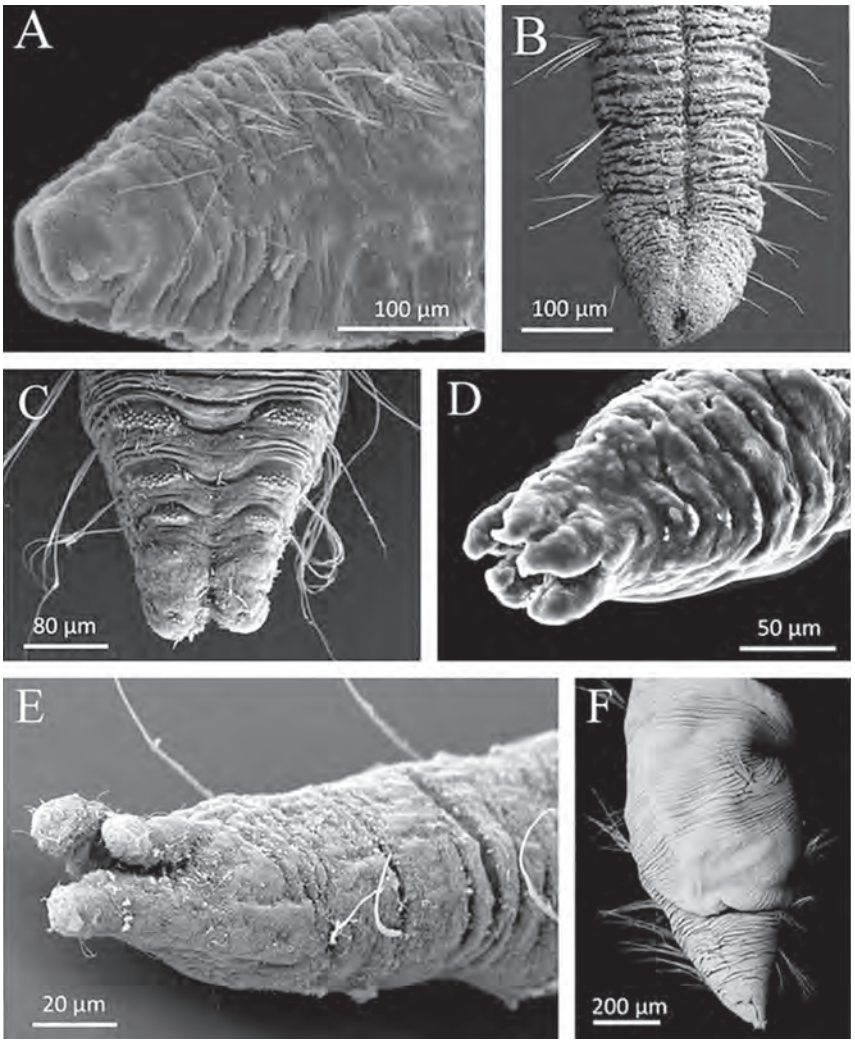


**Fig. 4.1.8:** SEM of the posterior end of some representative species of Oweniidae genera. A, *Myriochele* aff. *olgae*, ventrolateral view. B, *Myriochele australiensis*, ventral view. C, *Myriochele heruensis*, ventral view. D, *Galathowenia scotiae* (Hartman, 1978), ventral view. E, *Galathowenia annae*, ventrolateral view. F, *Owenia* sp., dorsal view. A, B from Ford and Hutchings (2005); C, E after Capa *et al.* (2012); D, F original.

verifying their absence (Purschke 2005). It may be possible that their absence should be regarded as the plesiomorphic condition in the group Oweniidae (together with Magelonidae) as these families are positioned at the base of the annelid tree (Weigert *et al.* 2014). Eyespots are present in the head of adult worms in many species. Due to their close association with the brain, they have been considered as cerebral eyes (Purschke *et al.* 2006, Capa *et al.* 2012). However, it is still unclear if they have a prostomial or peristomial origin (Capa *et al.* 2012).

## Reproduction and development

**Gametes and fertilization.** Most reproductive and developmental published information is based on the study of the species of *Owenia*. Sexes are separate, and gametes are movable between segments, although generally concentrated in midabdominal segments in mature specimens (Smart and Dassow 2009). Males produce ect-aquasperm with a small head (4 µm) and a long flagellum (30 µm) (Rouse 1988, Smart and Dassow 2009). Females produce primary oocytes after extraovarian oogenesis (Dales 1958, Eckelbarger 1983). They have several reproductive cycles during their life span, and while in some geographic regions, populations show discrete seasonal spawning (Wilson 1932, Cazaux 1973, Buchanan *et al.* 1978, Gentil *et al.* 1990), other populations (potentially different species) breed throughout the year (McNulty and López 1969). Individuals can reach maturity after the first year of benthic life (Gentil *et al.* 1990). *Owenia* spp. are broadcast spawners, and sperm in the water column seems to stimulate the discharge of gametes of other males and females (Watson 1901). Both males and females expose the posterior end of the body through the anterior end of a tube and discharge spermatozoa and primary oocytes though paired posterior openings, assisting their dispersion with vigorous movements (Watson 1901, Wilson 1932, Smart and Dassow 2009). In contact with sea water, newly released eggs undergo some transformations and become spherical,

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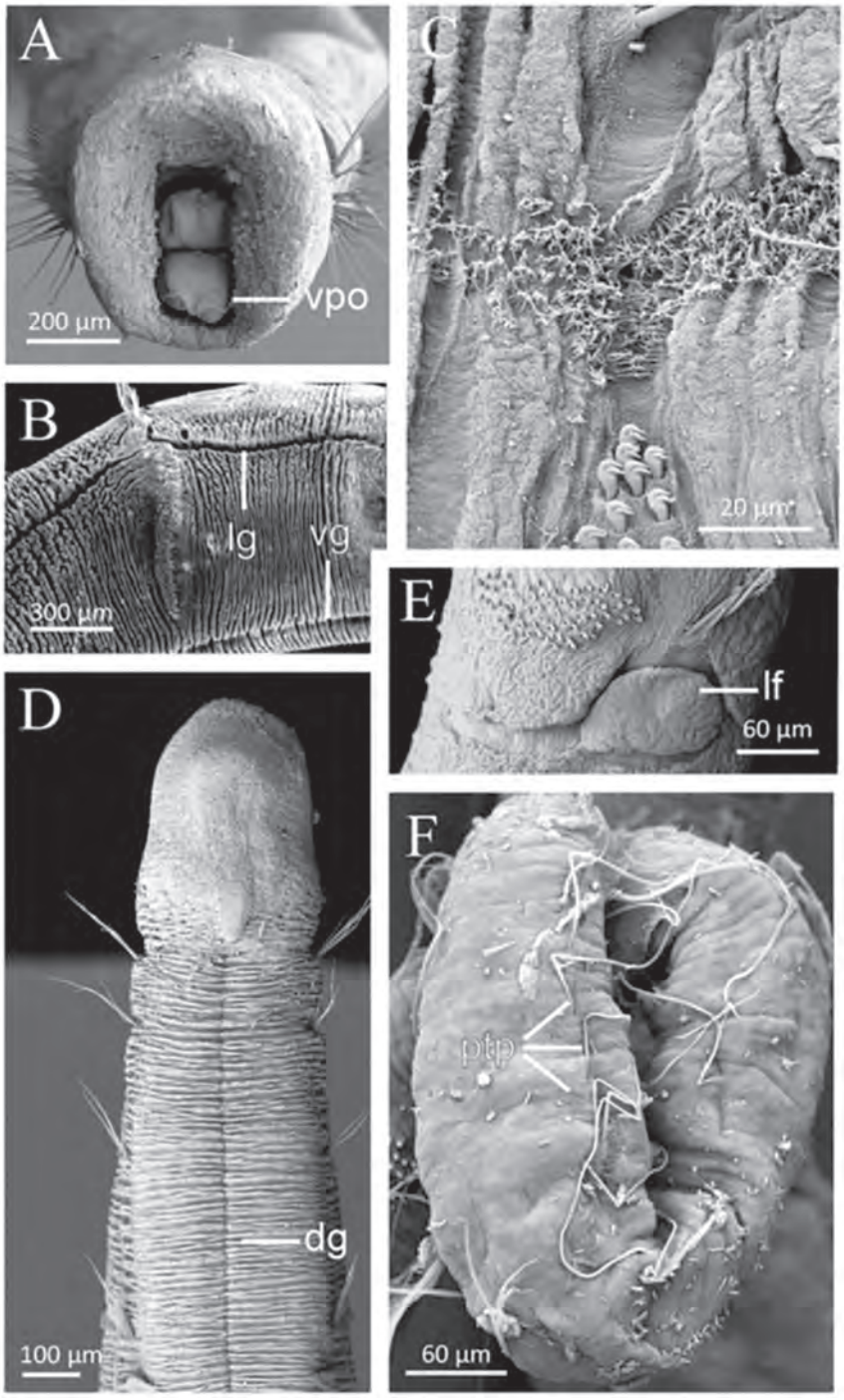


**Fig. 4.1.9:** SEM of several body structures in Oweniidae. A, Open mouth of *Galathowenia arafurensis* showing ventral pharyngeal organ (vpo). B, Ventrolateral view of midbody region at 3rd biramous chaetiger in *Myriochele riojai* Parapar, 2003 showing lateral groove (lg) and ventral groove (vg). C, Detail of lateral ciliary band in *Myriochele australiensis*. D, Dorsal view of anterior end of *M. australiensis* showing dorsal groove (dg). E, Detail of lateral flap (lf) in second biramous chaetiger in *Galathowenia* sp. F, Midbody region with parapodial tubular projections (ptp). A, C–F from Capa *et al.* (2012); B from Parapar (2003c).

lose the jelly coat, and the germinal vesicle collapses. Fecundity seems correlated with the size of females, ranging from 6,000 to 85,000 eggs in 40–110-mm females, respectively (Gentil *et al.* 1990, Thiébaut and Dauvin 1991).

**Embryonic and larval development.** *Owenia fusiformis* and *Owenia collaris* Hartman, 1955 exhibit modified embryonic and larval morphology and development compared to the typical annelid pattern (Wilson 1932, Smart and Dassow 2009). Embryos undergo holoblastic spiral cleavage to form a coeloblastula, similar to other annelids (Okada 1970, Smart and Dassow 2009), but unlike other protostomes, the stomodeum (precursor of the mouth) does not appear to be derived from either the blastopore or the area in which the blastopore forms. Instead, the anus develops from the blastopore, like deuterostomes

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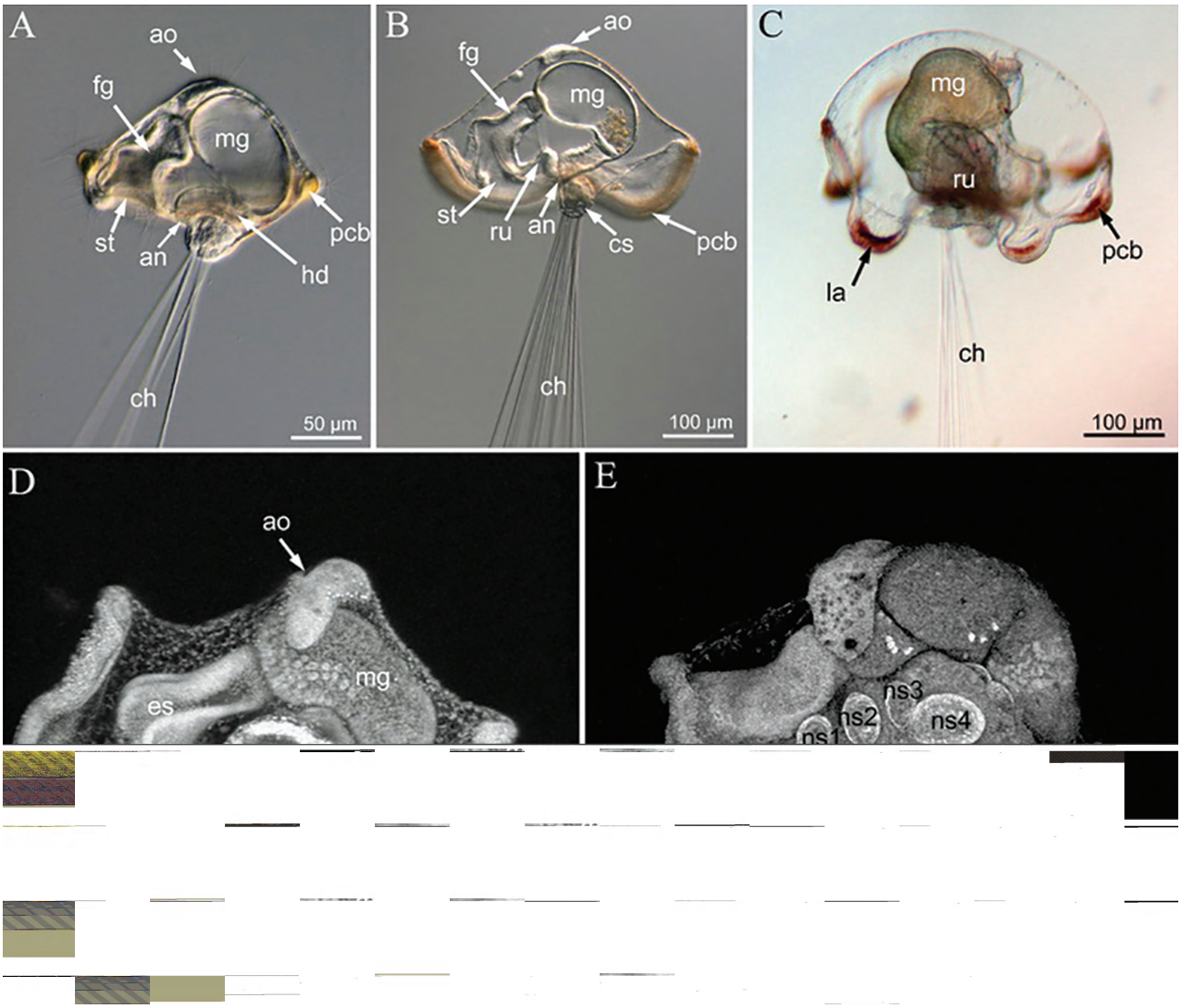


**Fig. 4.1.10:** Micrographs of mitraria larvae in *Owenia collaris*. A, 60-hour lab-reared larva showing the complete digestive tract, from stomodeum (st), with oral ciliation, to anus (an), with forgut (fg), midgut (mg), and hindgut (hg); primary ciliated band with beat (pcb); apical organ (ao); and chaetal sac with first two pairs of larval chaetae (ch). B, Wild-caught larva, about 2 weeks old, showing the beginnings of the juvenile rudiment (ru). C, More advanced larva showing a developing rudiment (ru) and elongated ciliary bands forming lappets (la). D, Confocal projection of a 17-day larva stained with phalloidin and Hoechst, with fully developed ciliary band system consisting on the primary ciliated band (pcb) and the secondary ciliated band (scb) on the lappets (la); the rudiment invagination (in) fills the hyposphere below the digestive system. E, 27-Day larvae with fully developed rudiment and four sets of nephridial sacs (ns). A, B originals by George von Dassow; C–E originals by Tracey Smart.

(Smart and Dassow 2009). The mouth is formed as a secondary opening as either an extension of the blastopore or, most likely, as a secondary invagination (Smart and Dassow 2009). Ciliogenesis is initiated later than in other annelids, and the ciliated bands differ from those present in the typical trochophore. The primary ciliated band in early larvae of *Owenia,* analogous to the prototroch, develops through continued proliferation of cells, forming a double row of simple cilia uniformly arranged around the embryo (Fig. 4.1.10 A–E). Cilia are shorter than in other protostomes, and there is no evidence of compound cilia. Nevertheless, the band covers about the same fraction of the total surface area of the larva when compared with early trochophores of other polychaetes (Smart and Dassow 2009).

Twenty-four hours after fertilization, the characteristic mitraria larva develops completely (in cultured conditions) and is able to swim. Larvae are still protected by the spawning membrane when the larvae start swimming. At this stage, the mouth and anus seem to be already opened and located close to each other, leading

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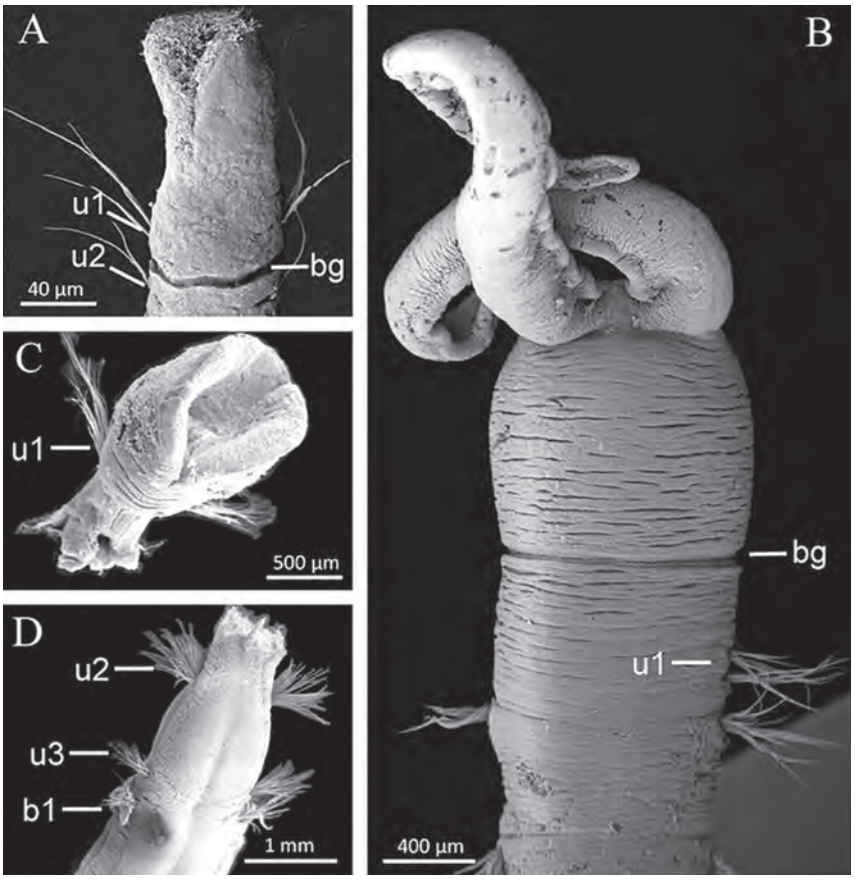


**Fig. 4.1.11:** SEM of several aspects of the regeneration process in Oweniidae. A, Ventral view of *Galathowenia annae* showing the breakage groove (bg) between first and second uniramous chaetigers (u1 and u2). B, Anterior end of *Myriowenia* sp. showing the breakage groove (bg) located anterior to first uniramous chaetiger (u1), dorsal view. C, Detached head of *Galathowenia scotiae* with attached first uniramous chaetiger. D, Anterior end of *G. scotiae* with head detached at the level of second uniramous chaetiger (u2). A, B from Capa *et al.* (2012); C, D original.

to a horseshoe-shaped gut and a more developed dorsal surface of the larvae, or episphere, compared to the ventral surface (Fig. 4.1.10 A). In the following two or three days, the mitraria forms two or three pairs of chaetae, the chaetal sacs and esophagus become muscularized, and eyespots are present in the apical organ (Fig. 4.1.10 B). After some days, the primary ciliary band folds, forming lappets and another ciliated band (analogous to the metatroch), and food grove complete the ciliated band system (Smart and Dassow 2009; Fig. 4.1.10 D).

Two weeks after fertilization, an invagination, known as the rudiment, grows on the ventral surface, occupying most of the hyposphere, forming a pocket (Fig. 4.1.10 B, C). Inside, small sacs are formed and will develop into the adult nephridia (Fig. 4.1.10 E). Lateral edges of the pocket fuse around the gut, while nephridia, chaetae, and body wall musculature develop. The coelomic lining develops as a thin layer around the rudiment. Metamorphosis starts about 4 weeks after fertilization with the protrusion of the trunk segments from the larval hyposphere, while the episphere retracts, becoming incorporated into the juvenile's head, the larval ciliary bands disintegrate, and the chaetal sac is reabsorbed (Smart and Dassow 2009). Other transformations involve the relative position of the nephridia and digestive system to the ectoderm and mesoderm.

Juveniles after metamorphosis are provided with a head (fused prostomium and peristomium), a uniramous segment with two sets of chaetae, six or seven biramous segments each with a single pair of chaetae and one pair of uncinal tori, and a pygidium. Soon after metamorphosis, the juvenile begins to gather materials with its anterior end for building its tube while pairs of buds start groups to form three pairs of unbranched prostomial tentacles after 2 weeks.

Asexual reproduction has been suggested as occurring in some oweniids. Adults of several species have been observed with a breakage groove between the first and the second chaetigers (Fig. 4.1.11 A), between the head and the first chaetiger (Fig. 4.1.11 B) (Aguirrezabalaga *et al.* 2000, Parapar 2001, 2003a, Capa *et al.* 2012) or between chaetigers 6 to 8 (Oliver 1984). Several specimens have been found already broken at this level (Fig. 4.1.11 C, D) (Parapar 2001, 2003c). Some specimens of *Myriochele heruensis*, *Myriochele* aff. *olgae* and *Myriowenia* sp. displayed anterior and posterior ends regenerating at different stages (Fig. 4.1.12 A–D), with anterior regeneration being the most common. In several of these specimens, hooks

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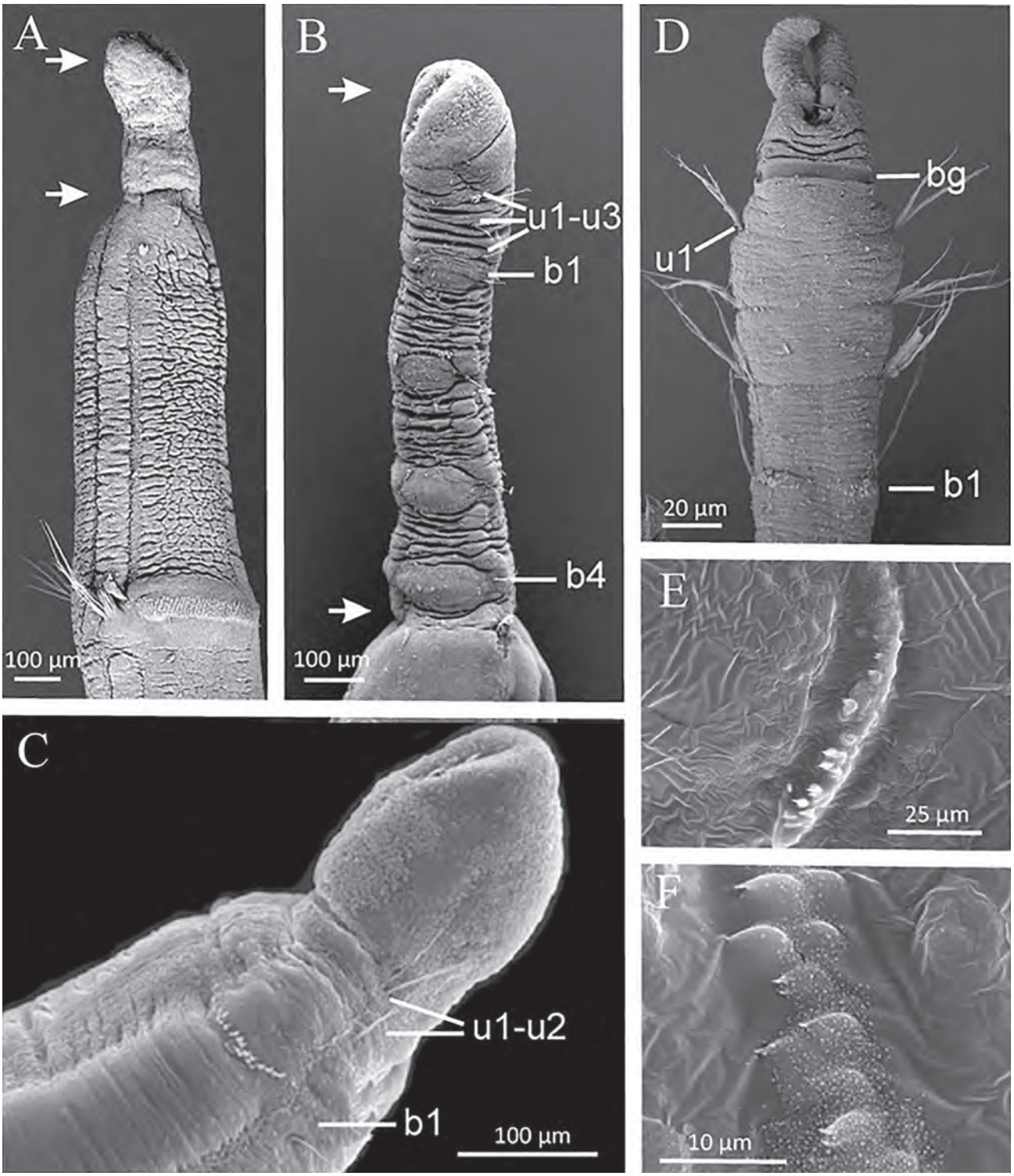


**Fig. 4.1.12**: SEM of several aspects of the regeneration process in Oweniidae. A, Anterior end in the early stage of regeneration in *Myriochele heruensis* (arrows). B, Anterior end in the more advanced stage of regeneration (arrows) in *M. heruensis*, involving all uniramous (u1–u3) and first four biramous chaetigers (b1–b4). C, Anterior end in the early stage of regeneration of Myriochele aff. *olgae* showing first normal biramous chaetiger (b1) and two thoracic uniramous chaetigers (u1–u2) still not fully developed. D, Regenerating anterior end in *Myriowenia* sp. showing small head anterior to the breakage groove (bg). E–F, Regenerating neuropodium in *M.* aff. *olgae* showing hooks piercing the epidermis. A, B, and D from Capa *et al.* (2012); C from Parapar (2006); E–F from Parapar (2001).

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piercing the epidermis could be seen in regenerating neuropodia (Fig. 4.1.12 E, F).

## Biology and ecology

Oweniids have been reported from a wide range of habitats, many geographical areas, and over a large bathymetric range, although they are more common in intertidal to continental shelf sediments (Day 1973, Fauchald 1977, Pettibone 1982). Some deep-sea species, such as *Galathowenia australis* (Grube, 1866), *Galathowenia oculata* (Zachs, 1923), and *Galathowenia pygidialis* (Hartman, 1960), are commonly reported below 1,800 m (Blake 2000), with the deepest reported species being *Myriochele* sp. from the Kermadec Trench at 8,300 m (Kirkegaard 1956). The four currently accepted genera (Capa *et al.* 2012) have broad distributions, while individual species seem to have more restricted environmental requirements and therefore show narrower distribution ranges. A few recent studies have dealt with some of these supposedly broadly distributed species and have shown that they represent complexes of morphologically similar species, for example, *G. oculata* and *Myriochele heeri* Malmgren, 1867 (Parapar 2003a,b,c, 2006, and references therein). Another well-known case is *O. fusiformis* originally described from the Mediterranean but reported as cosmopolitan (e.g., Hartman 1959, Hutchings and Rainer 1979, Day and Hutchings 1984, Hutchings and Murray 1984, Dauvin and Thiébaut 1994) and later split into several species (Blake 2000, Koh and Bhaud 2001, Koh *et al.* 2003, Ford and Hutchings 2005). Jolly *et al.* (2006) studied the population connectivity of several populations of *Owenia* in the northeast Atlantic, using cytochrome c oxidase subunit I (COI) sequences. They concluded that there could be several species (at least three) that were distinct from those occurring in the Mediterranean.

Oweniids are tube-dwelling annelids that build a translucent and flexible tube of secreted mucus to which they attach sediment particles, foraminiferans, or small shell fragments (Fig. 4.1.13 A– F). Tentacles, lips, and other buccal structures play an important role in the manipulation and selection of sediment particles for tube building (e.g., Watson 1901, Wilson 1932, Dales 1957). It is characteristic of *Owenia* that the tube particles are arranged in an imbricated manner (Signor and McMenamin 1988, Gambi 1989), with elements cemented to the tube along a single edge (Fig. 4.1.11 A–D). This way of attaching particles not only strengthens the tube but also facilitates flexibility to contortions or stretching, allowing the tube to double its length when the animal is burrowing (Watson 1901). There has been some speculation about the specificity of sediment used to construct the tubes (e.g., Blake and Dean 1973), but, contrary to Koh *et al.'s* (2003) opinion regarding *Owenia*, it seems that the selection of particles for tube construction in *Myriochele* depends on those available and shows intraspecific variability (Parapar 2003a, 2006; Fig. 4.1.11 A–F). What has been demonstrated in *Owenia* is that the animals select from the surrounding sediment coarse and flatter particles for tube building. This ability is fully developed after settlement of the larvae and persists throughout adult life, as these worms only build a single tube during their 2–3-year lifecycle (Noffke *et al.* 2009). The large number of hooks that some oweniids bear, estimated to be around 450,000 in *Owenia* species, is useful in ensuring that the tube moves with the animal as it burrows in the sediment (Watson 1901).

Tubes are oriented vertically in the sand and extend above the surface. They grow at the exposed end, where the head of the worm is generally located. No addition of sediment seems to occur at the posterior end, even though the animal is able to turn around inside its tube (Watson 1901). The building process, which includes both the buccal organ and the tentacular crown, has been observed in detail (Watson 1901, Gambi 1989). Both ends of the tube are provided with elastic tips, consisting of only the inner layer and no attached sediment. Species of *Owenia* seem to be largely nocturnal in habits, becoming active toward dusk and exposing the anterior end of the tube above the surface of the sediment and protruding their tentacular crown. The animals are able to burrow in the sediment without leaving the tube. They excrete feces or release gametes into the water column by executing a "U"-shaped turn within the tube (Watson 1901).

Oweniids are suspension or surface deposit feeders that collect particles at the sediment-water interface (Dales 1957, Blake 2000). Feeding habits in *Owenia* include direct ingestion of particles, bending over and collecting sand and detritus from the bottom surface with the ramified and highly motile tentacular crown, or ciliary feeding, using cilia on the tentacular crown to create water currents that direct suspended particles into the crown. There, the particles are carried toward the mouth by other ciliary currents arranged in channels (Gambi 1989). Lips, which are provided with strong muscles, are responsible for particle selection (Dales 1962). Mucous gland secretions in the tentacular crown assist in the retention and movement of the particles. Particles smaller than 200 μm are ingested and larger ones are either rejected or incorporated into the tube (Dales 1957). The buccal organ is used for attaching the sediment grains to the tube (Watson 1901). Other oweniids that lack a tentacular crown collect particles by direct ingestion. *Myriowenia* may use its long

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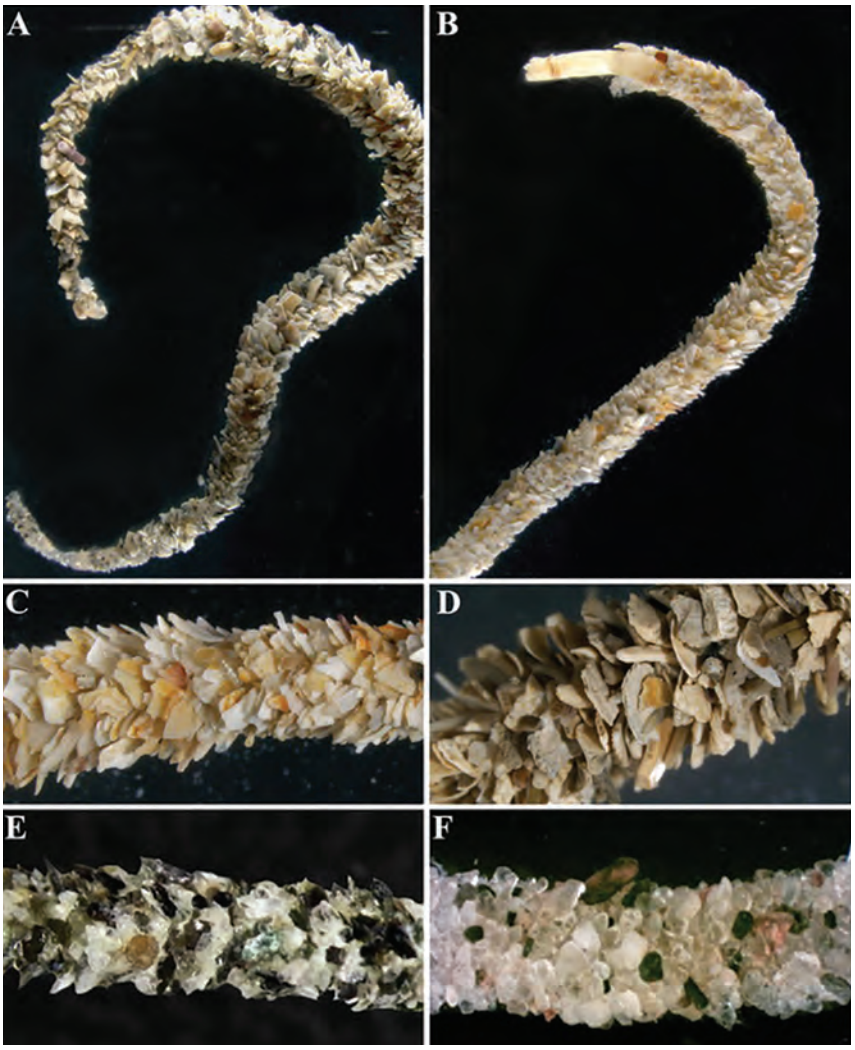


**Fig. 4.1.13:** Micrographs of *Owenia* sp. tubes from Norwegian waters, A, B, Tube opening is on top; C–F, on the left. E, F originals by Torjus Haukvik.

palps to gather particles in a manner similar to spionids, but there have been no direct studies of its feeding biology (Blake 2000).

The well-irrigated tentacular crown in *Owenia*, which sometimes is protruded from the tube entrance into the water column, is also used for respiration. *Owenia* possesses a blood pigment, erythrocruorin (extracellular hemoglobin), that allows them to withstand prolonged anoxia as they are able to switch to anaerobic metabolism (Watson 1901, Warren and Dales 1980, Wells *et al.* 1981). This allows them to survive, if buried by the wave action, in anoxic conditions for prolonged periods of time (up to 21 days, von Brand 1927).

Some oweniids can form dense aggregations. *Owenia fusiformis* has been reported as reaching up to 1000 individuals per $m^2$ in the Bay of Seine, eastern English Channel (Ménard *et al.* 1989), and aggregations of *G. oculata* have been reported with 707 and 348 individuals per $m^2$ in the vicinity of the Doggerbank (Kirkegaard 1969, Künitzer 1990, respectively). Fiege *et al.* (2000) found lower numbers for *Galathowenia fragilis* (Nilsen and Holthe 1985), with 116 individuals per $m^2$ in the Ierapetra basin. However, these numbers are still remarkable when considering the extreme oligotrophy of the eastern Mediterranean Sea. Oweniids have been reported as stabilizers of sediments when forming dense aggregations (Fager 1964, Eckman *et al.* 1981, Somaschini 1993). They also increase the heterogeneity of the sediments and, consequently, the diversity of the community (Somaschini 1993). *Owenia* is reported as a common prey item for some flat fishes in areas where the population is abundant (Ménard *et al.* 1989).

## Phylogeny and taxonomy

### Phylogeny

Due to the simplified but peculiar morphology, ontogeny, and their characteristic mitraria larvae, the position of

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the Oweniidae in the annelid tree has been debated for many years, (Liwanow and Porfirjewa 1967, Bubko 1973, Rieger 1976, 1988, Smith *et al*. 1987, Minichev and Bubko 1992, Westheide 1997, Eeckhaut *et al*. 2000, Rousset *et al*. 2004, Struck *et al*. 2007, 2008, Zrzavý *et al*. 2009, Capa *et al*. 2012).

Oweniids were considered as being related to siboglinids (previously pogonophorans) due to the presence of an intraepidermal nerve cord that is unique among annelids (Livanov and Porfireva 1967). This relationship has been later supported by other authors who found the absence of parapodia in the posterior segments and chaetae projecting directly from the body wall together with other shared features (although homoplastic and shared with other annelids). There is also molecular evidence for this sister group relationship and support for the concept of oweniids being derived annelids (Eeckhaut *et al*. 2000, Rousset *et al*. 2004, Struck *et al*. 2007, 2015, Andrade *et al*. 2015).

Unspecialized monociliated cells are present in the epithelia and nephridia of *Owenia* and *Myriowenia* (Gardiner 1978, Smith *et al*. 1987, Westheide 1997). This feature also occurs in the larval feeding tentacles of *Magelona mirabilis* (see Johnston 1865, Bartolomaeus 1995). Relationships between magelonids and oweniids and their position in the Annelida are still the subject of intense debate. Some authors argue that an epithelium consisting mostly of unspecialized monociliated cells represents a basal condition within Metazoa (e.g., Rieger 1976, Gardiner 1978, Westheide 1997). Others, however, state that this condition is convergent and derived in the two groups, resulting from truncated ciliogenesis that suppresses the formation of additional cilia in cells that were previously multiciliated (Bartolomaeus 1995). The position of the Oweniidae at the base of the annelid tree is supported by molecular or combined morphological and molecular data (e.g., Zrzavý *et al*. 2009). Recent phylogenomic analyses of the Annelida, using transcriptomics and the most comprehensive molecular data set assembled to date, recovers Oweniidae and Magelonidae as sister groups at the base of the annelid tree (Weigert *et al*. 2014, Andrade *et al*. 2015, Struck *et al*. 2015, Helm *et al*. 2018).

Phylogenetic analyses assess the monophyly of the Oweniidae, supported by the shared presence of (1) dorsolateral ciliary folds, (2) an intraepidermal nerve cord, (3) neuropodial patches with fields of densely concentrated bifurcated hooks, and (4) elongated but dissimilar median segments (Sene-Silva 2002, Capa *et al*. 2012). The family currently consists of four genera: *Owenia*, *Myriochele*, *Galathowenia*, and *Myriowenia* (Capa *et al*. 2012; Fig. 4.1.14). The suggested monophyly of *Owenia* and *Myriowenia* is based in large part on the presence of their characteristic head appendages (tentacular crown and grooved palps, respectively) and uncini (with teeth arranged side by side and vertically, respectively). A recent analysis by Capa *et al*. (2012) also recovered *Galathowenia* monophyletic. This conclusion is especially supported by the shape of the head and the presence of a ventral cleft (as suggested by Kirkegaard 1959, 1983, Fauchald 1977, Blake 1984, 2000, Parapar 2001, 2003b, 2006). Other authors, however, consider *Galathowenia* to be a junior synonym of *Myriochele* (e.g., Blake and Dean 1973, Nilsen and Holthe 1985, Hartmann-Schröder 1996, Cantone and Di Pietro 1998, Sene-Silva 2002). In the same study by Capa *et al*. (2012), *Myriochele* was shown to be a paraphyletic taxon, containing species of *Myrioglobula* nested within the clade of *Myriochele*. Consequently, the two genera were synonymized (Capa *et al*. 2012). *Myriochele*, as currently conceived, is characterized by the presence of acicular chaetae with an elongated tapering distal end and a smooth surface and by the shape of the head, similar in width to the segments and with a rounded anterior margin (Capa *et al*. 2012).

## Taxonomy

### Oweniidae Rioja, 1917

**Diagnosis:** Body cylindrical. Prostomium and peristomium fused forming the head. Nuchal organs absent. Mouth terminal or shifted ventrally. Segments of unequal length. Anterior region with one to three short, contiguous or not, uniramous segments, following segments biramous. Notopodial chaetae emerging from body wall, capillaries with characteristic structure of the cortex, resembling small imbricated scales and, occasionally, smooth acicular chaetae. Neuropodia as low tori with irregular rows of bidentate uncini. Parapodial branchiae or cirri absent. Tube as a thin secreted layer encrusted with foreign objects. Distinct mitraria larva. Intraepidermal nerve cord present.

### *Galathowenia* Kirkegaard, 1959

**Type species:** *Galathowenia africana* Kirkegaard, 1959, by original designation.

**Synonyms:** *Clymenia* Ørsted, 1844 (not Münster [Ammonoidea]); *Psammocollus* Grube, 1866.

Twelve described species (Parapar 2003b, Capa *et al*. 2012). A genus reported worldwide.

**Diagnosis:** Head cylindrical, anteriorly truncated, terminal mouth extending midventrally as an elongated slit and with ventral pharyngeal organ. Breakage groove between first and second chaetigers. Esophageal commissure Y-shaped. First three segments generally uniramous, with capillaries on notopodia. Following segments biramous; notopodia with capillary chaetae only and neuropodial uncini with two teeth generally arranged obliquely.

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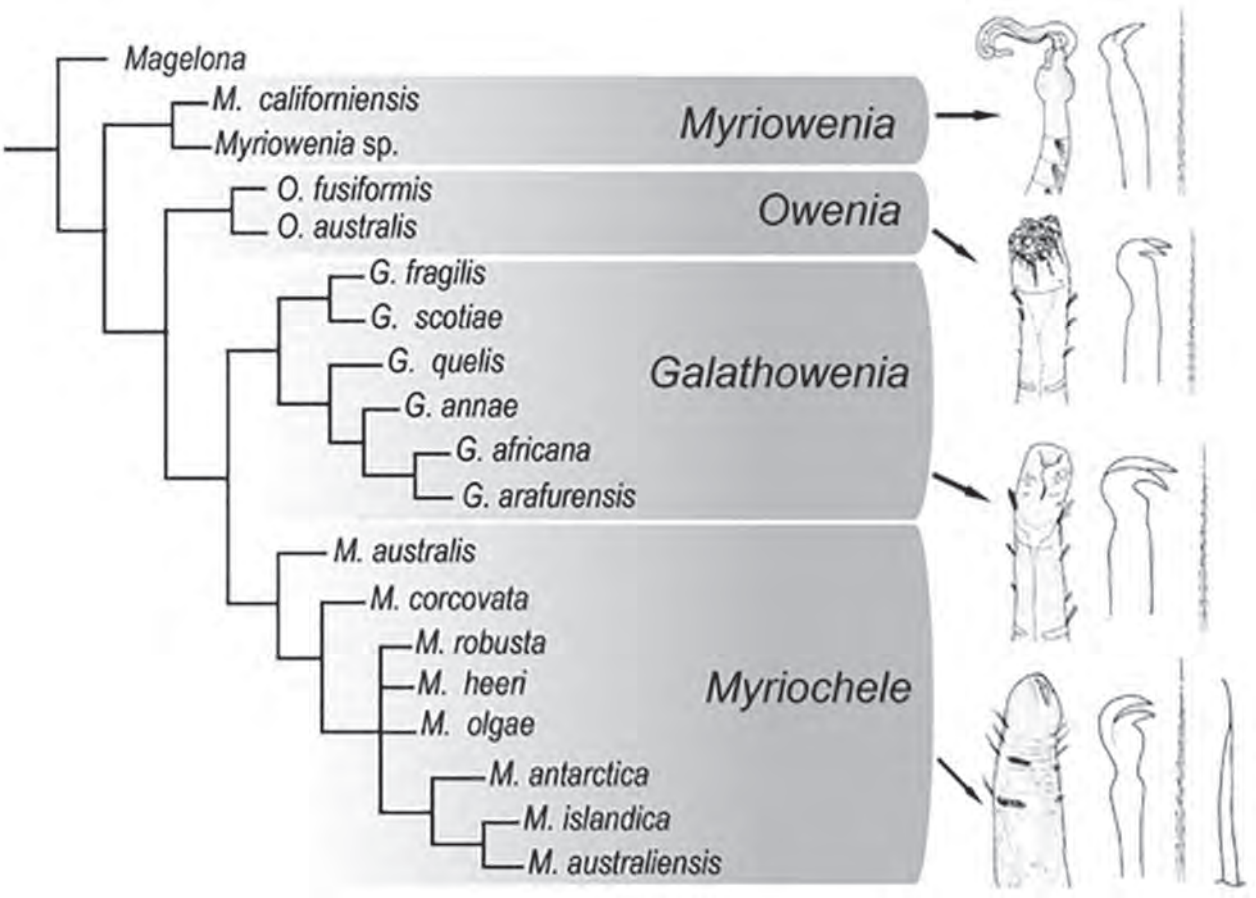


**Fig. 4.1.14:** Phylogenetic hypothesis (strict consensus of most parsimonious trees) of morphological data, after weighting less homoplasious (implied weighting, concavity constant k = 3–4), with some of the morphological features characteristic of genus. After Capa *et al.* (2012).

***Myriochele* Malmgren, 1867**

**Type species:** *Myriochele heeri* Malmgren, 1867, by original designation.

**Synonyms:** *Myrioglobula* Hartman, 1967.

Twenty-three species described (Parapar 2003a, Capa *et al.* 2012). A genus reported worldwide.

**Diagnosis:** Body short and thick, tapering at both ends (cigar-like). Head with anterior end rounded, lacking appendages. Mouth terminal or slightly elongated ventrally but without a ventral slit and developed lips on the sides. Anterior one to three segments uniramous, subsequent segments biramous. Notopodia with capillary and acicular chaetae (latter type often absent in anterior-most chaetigers). Neuropodial tori with uncini bearing two similarly sized teeth generally arranged vertically but obliquely in some species.

**Remarks:** A phylogenetic analysis, using morphological features, by Capa *et al.* (2012) suggested that *Myrioglobula* should be considered as a junior synonym of *Myriochele*. Although the support value for this clade was not strong, the synonymization was justified because the only feature distinguishing these two genera was the number of anterior uniramous segments. However, this character is now known to vary and overlaps between *Myrioglobula* and *Myriochele* (Capa *et al.* 2012). Moreover, several other features such as the shape of the body and head, the presence of acicular chaetae, and the arrangement of uncinal teeth are shared between the two groups.

***Myriowenia* Hartman, 1960**

**Type species:** *Myriowenia californiensis* Hartman, 1960, by original designation.

Two species described (Capa *et al.* 2012). A genus rarely reported (California, Gulf of Mexico, Australia).

**Diagnosis:** Head with pair of large grooved palps and bilobed prostomium; mouth anteroventral, with ventral pharyngeal organ. Breakage groove between head and first segment. First three segments uniramous, with capillary notochaetae. Biramous segments with capillaries on notopodia and neuropodial tori with fewer than five

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rows of bidentate uncini, with teeth arranged in a vertical position, dissimilar in size with proximal tooth larger.

### *Owenia* Delle Chiaje, 1844

**Type species:** *Owenia fusiformis* Delle Chiaje, 1844, by original designation.

**Synonyms:** *Ammochares* Grube, 1846; *Ops* Carrington, 1865 Eighteen species described (Ford and Hutchings 2005, Parapar and Moreira 2015, Silva and Lana 2017). A genus reported worldwide.

**Diagnosis:** Body thick and rigid. Head with prostomial tentacular crown. Anterior elongated mouth surrounded by membranous lips. Anterior three segments with capillaries only; third notopodia dorsal with respect to other anterior notopodia. Biramous segments with capillaries on notopodia and more than 20 irregular rows of bidentate uncini with teeth arranged side by side on neuropodial tori. Pygidium as a terminal rim or with a pair of weakly developed lobes. Tube generally tapering toward both ends and covered with foreign objects imbricated like roof tiles.

**Remarks:** Although a number of species of *Owenia* have been described, Hartman (1959) synonymized many of these with *O. fusiformis* without providing any justification, and this has been widely accepted. However, recent studies suggest that *O. fusiformis* has a restricted distribution to North Atlantic waters (e.g., Koh and Bhaud 2001, Koh *et al.* 2003, Ford and Hutchings 2005). Therefore, this "cosmopolitan" taxon actually represents a suite of sibling species. A global revision of the genus should be performed.

### Key to Oweniid Genera

| | |
|---|---|
| 1. Head with tentacular crown | *Owenia* |
| Head without tentacular crown | 2 |
| 2. Head with pair of long, grooved palps | *Myriowenia* |
| Head without palps | 3 |
| 3. Head rounded, mouth terminal or slightly elongated ventrally, not forming ventral slit, capillary and acicular chaetae present | *Myriochele* |
| Head elongated and truncated anteriorly, mouth terminal continuing ventrally as slit; only capillary chaetae present | *Galathowenia* |

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### References

Aguirrezabalaga, F., Gil, J. & Viéitez, J.M. (2000): Presence of *Myriochele danielsseni* Hansen, 1879 (Polychaeta, Oweniidae) en las costas de la Península Ibérica. *Boletín de la Real Sociedad Española de Historia Natural* 96: 57–68.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Bartolomaeus, T. (1995): Secondary monociliarity in the Annelida: monociliated epidermal cells in larvae of *Magelona mirabilis* (Magelonida). *Microfauna Marina* 103: 27–332.

Bartolomaeus, T. (1998): Chaetogenesis in polychaetous Annelida – significance for annelid systematics and the position of the Pogonophora. *Zoology* 100: 348–364.

Berkeley, E. (1949): Morphological characters of *Myriochele heeri* Malmgren. *Nature* 164: 239.

Blake, J.A. (1984): Polychaeta Oweniidae from Antarctic seas collected by the United States Antarctic Research Program. In: Hutchings P.A. (ed.) *Proceedings of the First International Polychaete Conference*. The Linnean Society of New South Wales, Sydney: 112–117.

Blake, J.A. (2000): Chapter 5. Family Oweniidae Rioja, 1917. In: Blake, J.A, Hilbig, B. & Scott, P.V. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 7. The Annelida. Part 4: Polychaeta: Flabelligeridae to Sternaspidae.* Santa Barbara Museum Natural History, Santa Barbara, CA: 97–127.

Blake, J.A. & Dean, D. (1973): Polychaetous annelids collected by the R/V Hero from Baffin Island, Davis Strait, and west Greenland in 1968. *Bulletin of the Southern California Academy of Sciences* 72: 31–39.

von Brand, T.F. (1927): Stoffbestand und Ernahrung einiger Polychaten und anderer mariner Wiirmer. *Zeitschrift fur Vergleichende Physiologie* 5: 643–698.

Bubko, O. (1973): On systematic position of Oweniidae and Archiannelida (Annelida). *Zoologischeskii Zhurnal* 52: 1286–1296 [in Russian].

Bubko, O.V. & Minichev, Y.S. (1972): The nervous system of Oweniidae (Polychaeta). *Zoologischeskii Zhurnal* 51: 1288–1299 [in Russian].

Buchanan, J.B., Sheader, M. & Kingston, P.F. (1978): Sources of variability in the benthic macrofauna off the South Northumberland coast, 1971–1976. *Journal of the Marine Biological Association of the United Kingdom* 58: 191–209.

Cantone, G. & Di Pietro, N. (1998): A new species of *Myriochele* (Polychaeta, Oweniidae) from Antarctica, with considerations on Antarctic oweniids. *Polar Biology* 19: 421–423.

Capa, M., Hutchings, P.A., Aguado, M.T. & Bott, N.J. (2011): Phylogeny of Sabellidae (Annelida) and relationships with other taxa inferred from morphology and multiple genes. *Cladistics* 27: 447–557.

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Capa, M., Parapar, J. & Hutchings, P. (2012): Phylogenetic analyses of Oweniidae (Polychaeta) and taxonomic revision of Australian fauna reveals relationships and undocumented diversity within this enigmatic group of marine worms. *Zoological Journal of the Linnean Society* 166: 236–278.

Carrington, B. (1865): On the chaetopod annelids of the Southport sands. *Proceedings of the Literary and Philosophical Society of Manchester* 1865: 176–188.

Cazaux, C. (1973): Cycle et distribution des larves de Polychètes caractères du méroplancton des différents types de masses d'eaux du Bassin d'Arcachon. *Bulletin Ecologie* 4: 257–274.

Coulon, J. & Bessone, R. (1979): Autoradiographic detection of indolamine and catecholamine neurons in the nervous system of *Owenia fusiformis* (Polychaeta, Annelida). *Cell and Tissue Research* 198: 95–104.

Dales, R.P. (1957): The feeding mechanism and structure of the gut of *Owenia fusiformis* Delle Chiaje. *Journal of the Marine Biological Association of the United Kingdom* 36: 81–89.

Dales, R.P. (1958): Survival of anaerobic periods by two intertidal polychaetes, *Arenicola marina* (L) and *Owenia fusiformis* delle Chiaje. *Journal of the Marine Biological Association of the United Kingdom* 37: 521–529.

Dales, R.P. (1962): The polychaete stomodeum and the interrelationships of the families of Polychaeta. *Proceedings of the Zoological Society of London* 139: 389–428.

Dauvin, J.C. & Thiébaut, E. (1994): Is *Owenia fusiformis* Delle Chiaje a cosmopolitan species? Actes de la 4ème Conference Internationale de Polychètes. *Memoires Du Muséum National d'Histoire Naturelle (Zoologie)* 162: 383–404.

Day, J. (1973): New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Technical Report NMFS CIRC* 375: 1–140.

Day, J.H. & Hutchings, P.A. (1984): Descriptive notes on the fauna and flora of Merimbula, Pambula and Back Lakes, New South Wales. *Australian Zoologist* 21: 269–289.

Delle Chiaje, S. (1844): *Descrizione e Notomia degli Animali Invertebrati della Sicilia Citeriore osservati vivi negli anni 1822–1830*. Tomo Ottavo. Appendice, Osservazioni Critiche, Indice Generale. Stabilimento Tipografico di C. Batelli e Comp. Napoli. Available at: http://www.biodiversitylibrary. org/item/40601#page/319/mode/1up.

Eeckhaut, I., McHugh, D., Mardulyn, P., Tiedemann, R., Monteyne, D., Jangoux, M. & Milinkovitch, M.C. (2000): Myzostomida: a link between trochozoans and flatworms? *Proceedings of the Royal Society of London B* 267: 1383–1392.

Eckelbarger, K.J. (1983): Evolutionary radiation in polychaete ovaries and vitellogenic mechanisms: their possible role in life history patterns. *Canadian Journal of Zoology* 61: 487–504.

Eckman, J.E., Nowell, A.R.M. & Jumars, P.A. (1981) Sediment destabilization by animal tubes. *Journal of Marine Research* 39: 361–374.

Fager, E.W. (1964): Marine sediments: effects of tube-dwelling polychaete. *Science* 143: 356–359.

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

Fiege, D., Kröncke, I. & Barnich, R. (2000): High abundance of *Myriochele fragilis* Nilsen & Holthe, 1985 (Polychaeta: Oweniidae) in the deep sea of the Eastern Mediterranean. *Hydrobiologia* 426: 97–103.

Fontés, M., Coulon, J. & Delgross, M.H. (1983): Muscle dedifferentiation and contractile protein synthesis during post-traumatic regeneration by *Owenia fusiformis* (Polychaete: Annelid). *Cell Differentiation* 13: 267–282.

Ford, E. & Hutchings, P. (2005): An analysis of morphological characters of *Owenia* useful to distinguish species: description of three new species of *Owenia* (Oweniidae: Polychaeta) from Australian waters. *Marine Ecology* 26: 181–196.

Fransen, M.E. (1988): Coelomic and vascular systems. *Microfauna Marina* 4: 199–213.

Gambi, M.C. (1989): Osservazioni su morfologia funzionale e comportamento trofico di *Owenia fusiformis* delle Chiaje (Polychaeta, Oweniidae) in rapporto ai fattori ambientali. *Oebalia* XV-1: 145–155.

Gardiner, S.L. (1978): Fine structure of the ciliated epidermis on the tentacles of *Owenia fusiformis* (Polychaeta, Oweniidae). *Zoomorphologie* 91: 37–48.

Gardiner, S.L. & Rieger, R.M. (1980): Rudimentary cilia in muscle cells of annelids and echinoderms. *Cell and Tissue Research* 213: 247–252.

Gentil, F., Dauvin, J.C. & Menard, F. (1990): Reproductive biology of the polychaete *Owenia fusiformis* Delle Chiaje in the Bay of Seine (eastern English Channel). *Journal of Experimental Marine Biology and Ecology* 142: 13–24.

Gibbs, P.E. (1972): Polychaete annelids from the Cook Islands. *Journal of Zoology, London* 168: 199–220.

Grube, A.E. (1846): Beschreibungen neuer oder wenig bekannter Anneliden. Zweiter Beitrag: *Canephorus elegans* Gr., *Ammochares ottonis* Gr, *Dasymallus caducus* Gr., *Scalis minax* Gr. Archiv Für Naturgeschichte, Berlin 12: 161–171.

Grube, A.E. (1866): Beschreibungen neuer von der Novara – Expedition mitgebrachter Anneliden und einer neuen Landplanarie. *Verhandlungen Der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 16: 173–184.

Hartman, O. (1955): Endemism in the North Pacific Ocean, with emphasis on the distribution of marine annelids, and descriptions of new or little known species. In: Allan Hancock Foundation (ed.). *Essays in the Natural Sciences in Honor of Captain Allan Hancock on the Occasion of His Birthday July 26*, Los Angeles, University of Southern California Press, Los Angeles, CA: 39–60.

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

Hartman, O. (1960): Systematic account of some marine invertebrate animals from the deep basins of southern California. In: Hartman, O. & Barnard, J.L. (eds.) *The Benthic Fauna of The Deep Basins Off Southern California. Part II. Allan Hancock Pacific Expeditions, No. 22*. The University of Southern California Press, Los Angeles, CA: 69–215.

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

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

Hartman, O. (1969): *Atlas of the Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.

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Hartman, O. (1978): Polychaeta from the Weddell Sea Quadrant, Antarctica. Biology of the Antarctic Seas VI. *Antarctic Research Series* 26: 125–223.

Hartman, O. & Barnard, J.L. (1960): The benthic fauna of the deep basins off southern California. *Allan Hancock Pacific Expeditions* 22: 67–297.

Hartmann-Schröder, G. (1996): *Annelida, Borstenwürmer, Polychaeta*. In: Dahl, F. & Schumann, H. (eds.) *Die Tierwelt Deutschlands*. 2nd ed. Gustav Fischer Verlag, Jena: 58: 1–648.

Hartmann-Schröder, G. & Rosenfeldt, P. (1989): Die Polychaeten der 'Polarstern' Reise ANT III/2 in die Antarktis 1984. Teil 2: Cirratulidae bis Serpulidae. *Mitteilungen des Hamburgischen Zoologischen Museums und Institut* 86: 65–106.

Hartmann-Schröder, G. & Rosenfeldt, P. (1991): Die Polychaeten der "Walther Herwig"– Reise 68/1 nach Elephant Island (Antarktis) 1985. Teil 2: Acrocirridae bis Sabellidae. *Mitteilungen aus dem Hamburger zoologischen Museum und Institut* 88: 73–96.

Hartmann-Schröder G (1996) Annelida, Borstenwürmer, Polychaeta. (2. Aufl.) In: F. Dahl, Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und ihrer Lebensweise. Teil 58. Jena: Gustav Fischer Verlag. p. 648

Hausen, H. (2005a): Comparative structure of the epidermis in polychaetes (Annelida). *Hydrobiologia* 535/536: 25–35.

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

Helm, C., Beckers, P., Bartolomaeus, T., Drukewitz, S.H., Kourtesis, I., Weigert, A., Purschke, G., Worsaae, K., Struck, T.H., Bleidorn, C. (2018): Convergent evolution of th ladder-like nerve cord in Annelida. *Frontiers in Zoology* 15:36, 1–17.

Hutchings, P.A. (2000): Family Oweniidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.) *Polychaetes & allies: The Southern synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 173–176.

Hutchings, P.A. & Murray, A. (1984): Taxonomy of Polychaetes from the Hawkesbury River and the Southern Estuaries of New South Wales, Australia. *Records of the Australian Museum* Supplement 3: 1–118.

Hutchings, P.A. & Rainer, S. (1979): A key to estuarine Polychaetes in New South Wales. *Proceedings of the Linnean Society of New South Wales* 104: 35–48.

Imajima, M. & Morita, Y. (1987): Oweniidae (Annelida, Polychaeta) from Japan. *Bulletin of the National Science Museum, Tokyo Series A* 13: 85–102.

Jolly, M.T., Viard, F., Gentil, F., Thiébaut, E. & Jollivet, D. (2006): Comparative phylogeography of two coastal polychaete tubeworms in the Northeast Atlantic supports shared history and vicariant events. *Molecular Ecology* 15: 1841–1855.

Johnston, G. (1865): A catalogue of the British non-parasitical worms in the collection of the *British Museum. British Museum. London* 1–365.

Kirkegaard, J.B. (1956): Benthic polychaeta from depths exceeding 6000 meters. *Galathea Report* 2: 63–75.

Kirkegaard, J. (1959): The Polychaeta of West Africa. Part I. Sedentary species. *Atlantide Reports* 5: 10–117.

Kirkegaard, J.B. (1969): A quantitative investigation of the central North Sea. *Polychaeta. Spolia* 29: 1–285.

Kirkegaard, J. (1983): Bathyal benthic polychaetes from the N. E. Atlantic Ocean, S. W. of the British Isles. *Journal of the Marine Biological Association of the United Kingdom* 63: 593–608.

Koh, B.S. & Bhaud, M. (2001): Description of *Owenia gomsoni* n. sp. (Oweniidae, Annelida Polychaeta) from the Yellow Sea and evidence that *Owenia fusiformis* is not a cosmopolitan species. *Vie et Milieu* 51: 77–87.

Koh, B.S., Bhaud, M. & Jirkov, I. (2003): Two new species of *Owenia* (Annelida: Polychaeta) in the northern part of the north Atlantic Ocean and remarks on previously erected species from the same area. *Sarsia* 88: 175–188.

Künitzer, A. (1990): *Zur Verbreitung und Populationsdynamik der Bodenfauna der zentralen Nordsee*. Dissertation, Universität Bremen.

Liwanow, N.A. & Porfirjewa, N.A. (1967): Die Organisation der Pogonophoren und deren Beziehungen zu den Polychäten. *Biologisches Zentralblatt* 86: 177–204.

Milligan, M.R. (1984): Family Oweniidae Rioja 1917. In: Uebelacker, J.M. & Johnson, P.G. (eds.) *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico. Vol. VI. Mobile: Barry A. Vittor and Associates*: 46.1–46.12.

Malmgren, A.J. (1867): Annulata Polychaeta Spetsbergiae, Grönlandiae, Islandiae et Scandinaviae hactenus cognita. Öfversigt af Kongligen. *Vetenskaps-Akademiens Förhandlingar* 24: 127–235.

Martín, D. (1989): Revisión de las especies de Owenidae (Annelida, Polychaeta) de la Península Ibérica. *Scientia Marina* 53: 47–52.

Martin D., Koh B.S., Bahud M., Dutrieux E. & Gil J. (2006): The genus *Owenia* (Annelida: Polychaeta) in the Persian Gulf, with description of *Owenia persica* sp. nov. *Organisms Diversity and Evolution* 6: 1–21.

McNulty, J.K. & López, N.N. (1969): Year-round production of ripe gametes by benthic polychaetes in Biscayne Bay, Florida. *Bulletin of Marine Science* 19: 945–954.

Ménard, F., Gentil, F. & Dauvin, J.C. (1989): Population dynamics and secondary production of *Owenia fusiformis* Delle Chiaje (Polychaeta) from the Bay of Seine (eastern English Channel). *Journal of Experimental Marine Biology and Ecology* 133: 151–167.

Meyer, K. & Bartolomaeus, T. (1996): Ultrastructure and formation of the hooked setae in *Owenia fusiformis* delle Chiaje, 1842: implications for annelid phylogeny. *Canadian Journal of Zoology* 74: 2143–2153.

Minichev, Y.S. & Bubko, O.V. (1992): Are the Oweniidae polychaetes? Polychaetes and their ecological significance. *Academy of Sciences, Explorations of the Fauna of the Seas* 43: 47–51 [in Russian].

Nilsen, R. & Holthe, T. (1985): Arctic and Scandinavian Oweniidae (Polychaeta) with comments on the phylogeny of the family. *Sarsia* 70: 17–32.

Noffke, A., Hertweck, G., Kröncke, I. & Wehrmann, A. (2009): Particle size selection and tube structure of the polychaete *Owenia fusiformis*. *Estuarine, Coastal and Shelf Science* 81: 160–168.

Oliver, J.S. (1984): Selection for asexual reproduction in an Antarctic polychaete worm. *Marine Ecology Progress Series* 19: 3–38.

Okada, K. (1970): Annelida. In: Kume, M. & Dan, K. (eds.) *Invertebrate Embryology*. Bai Fu Kan Press, Tokyo: 192–241.

Orrhage, L. (1964): Anatomische und morphologische Studien über die Polychaeten familien Spionidae, Disomidae und Poecilochaetidae. *Zoologiska Bidrag Från Uppsala* 36: 335–405.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Orrhage, L. (1978): On the structure and evolution of the anterior end of the Sabellariidae (Polychaeta Sedentaria): with some remarks on the general organisation of the polychaete brain. *Zoologische Jahrbücher, Anatomie und Ontogenie der Tiere* 100: 343–374.

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

Ørsted, A.S. (1844): Zur classification der Annulaten mit Beschreibung einiger neuer oder unzulänglichbekannter Gattungen und Arten. Archiv Für Naturgeschichte. *Berlin* 10: 99–112.

Parapar, J. (2001): Revision of five species referred to *Myriochele* and *Galathowenia* (Polychaeta: Oweniidae) from the Antarctic Seas based upon type material. *Proceedings of the Biological Society of Washington* 114: 403–413.

Parapar, J. (2003a): Oweniidae (Annelida, Polychaeta) from Icelandic waters, collected by the BIOICE project, with the description of *Myrioglobula islandica* n. sp. *Sarsia* 88: 274–290.

Parapar, J. (2003b): Resurrection of *Galathowenia australis* (Polychaeta, Oweniidae) based upon type material. *Cahiers de Biologie Marine* 44: 249–255.

Parapar, J. (2003c): Two new species of *Myriochele* (Polychaeta: Oweniidae) from the Bransfield Strait (Antarctica). *Antarctic Science* 15: 219–226.

Parapar, J. (2006): The genera *Myriochele* and *Myrioglobula* (Polychaeta, Oweniidae) in Icelandic waters with the revision of type material of *Myriochele heeri* Malmgren, 1867, and the description of a new species. *Journal of Natural History* 40: 523–547.

Parapar, J.& Moreira, J. (2015): The Oweniidae (Annelida; Polychaeta) from Lizard Island (Great Barrier Reef, Australia) with the description of two new species of *Owenia* Delle Chiaje, 1844. *Zootaxa* 4019(1): 604–620.

Pettibone, M.H. (1982): Annelida. In: Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill Book Co, New York: 1–43.

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

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

Purschke, G. & Tzetlin, A.B. (1996): Dorsolateral ciliary folds in the polychaete foregut: structure, prevalence and phylogenetic significance. *Acta Zoologica* 77: 33–49.

Rieger, R.M. (1976): Monociliated epidermal cells in Gastrotricha: significance for concepts of early metazoan evolution. *Zeitschrift Fiir Zoologische Systematik und Evolutionsforschung* 14: 198–226.

Rieger, R.M. (1988): Comparative ultrastructure and the Lobatocerebridae: keys to understand the phylogenetic relationships of Annelida and the acoelomates. *Meiofauna Marina* 4: 373–382.

Rioja, E. (1917): Datos para el conocimiento de la fauna de anélidos poliquetos del Cantábrico. Trabajos del Museo Nacional de Ciencias Naturales. *Serie Zoológica* 29: 1–111.

Rouse, G.W. (1988): An ultrastructural study of the spermatozoa from *Prionospio* cf. *queenslandi* and *Tripolydora* sp.: two spionid polychaetes with different reproductive methods. *Acta Zoologica* 69: 205–216.

Rouse, G.W. (2001): Oweniidae. Pp. 185–188. In: Rouse, G.W. & Pleijel, F. (eds.) *Polychaetes*. Oxford: Oxford University Press.

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

Rousset, V., Rouse, G.W., Siddall, M.E., Tillier, A. & Pleijel, F. (2004): The phylogenetic position of Siboglinidae (Annelida) inferred from 18S rRNA, 28 S rRNA and morphological data. *Cladistics* 20: 518–533.

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

Sene-Silva, G. (2002): Phylogenetic relationships within Oweniidae Rioja (Polychaeta, Annelida). *Revista Brasileira De Zoologia* 19: 999–1010.

Signor, P.W. & McMenamin, M.A.S. (1988): The early Cambrian worm tube *Onuphionella* from California and Nevada. *Journal of Palaeontology* 62: 233–240.

Silva, L. & Lana, P. (2017). *Owenia caissara* sp. n. (Annelida, Oweniidae) from Southern Brazil: addressing an identity crisis. *Zoologia* 34: 1–7.

Smart, T.I. & Dassow, G.V. von (2009): Unusual development of the mitraria larva in the polychaete *Owenia collaris*. *Biological Bulletin* 217: 253–268.

Smith, P.R., Ruppert, E.E. & Gardiner, S.L. (1987): A deuterostome-like nephridium in the mitraria larva of *Owenia fusiformis* (Polychaeta, Annelida). *Biological Bulletin* 172: 315–323.

Somaschini, A. (1993): A Mediterranean fine-sand polychaete community and the effect of the tube-dwelling *Owenia fusiformis* Delle Chiaje on community structure. *Internationale Revue der Gesamten Hydrobiologie* 78: 219–233.

Storch, V. (1988): Integument. In: Westheide, W. & Hermans, C.O. (eds.) The ultrastructure of Polychaeta. *Microfauna Marina* 4: 13–36.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015). The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology*, 25(15): 1993–1999.

Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular, Phylogenetics and. Evolution* 48: 628–645.

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

Thiébaut, E. & Dauvin, J.C. (1991): Modelling of population dynamics of *Owenia fusiformis* (Annelida, Polychaeta) in eastern Bay of Seine. In: Herman, P.M.J., *et al.* (eds.) *Report of the Workshop Modelling the Benthos*. Delta Institute Communication, Yerseke 538: 189–190.

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

Tzetlin, A.B. & Filippova, A.V. (2005): Muscular system in polychaetes (Annelida). *Hydrobiologia* 535/536:113–126.

Tzetlin, A.B. & Purschke, G. (2005): Pharynx and intestine. In: Bartolomaeus, T. & Purschke, G. (eds.) Morphology, molecules, evolution and phylogeny in Polychaeta and related taxa. *Hydrobiologia* 535/536: 199–225.

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Villalobos-Guerrero, T.F. (2009): 34. Oweniidae Rioja, 1917. In: de León-González, J.A., Bastida-Zavala, J.R., Carrera-Parra, L.F., García-Garza,M.E., Peña-Rivera, A., Salazar-Vallejo, S.I. & Solís-Weiss, V (eds.) *Poliquetos (Annelida: Polychaeta) de México y América Tropical. Universidad Autónoma de Nuevo León*. Monterrey: 391–402.

Warren, L.M. & Dales, R.P. (1980): Glucose degradation in the polychaete annelid *Owenia fusiformis* Delle Chiaje under anaerobic conditions. *Comparative Biochemistry and Physiology B* 65: 443–445.

Watson, A.T. (1901): On the structure and habits of the Polychaetae of the family Ammocharidae. *Journal of the Linnean Society* 28: 230–260.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Wells, R.M.G., Dales, R.P. & Warren, L.M. (1981): Oxygen equilibrium characteristics of the erythrocruorin (extracellular haemoglobin) from *Owenia fusiformis* Delle Chiaje (Polychaeta: Oweniidae). *Comparative Biochemistry and Physiology A* 70A: 111–114.

Westheide, W. (1997): The direction of evolution within the Polychaeta. *Journal of Natural History* 31: 1–15.

Wilson, D.P. (1932): On the mitraria larva of *Owenia fusiformis* Delle Chiaje. *Philosophical Transactions of the Royal Society of London, Series B* 221: 231–334.

Zachs, I.G. (1923): Sur un nouveau Ammocharidae (*Myriochele oculata* n. sp.) provennant de l'expédition du Prof. Deruguine dans la Mer-Blanche en 1922. *Trudy Petrogradskogo Obshchestva Estestvoispytatelei* 53: 171–174.

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

Kate Mortimer

# 4.2 Magelonidae Cunningham & Ramage, 1888

## Introduction

The Magelonidae is a relatively small family of annelid worms containing 68 species in two genera: the type genus *Magelona* F. Müller, 1858 (possessing a thoracic region of nine chaetigers, Fig. 4.2.1 B) and the monotypic *Octomagelona* Aguirrezabalaga, Ceberio & Fiege, 2001 (possessing eight thoracic chaetigers). However, at least a further three undescribed species of the latter genus are believed to exist in Mexican, Australian, and West African (Fig. 4.2.20) waters (Brasil, Glasby, and author, personal communication, respectively). A third genus, *Meredithia* Hernández-Alcántara & Solís-Weiss, 2000, was synonymized with *Magelona* by Mortimer and Mackie (2006). All previously introduced generic names for the group (*Maea* Johnston, 1865; *Rhynophylla* Carrington, 1865) and the family name (Maedae Johnston, 1865) have been similarly synonymized. The family is characterized by the presence of distinct shovel-shaped prostomia and paired papillated palps.

Comprehensive work on the group consists of a series of papers by McIntosh (1877, 1878, 1879, 1911) and Jones (1963, 1968, 1971, 1977, 1978) and more recently those by Mortimer and Mackie (2003, 2006, 2009, 2014), Mortimer (2010), Mortimer *et al.* (2011, 2012), and Zhou and Mortimer (2013), for example. Additionally, Brasil (2003) examined the phylogeny of the group based on 53 magelonid taxa.

Unique terminology has been applied to the group, introduced and subsequently modified by Jones (1963, 1971, 1978). However, there has been confusion during its use and it has been inconsistently and incorrectly applied in several species descriptions (Mortimer and Mackie 2003: 172). Rouse (2001) additionally felt that its continued use could obscure potential homologues with conditions seen in other annelid groups, and Mortimer and Mackie (2003) suggested that it encouraged synoptic descriptions, rather than detailed examinations. Subsequent authors have either abandoned its use or otherwise qualified it with positional information, particularly with regard to the lamellae and cirri.

## Morphology

### External morphology

**Size.** Adult magelonids are generally long and thin, less than 1 mm wide; however, more robust, stout species such as *Magelona alleni* Wilson, 1958, *Magelona cincta* Ehlers, 1908, and *Magelona symmetrica* Mortimer & Mackie, 2006 can attain greater widths. Magelonids may reach 150 mm in length, although average lengths for most species are unknown, due to their fragility upon collection. Fiege *et al.* (2000) recorded lengths of up to 170 chaetigers for *Magelona mirabilis* (Johnston, 1865), and 142 chaetigers were recorded for the type specimen of *Magelona filiformis* Wilson, 1959, although lengths of approximately 60–80 chaetigers are more common. However, more stout species often have a fewer number of chaetigers.

**Body regions.** The body of magelonids can be clearly divided into separate regions (Fig. 4.2.1): the head formed from the prostomium and peristomium, with the latter being limited to the buccal region (see Rouse and Fauchald 1997); a thorax with an achaetous first segment (previously regarded as the peristomium, although note comment earlier) and eight or nine chaetigers; and an abdomen comprising of many chaetigers terminating in the pygidium. The thoracic/abdominal junction is often clearly marked

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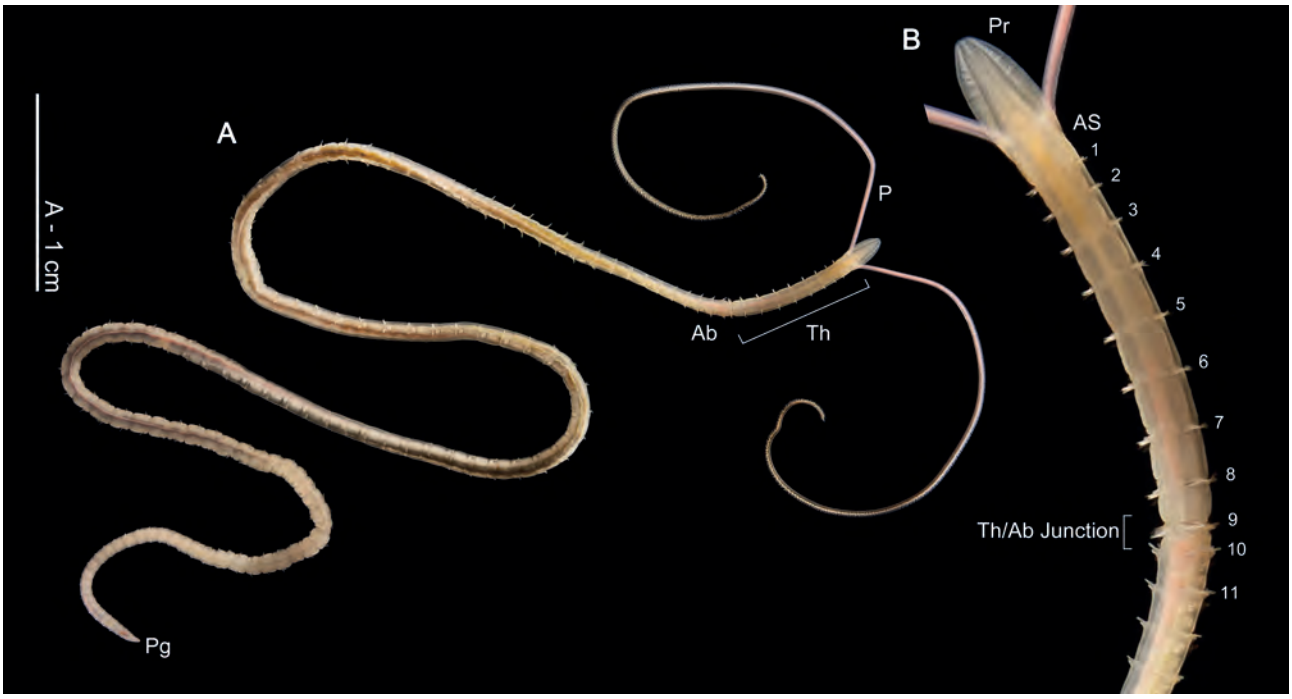


**Fig. 4.2.1:** *Magelona mirabilis* (Berwick-upon-Tweed, NMW.Z. 2013.037.0020). A, Whole body. B, Anterior, showing thoracic/abdominal junction between chaetigers 9 and 10 (Andrew Mackie, Mortimer & Mackie 2014). Ab, abdomen; AS, achaetous segment; P, palp; Pg, pygdium; Pr, prostomium; Th, thorax.

with a distinct differentiation between the two main body regions (Fig. 4.2.1) and constricted around chaetiger nine (*Magelona*). This junction is also marked by a change in chaetal type. Invariably, the abdominal width and depth are greater than those of the thorax, but stouter species, often those possessing characteristic rounded and bulbous thoracic chaetigers such as *M. cincta* (see Mortimer and Mackie 2009), have a wider thoracic region. In some species, the parapodia of chaetiger nine are obscured in a furrow between these two body regions. The exact nature of this junction, however, can be affected by contraction caused by preservation and fixation. The thorax carries capillary chaetae only, although those of chaetiger nine may be specialized, while the abdomen possesses only hooded hooks.

**Prostomium.** Magelonids are easily recognized for their characteristic flattened prostomia utilized for burrowing, giving rise to the group's common name, the shovelhead worms. However, there is great variation in their shape, as well as the length-to-width ratio, and thus is one of the most prominent features in separating species (Fig. 4.2.2). Brasil (2003) recognized three categories of prostomia based on the length-to-width ratio: those longer than wide (Fig. 4.2.2 A), those with similar widths to lengths (Fig. 4.2.2 D–I), and lastly, those wider than long (Fig. 4.2.20). This generalized pattern fits most magelonid species; however, the shape of the prostomium can be further categorized. The lateral prostomial margins may be rounded (Fig. 4.2.2 C), straight (Fig. 4.2.2 D) (as often seen in species with more triangular prostomia), or wavy (Fig. 4.2.2 M). In some species, the proximal corners of the prostomium may encircle the bases of the palps, such as in *Magelona capax* Hartman, 1965, named for its cape-like prostomium. Often, during collection, these edges become damaged and/or flattened out, giving the appearance of a greater prostomial width (see the right hand side of Fig. 4.2.2 H). The most conspicuous prostomial character is the presence or absence of horns of the anterior margin. These may be rudimentary (Fig. 4.2.2 I), as seen in species like *M. cincta*, or much more conspicuous, such as in *Magelona montera* Mortimer *et al.*, 2012 or *Magelona sinbadi* Mortimer *et al.*, 2012 (Fig. 4.2.2 L, M). The degree of separation between the horns and the anterior prostomial margin can also be quite marked; see for example Fig. 4.2.2 L, *Magelona pacifica* Monro, 1933 (see redescription by Mortimer *et al.* 2012, Fig. 4.2.2 J) and *Magelona posterelongata* Bolívar & Lana, 1986.

The anterior prostomial margin may be straight (Fig. 4.2.2 D, E), e.g., *Magelona falcifera* Mortimer & Mackie, 2003; rounded (Fig. 4.2.2 A), e.g., *M. mirabilis*; or medially indented as in *M. symmetrica* (Fig. 4.2.2 H). Those species possessing prostomial horns may have triangular anterior

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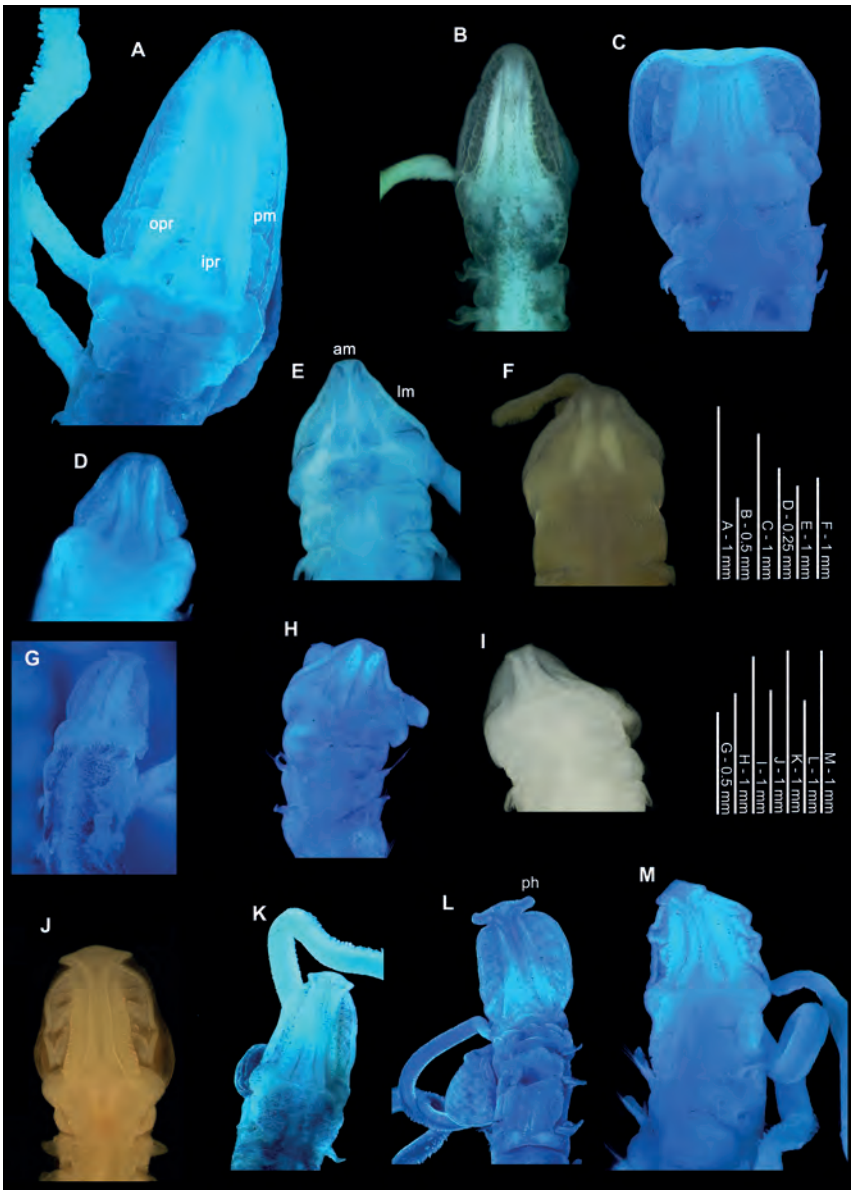


**Fig. 4.2.2:** Magelonid prostomia. A, *Magelona obockensis* (BMNH:ZB.1971.54). B, *Magelona parochilis* (NMW.Z.2012.033.0001). C, *Magelona conversa* (BMNH.2010.234). D, *Magelona* cf. *falcifera* (NMW.Z.2010.037.0010b). E, *Magelona alleni* (Morocco). F, *Magelona equilamellae* Harmelin, 1964 (SMF4675). G, *Magelona crenulifrons* (NMW.Z.2010.037.0024). H, *Magelona symmetrica* (NMW.Z.2010.037.0047b). I, *Magelona* cf. *cincta* (Iran, NMW.Z.2015.012.0004). J, *Magelona pacifica* (BMNH Type 1933.7.10.65/70). K, *Magelona pulchella* (BMNH 1969.391). L, *Magelona montera* (MNHN TYPE 1548, previously recorded as A895). M, *Magelona sinbadi* (NMW.Z.2010.037.0001). ipr, inner prostomial ridges; opr, outer prostomial ridges; pm, prostomial markings; am, anterior margin; lm, lateral margin; ph, prostomial horns. Adapted from Mortimer *et al.* (2012) and Zhou and Mortimer (2013). A–E, G, H, K–M stained with Methyl Green.

margins, which may be distinctly pointed as in *M. sinbadi* (Fig. 4.2.2 M) or rounded triangular as in *Magelona pulchella* Mohammad, 1970 (Fig. 4.2.2 K). Those with rudimentary horns often possess straight anterior margins (Fig. 4.2.2 I). Lastly, the anterior margin may be smooth or crenulated. However, the degree of crenulation can be variable, as was noted for *Magelona crenulifrons* Gallardo, 1968 in the Persian Gulf and the Gulf of Oman (Shakouri *et al.* 2017, from minutely wavy to distinct crenulations, and also in the number of crenulations present). This character has been incorrectly described as absent in some species, for example, *Magelona cornuta* Wesenberg-Lund, 1949 (Mortimer and Mackie 2009).

Generally, two pairs of longitudinal prostomial ridges are present along the mid prostomium (Fig. 4.2.2), the outer pair of which is generally shorter and abutting the inner pair for the majority of their lengths. The inner pair is typically more distinct; they may abut each other for their entire or majority of their lengths, or may be slightly separated. In species with prostomial horns, the inner pair of ridges often diverges into the corners of the horns (Fig. 4.2.2 J–M). In some species, they show distinct transverse ridging, e.g., *M. sinbadi* and *M. montera* (Fig. 4.2.2 L, M). Prostomial ridges can be extremely conspicuous, particularly in those species that have larger prostomia (see, for example, Fig. 4.2.2 J). Conversely, they can be quite indistinct, particularly the outer pair, which at times can be difficult to discern (Fig. 4.2.2 F) or entirely lacking. The exact nature of these ridges is not entirely resolved, but they are often described as muscular, and

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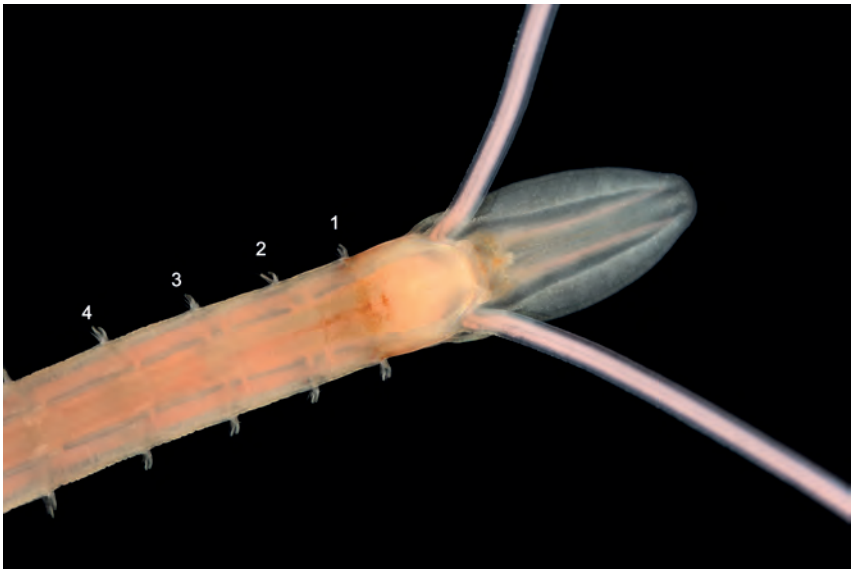


**Fig. 4.2.3:** Photograph of the anterior region (ventral view) of a live *Magelona johnstoni* (Berwick-upon-Tweed). Circulatory system and blood clearly visible, chaetigers 1–4 marked. (©Fredrik Pleijel).

Jones (1968) stated that their "inner surfaces, particularly dorsally and ventrally, are provided with longitudinal muscles". He further described them as hollow, cylindroid structures, presuming them to be fluid filled. This appears to be corroborated by live photographs of *Magelona johnstoni* Fiege, Licher & Mackie, 2000, in which they appear to be filled with the same pink blood as seen in the rest of the circulatory system (Fig. 4.2.3).

Either side of the longitudinal ridges, the prostomium often carries distinct markings (Fig. 4.2.2 A, C, J, L, M), which may be, for example, oblong, triangular, quadrangular, or reniform in shape. The pattern of these prostomial markings is often extremely characteristic within a species; for example, see *Magelona cepiceps* Mortimer & Mackie, 2006, named for its "onion-like" arched markings. Prostomial markings may be conspicuous, indistinct, or entirely absent.

**Sensory organs.** No eyes or nuchal organs have been recorded in adult magelonids. Hausen (2001) confirmed the absence of nuchal organs in two species of *Magelona* (*Magelona minuta* Eliason, 1962 and *M. mirabilis*), and Bleidorn *et al.* (2015) stated that they are completely lacking within the family. Similarly, Brasil (2003) regarded nuchal organs to be absent in all 53 taxa observed in her cladistic analysis of the group. Although eyes are absent in adult animals, ciliary sense organs, presumed to be light sensitive, are recorded in the larvae of *M. mirabilis* (see Hausen 2007). Wilson (1982) also recorded eyespots as present in the larvae of *M. alleni*, *M. filiformis*, and *M. mirabilis* from British waters.

The buccal region of magelonids has been extensively described by Dales (1962, 1977) and Orrhage (1973). This region occurs on the ventral basal side of the prostomium (Figs. 4.2.3 and 4.2.5) consisting of three lips: the larger triangular upper lip surmounting two smaller lateral lips. This region has been shown to be extendable in some species, such as *M. mirabilis* (see Mortimer and Mackie 2014). However, further investigation with live material is warranted. As stated earlier, the peristomium of magelonids is thought to be limited to the buccal region.

**Burrowing organ.** Magelonids have long been regarded to possess a ventral eversible proboscis. However, Orrhage (1973) noted the presence of an additional dorsal buccal organ as being present, and Jones (1977) further concluded that "*Magelona* has not only a ventral proboscis but also a sort of buccal organ." Further doubt of the nature of the "proboscis" in magelonids came with a specimen of *Magelona fauchaldi* Shakouri, Mortimer & Dehani, 2017 from the Persian Gulf (see Mortimer *et al.* 2012, as *Magelona* cf. *agoensis*), which possessed an everted "buccal organ/tube" between the everted "proboscis" and prostomium. Observations on feeding by McMahon and Jones (1967), Jones (1968), and Mortimer and Mackie (2014) further concluded that the ventral "proboscis" played no part in feeding but functioned only in the burrowing behavior of observed animals. It is therefore preliminarily suggested that the term *burrowing organ* be applied to the structure traditionally described as the proboscis. The eversible and ventrally placed burrowing organ is generally heart shaped when fully everted and oval when only partially everted (Fig. 4.2.4). It usually carries longitudinal ridges inferiorly, while the superior surface often appears smooth.

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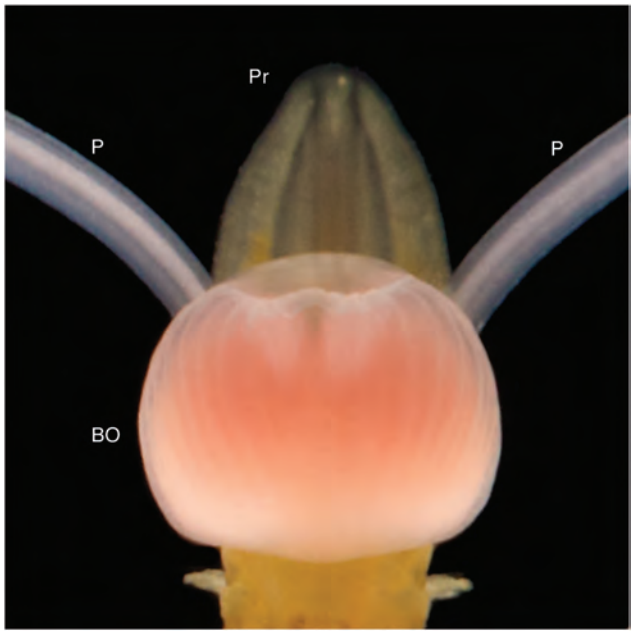


**Fig. 4.2.4:** Ventral view of the head end of a live *Magelona johnstoni* (NMW.Z. 2013.037.0018). P, Palp; Pr, Prostomium; BO, Burrowing Organ (partially everted). Andrew Mackie; adapted from Mortimer and Mackie (2014).

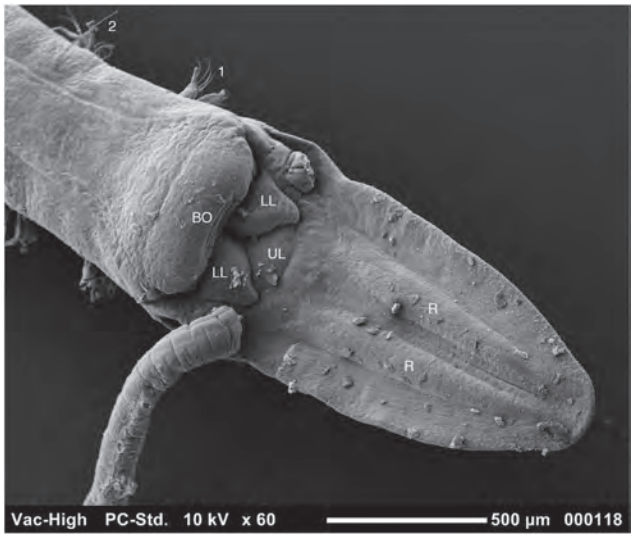


**Fig. 4.2.5:** Prostomium and first two chaetigers of *Magelona johnstoni* (NMW.Z.2013.037.0008, ventral view, showing buccal region). BO, Burrowing Organ; LL, Lateral Lip; UL, Upper Lip. Kate Mortimer; adapted from Mortimer and Mackie (2014).

**Palps.** Magelonids possess two long papillated palps, which arise ventro-laterally to the prostomium, one either side of the mouth, in all species. They are considered as peristomial, arising from the larval prototroch (Wilson 1982) and are unique among annelids in their ventral position, presence of papillae, and lack of a ciliated groove. Palp length is highly variable and species specific. Some species possess very long, slender palps, such as *M. johnstoni* (Figs. 4.2.1 A and 4.2.6 A), which are approximately half the length of the animal, while in other species (often shorter and stouter species such as *M. alleni*), they are relatively short and thick.

Papillae are generally ampuliform to digitform (Fig. 4.2.7) and vary in length. When papillae are long, it gives the palps a characteristic "frilly" appearance (often observed in species with shorter palp lengths). Papillae occur in rows along the length of palp, either side of an inconspicuous and nonciliated region. However, often termed a groove, in reality, its surface is relatively flat and no channel is present. Adjacent rows of papillae are slightly offset in an alternating pattern (see Jones 1968, Fig. 32). The number of rows is highly variable between species but is generally species specific. Brasil (2003) characterized species into three groups based on subject-predicate relations of the number of papillae (proximally and distally, being between 2 and 14 rows). Variation in the number of rows along the length of an individual palp also exists, often with proximal and distal ends carrying fewer rows than medially. The extreme proximal end is nonpapillated, and its length varies between species: often much longer in living animals than in preserved specimens. Palps are frequently lost upon collection, so details are often lacking within species descriptions.

**Thorax.** The segment directly behind the head is termed the *achaetous first segment* (Fig. 4.2.1 B), although larval studies of three species suggest that there may be one or two segments carrying chaetae, which subsequently become achaetous in latter larval stages (Wilson 1982). The size of this achaetous segment is variable within the group, although often of similar size or double the size of the first chaetiger.

As previously stated, the magelonid thorax has either eight (*Octomagelona*) or nine (*Magelona*) chaetigers. Chaetigers carry biramous parapodia with lateral lamellae, which may be equal in size between rami or larger in the notopodia. Although some species posses larger neuropodial than notopodial lamellae, this situation is infrequent. Notopodial lamellae are generally flattened postchaetal structures (filiform to foliaceous) that encircle the chaetal bundle, attaching to a low, often triangular or rounded, prechaetal lamellae, almost cuff-like (Fig. 4.2.8 A, E–H). However, in some species, the lamellae are somewhat subchaetal in position (Fig. 4.2.8 D, chaetiger 8), either for all or some of the thoracic chaetigers, for example, chaetiger 8 of *Magelona parochilis* Zhou &

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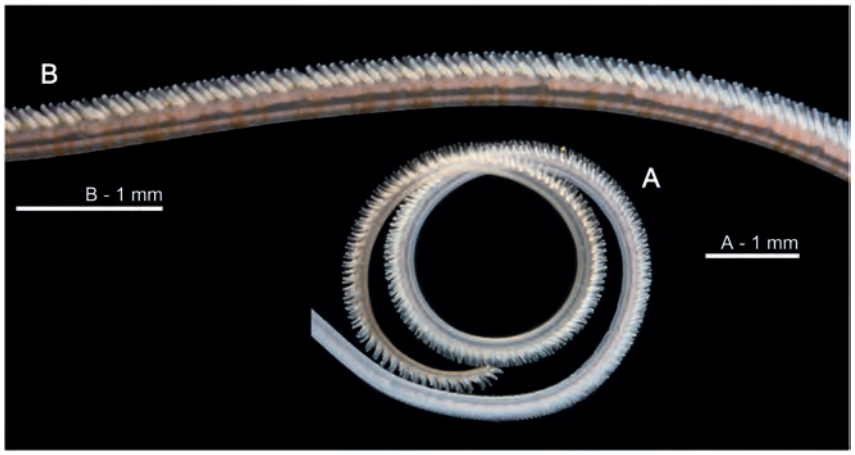


**Fig. 4.2.6:** Magelonid palps ($MgCl_2$-relaxed). A, *Magelona johnstoni,* distal portion (NMW.Z. 2013.037.0017, lateral view). B, *Magelona mirabilis*, median section showing transverse stripes (NMW.Z. 2013.037.002, lateral view). Andrew Mackie; adapted from Mortimer and Mackie (2014).

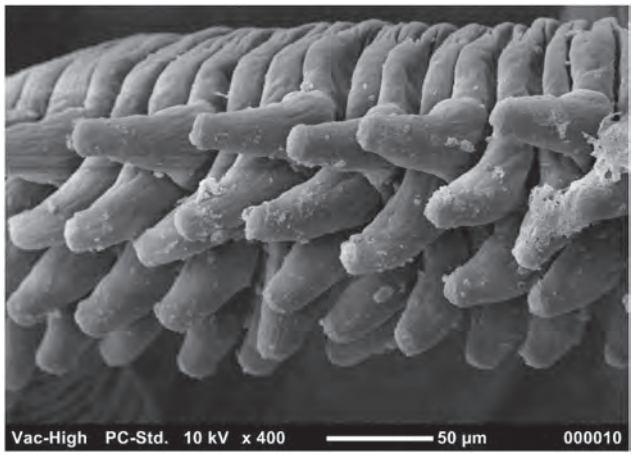


**Fig. 4.2.7:** Papillae of midpalp region of *Magelona johnstoni* collected in Berwick-upon-Tweed. Kate Mortimer; adapted from Mortimer and Mackie (2014).

Mortimer, 2013 or chaetigers 1 to 7 in *Magelona riojai* Jones, 1963 (see Brasil 2003). In these examples, the prechaetal lamellae are often well developed, attaching further along the length of the subchaetal lamellae, toward the distal tip. When viewed laterally, these lamellae form a U-shaped structure around the chaetae. Notopodial thoracic lamellar margins may be smooth (Fig. 4.2.8 E) or crenulated (Fig. 4.2.8 A, B, F, H) as in *M. johnstoni*. They may also be distinctly bilobed, as seen in *Magelona obockensis* Gravier, 1905 (Fig. 4.2.8 G).

Superior dorsal lobes (dorsal medial lobes of Jones) may be present, situated toward the top of the chaetal bundle, generally in a slightly prechaetal position. They are usually cirriform to digitiform in shape, but their size can vary greatly and can be particularly foliaceous in some species, e.g., *Magelona* sp. D of Uebelacker and Jones (1984) and *Magelona methae* Nateewathana & Hylleberg, 1991. Dorsal lobes may occur on all or just a few thoracic chaetigers such as *M. johnstoni*, in which they are present in the mid to posterior thorax only.

Thoracic neuropodial lateral lamellae may be of similar size and shape as their notopodial counterparts, in a distinctly postchaetal position (with low prechaetal lamellae). However, in many species, they are slender triangular in shape and ventral in position, directly underneath the chaetal bundle. Jones (1971, 1978) introduced the term *ventral neuropodial lobe* (VNL) to describe this form. However, the neuropodial lamellae may sit in a slightly prechaetal, ventral, or postchaetal position, and their position may change on different chaetigers along the thorax (often moving from a prechaetal position through to postchaetal in many species). Jones (1978) acknowledged the problems in using the term VNL and often qualified it, stating their position. However, subsequent authors have abandoned its use.

Ventral neuropodial lamellae are often attached to low pre- and postchaetal lamellae that encircle the chaetal bundles, cuff-like (Fig. 4.2.8 B–G). In some species, the postchaetal portion may be more expanded, often increasing in size toward the posterior thorax. In these cases, the postchaetal lamellae (generally of chaetigers 8 and 9) may be more triangular and of similar length to the neuropodial ventral lamella (Fig. 4.2.8 H, I). In *Magelona conversa* Mortimer & Mackie, 2003, the thoracic neuropodial lamellae are distinctly prechaetal, and those of chaetiger 8 are equal in size to large oblong postchaetal lamellae. On chaetiger 9 in some species, low inferior ridges are present, terminating in small ventral cirri/processes.

The nature of the thoracic lamellae across the whole thorax in terms of size, shape, and position is very species specific and thus extremely important in separating species. For example, the ventral neuropodial lamellae may decrease in size toward the posterior, only to the midthorax, or remain at a similar size throughout

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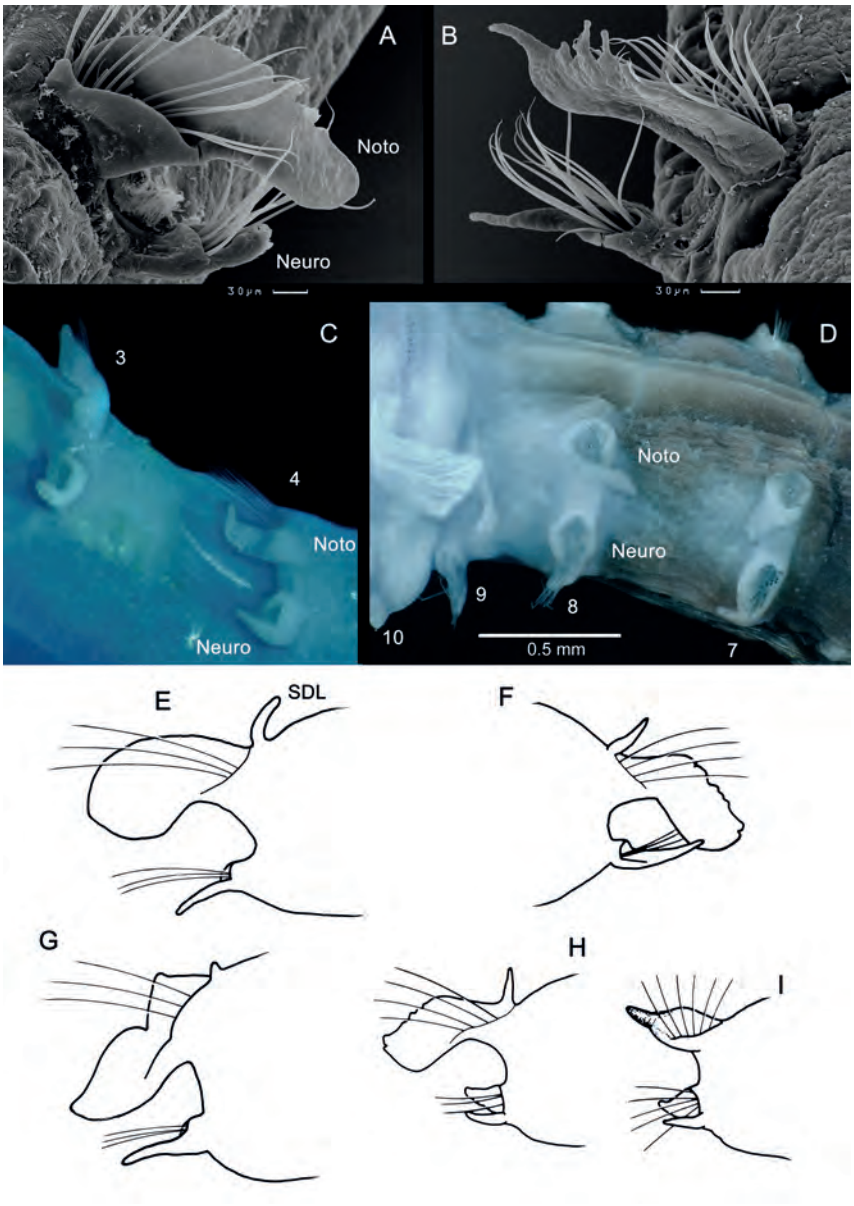


**Fig. 4.2.8:** Magelonid thoracic parapodia. A, B, *Magelona johnstoni* with crenulate upper edges (BMNH 1921.5.1.3023-43, from chaetiger 4, left, anterior view and SMF 4978, chaetiger 5, left, posterior view respectively). C, Chaetigers 3 and 4 of *Magelona alleni* from Morocco, showing ventral neuropodial lamellae and low pre- and postchaetal lamellae encircling chaetae cuff-like (ventral view, stained with Methyl Green). D, Same specimen, chaetigers 7–10 (lateral view). E, *Magelona sinbadi* (NMW.Z.2010.037.0001, from chaetiger 7, right, anterior view). F, H, I, *Magelona montera* (MNHN TYPE 1548, from chaetiger 4, left, anterior view, chaetigers 8 and 9, right, anterior views, respectively). G, *Magelona obockensis* (MNHN Type 1357, from chaetiger 2, right, anterior view) showing bilobed notopodial lamellae. Noto, Notopodia; Neuro, Neuropodia; SDL, Superior Dorsal Lobe. A, B, Fiege *et al.* (2000); E, F, H, I, Mortimer *et al.* (2012); G, Mortimer (2010).

the thorax. However, the parapodia of posterior thoracic chaetigers, especially those of chaetigers 8 and 9, in particular, are extremely important in distinguishing species and must be fully described.

Thoracic chaetigers bear capillary chaetae (Fig. 4.2.8 A, B), which are generally not specialized, apart from those of chaetiger 9 in some species (see Fig. 4.2.9). However, Brasil (2003) pointed out that many authors have undervalued the differences between magelonid thoracic chaetae, recognizing three subject-predicate relations: unilimbate, bilimbate, and lastly, bilimbate with an irregular blade along the longitudinal axis (a feature recorded for *Magelona variolamellata* Bolívar & Lana, 1986 and *M. riojai*). For some species, the chaetae of chaetiger 9 may be mucronate/spatulate (Fig. 4.2.9), as in *M. johnstoni* and *Magelona debeerei* Clarke, Paterson, Florence & Gibbons, 2010, or limbate chaetae with pennoned tips, which in *Magelona* sp. B of Uebelacker and Jones (1984) are asymmetrical. Thoracic chaetae can also be characteristically splayed within rami, and longer, particularly toward the posterior thorax in some species, see for example *M.* cf. *cincta* (see Mortimer *et al.* 2012, Shakouri *et al.* 2017).

Thoracic ventral pads are present in some species, for example, *M. mirabilis* (see Mortimer and Mackie 2014: Fig. 2B, visible on chaetigers 3 to 8). These are more prominent than those seen in the morphologically similar *M. johnstoni*. Distinct oval and reniform swellings were also noted for *M. obockensis* on the ventral thorax (Mortimer 2010). *Magelona crenulifrons* and *M. pulchella* are described as having distinct v and x shapes,

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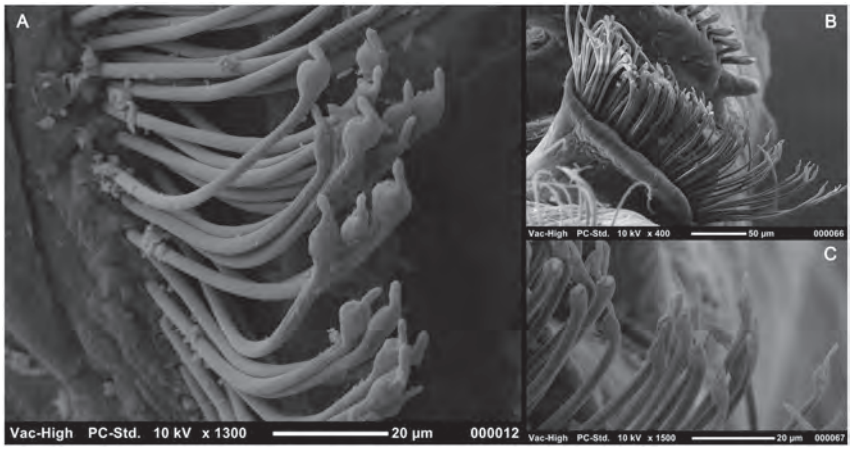


**Fig. 4.2.9:** Mucronate chaetae from chaetiger 9 in *Magelona johnstoni* (Berwick-upon-Tweed). A, NMW.Z.2013.037.0008c. B, C, NMW.Z.2013.037.0011b.

respectively, of the mid-ventral region (Fig. 4.2.16 A, B, D), which are particularly noticeable with Methyl Green as they remain unstained.

**Abdomen.** The abdominal region of magelonids consists of many chaetigers carrying biramous parapodia. In contrast to the thorax, the abdominal lateral lamellae of the notopodia and neuropodia are generally symmetrical and of similar size and shape. However, *M. alleni* has subequal abdominal lateral lamellae, those of the notopodia being somewhat larger. The size and shape of lateral lamellae vary between species, from pointed triangular to large, spatulate and sometimes foliaceous. Lamellae may be basally constricted (almost toad-stool shape in profile, Fig. 4.2.10 B) or broad-based, entirely lacking a constriction (Fig. 4.2.10 A). Lateral lamellae may be postchaetally expanded behind chaetal rows (Fig. 4.2.10 B), the apex of which may be rounded or triangular. Alternatively, postchaetal expansions may be entirely absent, with chaetae arising from a definite ridge (Fig. 4.2.10 A). At the inner margins of chaetal rows, triangular to digitiform processes may be present (Dorsal Medial Lobe DML and Ventral Medial Lobe VML of Jones). These can be difficult to discern in smaller species and have been incorrectly reported as absent in some species; however, in others, they are particularly long. Their conspicuousness is dependent on the size of the species/specimen and additionally may expand and contract with the coelomic pressure of the body (although this has not been verified). Uebelacker and Jones (1984) believed that they may occur universally across the family, but this is something that warrants further investigation and is not a view currently shared.

Abdominal chaetae occur in a single row for both notopodial and neuropodial rami, either unidirectional (Fig. 4.2.10 A) in a single group, or in two groups, hooks facing vis-à-vis (Fig. 4.2.10 B, number of chaetae per group may be equal or subequal). The number of chaetae per rami is variable and species specific. Chaetae arise from a ridge in between lateral lamellae and processes (when present), and this is more conspicuous in species without postchaetal expansions behind the chaetal rows.

Abdominal chaetae are hooded hooks, which may be bi-, tri-, or poly-dentate, with a main fang, surmounted by small secondary teeth (Figs. 4.2.10 and 4.2.11). The position of secondary teeth in relation to main fangs has been shown to vary, although this is not a feature widely reported in the group. For instance, Mortimer and Mackie (2009) reported that secondary teeth in *M. crenulifrons* are separated from main fangs by a large cleft, unlike other species, in which the angle between the two is much smaller.

Four polydentate species have been described; however, the number of secondary teeth per hook varies between each species (quadridentate, pentadentate, and hexodont hooks). Some carry more than one type of hook, and the proportion of each varies between species. For instance, *Magelona polydentata* Jones, 1963 possess predominately pentadentate hooks, while *Magelona* sp. I of Uebelacker and Jones (1984) additionally possesses tridentate hooded hooks (predominating in some specimens).

Greatly enlarged hooded hooks are present in a handful of species such as *M. falcifera* and *Magelona uebelackerae* (Hernández-Alcántara & Solís-Weiss, 2000), which are unidentate, lacking secondary teeth, and *Magelona magnahamata* Aguado & San Martín, 2003, which possesses strongly curved, large bidentate hooded hooks. *Magelona spinifera* (Hernández-Alcántara & Solís-Weiss, 2000) is reported as having one large recurved spine per ramus in the anterior abdomen associated with a smaller, similarly formed spine. Small rudimentary hooks, emerging at the bases of or adjacent to lateral lamellae (e.g., in

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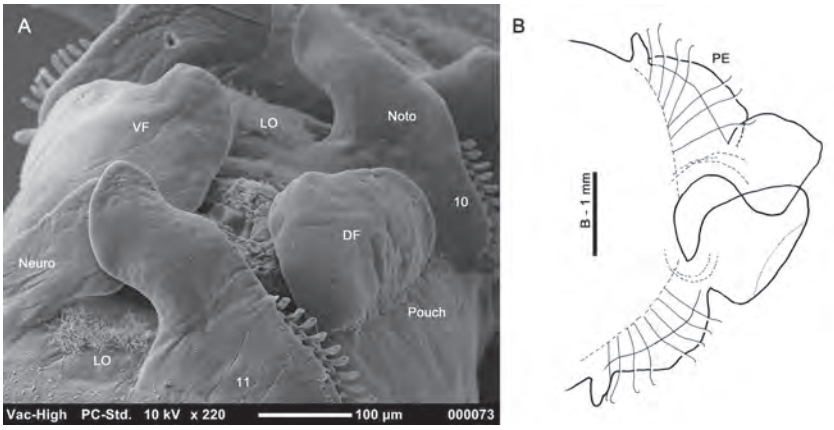


**Fig. 4.2.10:** Abdominal chaetigers. A, *Magelona johnstoni* (Berwick-upon-Tweed, NMW.Z.2013.037.0011b) chaetigers 10 and 11 (posterior view), lateral abdominal pouch. B, *Magelona crenulifrons* (Iran) parapodia from chaetiger 10 (left, anterior view, NMW.Z.2010.037.0034b). Noto, Notopodia; Neuro, Neuropodia; DF, Dorsal Flap; VF, Ventral Flap; LO, Lateral Organ; PE, Postchaetal Expansion of abdominal lamellae. B, Mortimer *et al.* (2012).

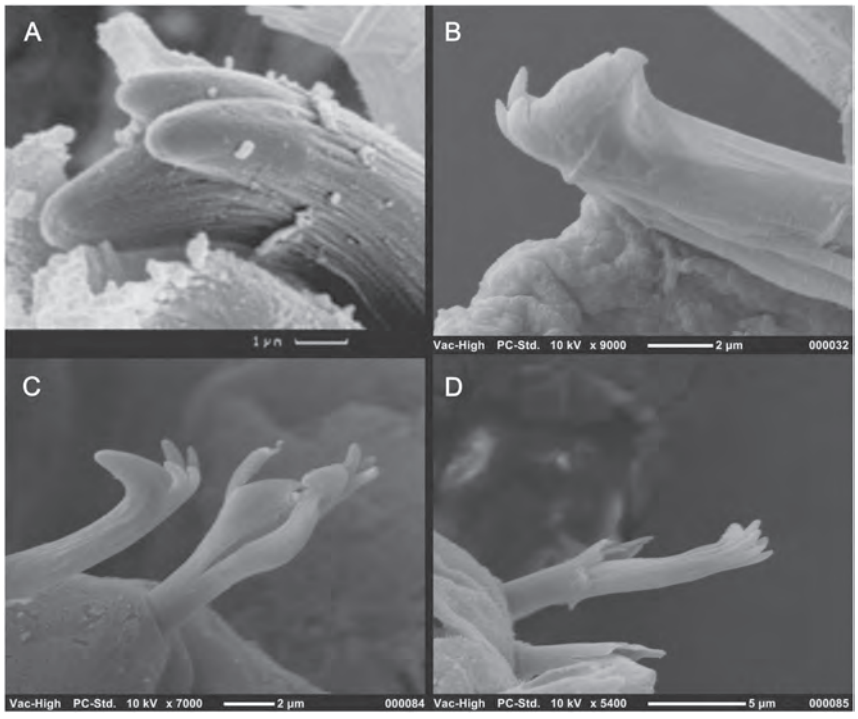


**Fig. 4.2.11:** Magelonid abdominal hooded hooks (hoods broken). A, tridentate hook of *Magelona mirabilis* (St Andrews, BMNH 1921.5.1.3023-43). B–D, Quadridentate, pentadentate, and hexodont hooded hooks of *Magelona fauchaldi* (Iran, NMW.Z.2015.012.0002d & e). A, Fiege *et al.* (2000); B–D, Shakouri *et al.* (2017).

*M. magnahamata*), and small curved support chaetae are described for several species, e.g., *M. cornuta* and *M. crenulifrons* (see Mortimer and Mackie 2009), although this is a feature that is poorly reported within the group. Brasil (2003), however, noted their presence and absence in 53 observed taxa.

In general, species possess abdominal chaetigers whose width is similar to their lengths; however, in some, their length may be much greater. *Magelona posterelongata* was the first species formally described with this situation.

Lateral pouches occur on the abdomen of many species, and their presence or absence is often a key diagnostic feature. The function of lateral abdominal pouches is unknown, but when present, they occur in males, females, and juveniles. Although several possible functions have been postulated, no definitive evidence has been found. Fiege *et al.* (2000) described two types of lateral pouch (Σ and C shaped) as being present. Σ-shaped pouches (Fig. 4.2.12) occur in the anterior abdomen, generally in pairs, on either side of the body (although occasional unpaired pouches have been reported, see, for example, *M. johnstoni*), and are anteriorly opening. Each pouch is bound dorsally and ventrally by a cuticular flap and contains a bag-like, relatively thick membrane, with a highly convoluted surface, the outer surface of which appears more convoluted than the inner. Although previous observations of this membrane

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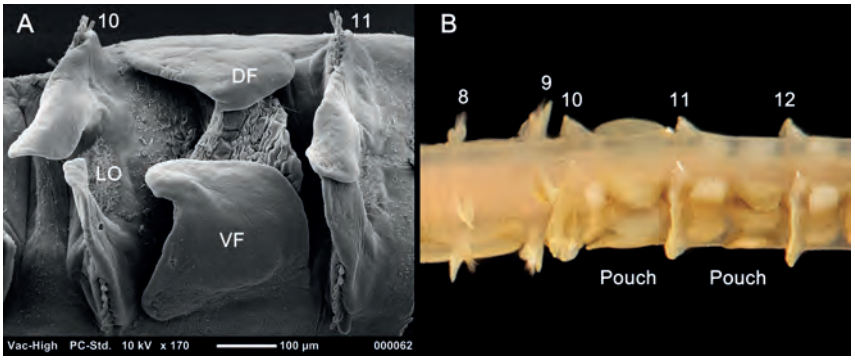


**Fig. 4.2.12:** Anteriorly open pouches of *Magelona johnstoni* (Berwick-upon-Tweed). A, Left-hand anteriorly opening pouch located between chaetigers 10 and 11 (lateral view, DF = dorsal flap, VF = ventral flap, LO = lateral organ, NMW.Z.2013.037.0011b). B, Left-hand pouches on consecutive segments, between chaetigers 10–11 and 11–12 (lateral view, NMW.Z. 2013.037.0018). Adapted from Mortimer and Mackie (2014).

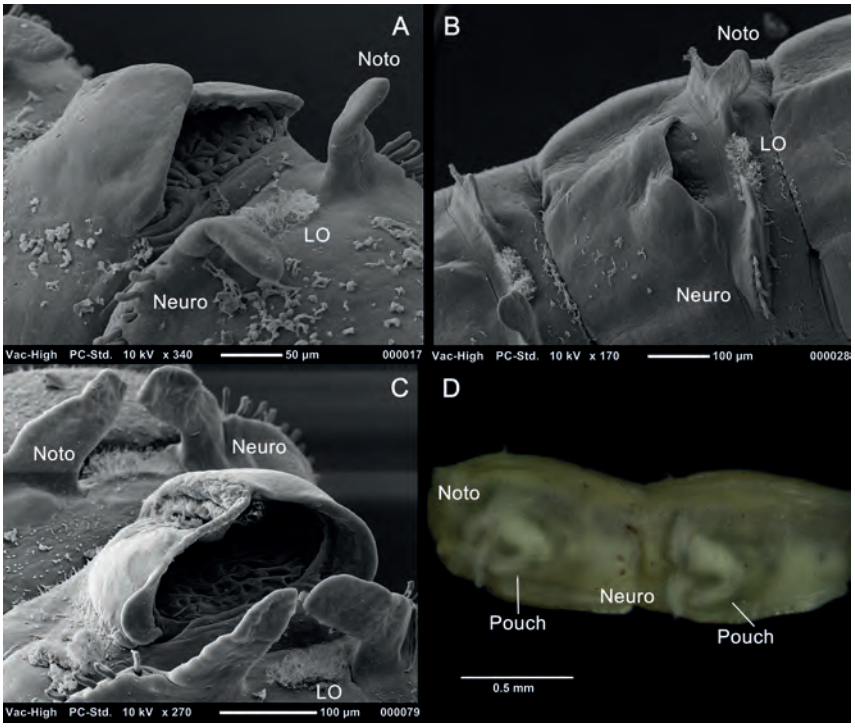


**Fig. 4.2.13:** Posteriorly open pouches. A–C, *Magelona johnstoni* (Berwick-upon-Tweed. A, B, NMW.Z.2013.037.0008c. C, NMW.Z.2013.037.0011d, ventral posterior, lateral, and posterior views, respectively). D, *Magelona pacifica* (BMNH Type 1933.7.10.65/70, lateral view, pouches on consecutive chaetigers, showing medial slits). Noto, notopodia; Neuro, neuropodia; LO, lateral organ. A, Mortimer and Mackie (2014); D, Mortimer *et al.* (2012).

using light microscopy were unclear, more recent SEM images of *M. johnstoni* have simplified the situation (Mortimer and Mackie 2014). The membrane is formed into a bag-like structure, whose open end points in an anterior direction. Σ-shaped pouches (more recently termed *anteriorly open pouches*, see subsequent note based on Mortimer and Mackie 2010) often start between chaetigers 11 and 12, although they have been additionally reported between chaetigers 9 and 10 and also between 10 and 11 in some species.

By contrast, C-shaped pouches (Fig. 4.2.13; more recently termed *posteriorly open pouches*) occur on median and posterior abdominal chaetigers, simple and pocket like, opening posteriorly. They may be unpaired, alternating from one side of the body to the other, on alternate segments, or paired occurring on consecutive segments (Fig. 4.2.14). In general, those species that possess Σ-shaped pouches have also C-shaped pouches, although the presence of the latter has yet to be confirmed in some species (i.e., those known only from posteriorly incomplete specimens). Additionally, Brasil (2003) recorded three species possessing only Σ-shaped pouches. The inner surface of posteriorly open (C-shaped) pouches in *M. johnstoni* has been shown to be somewhat convoluted (Mortimer and Mackie 2014; Fig. 4.2.13 A–C). Mortimer (2010) and Mortimer and Mackie (2014) thus suggested that a continuation between the two pouch morphologies exists. Particularly, the C-shaped pouches toward the anterior abdomen of *M. johnstoni* were shown to have slightly thicker dorsal and ventral portions, with a more textured region in between, more akin to Σ-shaped pouches (Fig. 4.2.13 C).

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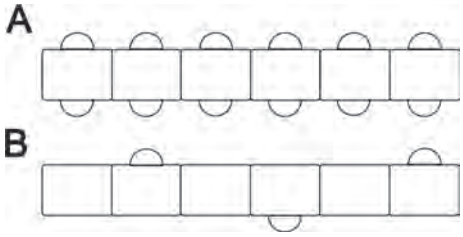


**Fig. 4.2.14:** Schematic diagram showing patterns of pouch locations for posteriorly opening abdominal pouches. A, Paired pouches occurring on consecutive segments. B, Unpaired pouches alternating from one side of the body to the other and on alternate segments.

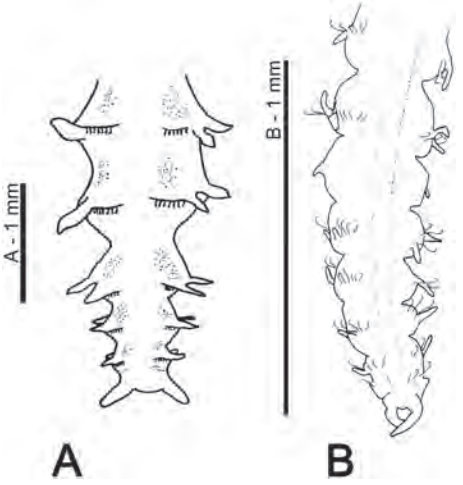


**Fig. 4.2.15:** Posterior regions. A, *Magelona conversa* (NMW.Z.2000.020.0001, dorsal view, Mortimer and Mackie 2003). B, *Magelona* cf. *falcifera* (Iran, NMW.Z.2010.037.0013, ventral view, Mortimer *et al.* 2012).

Since Fiege *et al.* (2000) characterized the two forms of pouches, further pouch morphologies have been described. The posteriorly open pouches of some species carry medial slits (Fig. 4.2.13 D) such as M. cornuta, while others possess thicker edges, for example, *Magelona mahensis* Mortimer & Mackie, 2006 (Mortimer 2010: 22). Mortimer (2010) suggested the abandonment of the terms *Σ* and *C shaped*; instead, pouch morphologies should be fully described according to the direction of opening (i.e., anteriorly/posteriorly opening), shape, size, nature, and location to enable the variation in pouch morphologies to be better understood.

The chaetiger of first presence of posteriorly open pouches between species varies greatly. In some species, they occur only in the extreme posterior region, such as *M. filiformis* or *Magelona dakini* Jones, 1978 (chaetiger 101–117 for the latter species). Therefore, the absence of these structures in species that are described from incomplete specimens cannot be stated with absolute certainty.

The presence, morphology, and location of pouches are unknown for many species and have been incorrectly reported in further species. However, the pouch location pattern is, in the main, very species specific. Mortimer and Mackie (2014) tabulated the current knowledge of lateral abdominal pouches in all described species based on literature records, categorizing species into five groups. The first consist of those without pouches (1), and the second, those possessing both anteriorly and posteriorly open pouches (2). The remaining species, i.e., those with posteriorly open pouches only (anteriorly open pouches absent), were divided into three groups: those with pouches on consecutive segments (3), those on alternating segments (4), and lastly, those occurring in the extreme posterior only (5).

Lateral organs (not the lateral organs of McIntosh 1879, 1911, 1915; see Mortimer and Mackie 2014) are present in magelonids on thoracic and abdominal chaetigers. Jones (1968) stated that they are present on all but the ninth chaetiger and comprise of nonmotile stereocilia between lateral lamellae, which project straight out in healthy specimens (Figs. 4.2.8 A, 4.2.10 A, 4.2.12 A, and 4.2.13 A–C.)

**Pygidium.** The pygidium is relatively uniform among magelonids, although the posterior region is unknown for many species due to the fragility of these animals. Drawings of magelonid pygidia are relatively uncommon in species descriptions but are present for the following species: *M. alleni*, *Magelona californica* Hartman, 1944, *M.* cf. *cincta* (see Mortimer and Mackie 2009), *M. conversa*, *M. falcifera* (see Mortimer *et al.* 2012), *M. fauchaldi, M. filiformis, M. magnahamata, M. mahensis, M. obockensis* (as *Magelona heteropoda*, see Mohammad 1973 and Mortimer 2010), *M. pacifica* (see Mortimer *et al.* 2012), *M. parochilis, M. pulchella* (see Mortimer 2010), *Magelona pygmaea* Nateewathana & Hylleberg, 1991 (see Mortimer and Mackie 2006), and *Magelona sacculata* Hartman, 1961. McIntosh (1878) provides a detailed drawing presumably of either *M. mirabilis* or *M. johnstoni* (as *Magelona papillicornis*). The magelonid anus is in a ventral to terminal position, with a pair of pygidial cirri (Fig. 4.2.15), which are generally digitiform in shape.

**Color.** Magelonids are generally white with a pinkish tinge, although the gut is often visible through the body wall and darker green (Figs. 4.2.1 and 4.2.3). Females of *M. johnstoni* that are a deeper yellow to orange color have been observed by the author. Additionally, coloration may be more obvious in larger specimens, with a cream

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to light reddish hue across the body. Some species, generally those that are stouter, such as *M. alleni,* possess a characteristic pigment band on posterior thoracic chaetigers, often deep reddish to brown in color. These pigment bands can persist for many years in preserved specimens, although now no longer visible on the type specimen of *M. cincta* (see Mortimer and Mackie 2009). However, the authors noted fading in specimens of *Magelona* cf. *cincta* of relatively freshly collected specimens also. Light pigmentation of posterior thoracic chaetigers was noted for *M. symmetrica* collected in Arabian waters (Mortimer *et al.* 2012) but appeared to be a sporadic/variable character between specimens. An *M. alleni*-like species from Senegal, Western Africa, that has distinct pigmentation above and below the pigment band in distinct transverse stripes, all the way to the pygidium, has been observed. This character clearly warrants investigating in live material and variability in pigmentation pattern with length of

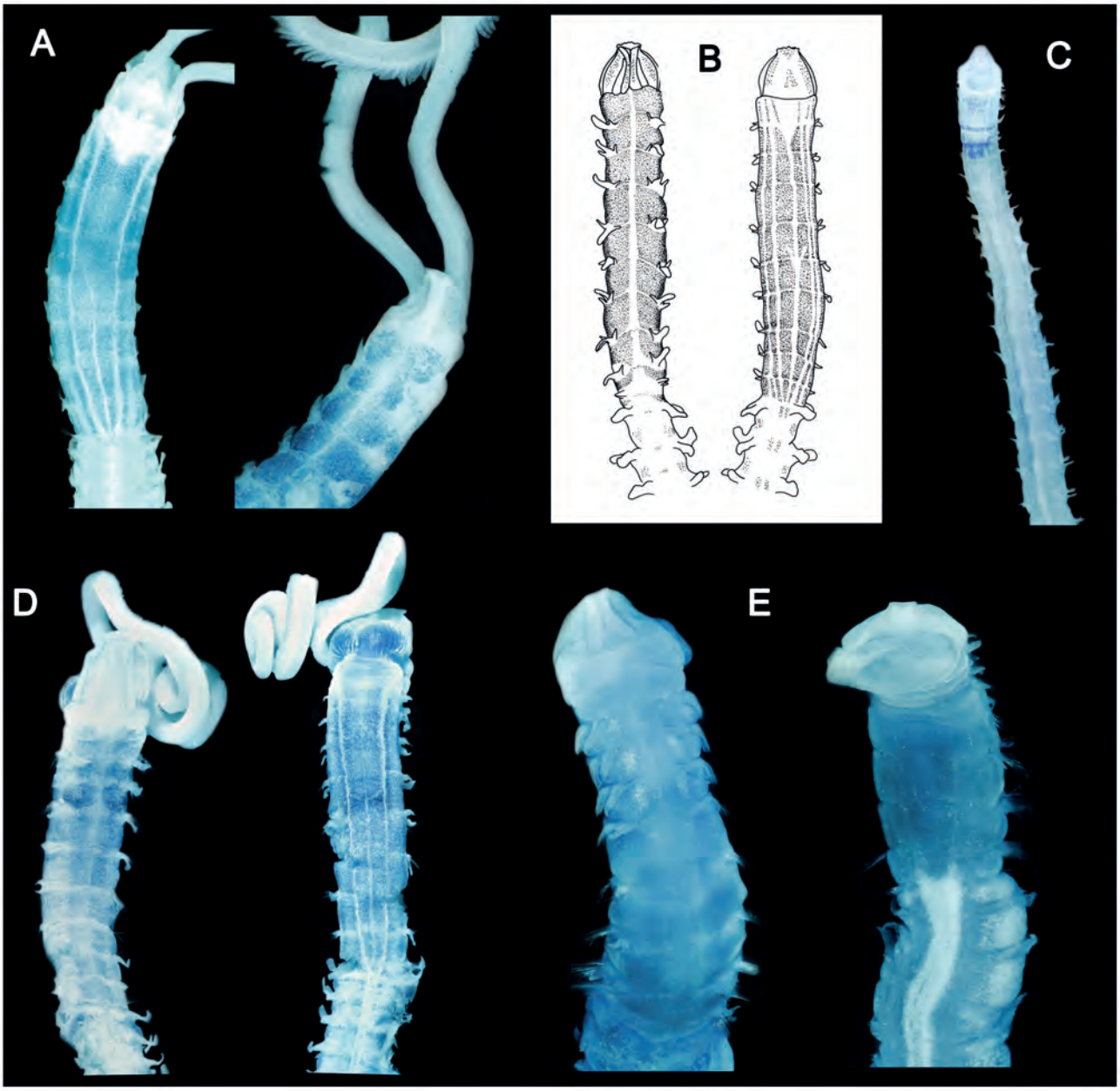


**Fig. 4.2.16:** Methyl Green staining patterns of the anterior region. A, *Magelona crenulifrons* (Iran, NMW.Z.2015.012.0003, ventral and dorsal views). B, *Magelona crenulifrons* (Hong Kong, dorsal and ventral views). C, *Magelona fauchaldi* (NMW.Z.2015.012.0002a, ventral view). D, *Magelona pulchella* (BMNH 1969.391, dorsal and ventral views). E, *Magelona* cf. *cincta* (Iran, NMW.Z.2015.012.0004, dorsal and ventral views). A, C–E, Shakouri *et al.* (2017); B, Mortimer and Mackie (2009).

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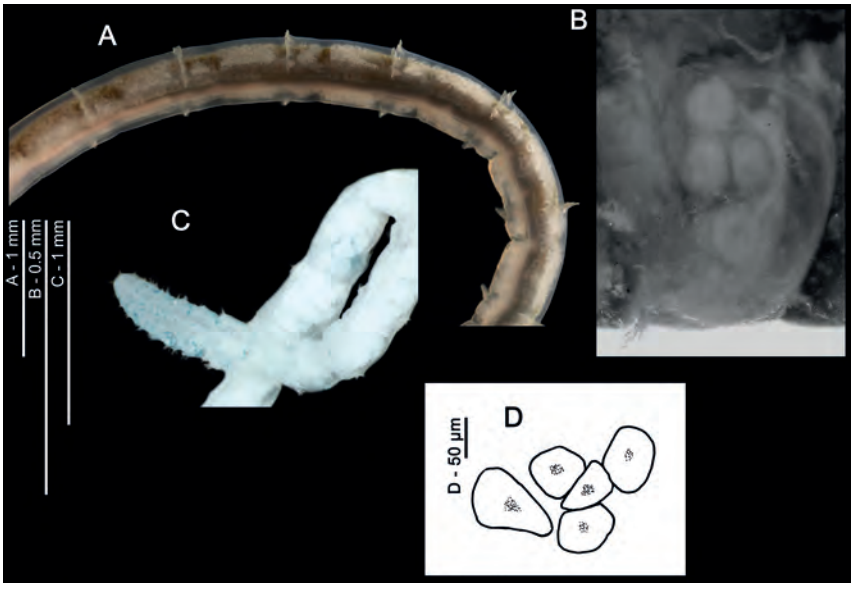


**Fig. 4.2.17:** Eggs. A, Within the abdomen of *Magelona johnstoni* (Berwick-upon-Tweed, NMW.Z. 2013.037.0015, Mortimer and Mackie 2014). B, Within an abdominal chaetiger of *Magelona obockensis* (MNHN Type 1357, Mortimer 2010). C, D, *Magelona fauchaldi* (NMW.Z.2015.012.0002a, in the posterior region, Shakouri *et al.* 2017).

time in preserving fluid. *Magelona mirabilis* has distinct striped markings on its palps (Fig. 4.2.6 B), allowing them to be distinguished from the morphologically similar *M. johnstoni*, in which the stripes are absent.

Methyl Green staining patterns (Fig. 4.2.16) are often species specific and can be extremely useful in separating and identifying species. For example, the staining pattern of *M. crenulifrons* (Fig. 4.2.16 B) shows longitudinal ventral stripes in the thoracic region (Mortimer and Mackie 2009, Shakouri *et al.* 2017). Staining patterns can be particularly useful for identifying smaller species in samples, as was noted for *M. fauchaldi* (Fig. 4.2.16 C, see also Mortimer *et al.* 2012: 14, as *M.* cf. *agoensis*). Nateewathana and Hylleberg (1991) described the staining patterns of specimens collected in Thailand using Methylene Blue, both before and after transfer to alcohol, noting that changes in patterns due to stain dissipation were also useful. Shakouri *et al.* (2017) detailed the persistence of stain between chaetigers 2 and 3 in *M. pulchella* (Fig. 4.2.16 D), even after much of the other thoracic stain had dissipated. Although some species show no distinct staining patterns, the stain can often highlight other features such as dorsal and ventral speckling (Fig. 4.2.16 E).

Staining patterns with rose bengal can also be conspicuous and species specific, aiding separation of species. Dorsal thoracic, transverse stripes have been recorded in several species stained with rose bengal, such as *M. crenulifrons* (see Mortimer and Mackie 2009).

White speckled areas (Fig. 4.2.16 E) dorsally and ventrally may be present in the thoracic region as well as glandular interparapodial regions in the abdomen and running along the midventral line, such as in *Magelona* cf. *cincta* (see Shakouri *et al.* 2017). The presence/absence and the location of these areas are of importance.

### Anatomy

Most knowledge of the anatomy of the group comes from McIntosh (1877, 1878, 1879, 1911, 1915, 1916) and Jones (1968). Filippova *et al.* (2005) investigated the musculature of *M.* cf. *mirabilis* by phalloidin labeling and confocal laser scanning microscopy, while Purschke (2016) reviewed the structure and evolution of the nervous system. The structure of the ventral nerve cord has been described by Helm *et al.* (2018) as consisting of medullary cords, paired in the thorax and unpaired in the abdomen. The blood of *Magelona*, which contains corpuscles, is described in detail by Benham (1896), with further notes by Jones (1968). The latter author also described in detail the well-developed, closed circulatory system of an undescribed magelonid species, consisting of an anterior dorsal vessel, divided into a series of chambers set apart by valves. A heavily muscularized portion of this dorsal vessel is largely responsible for movement of blood around the animal. The functioning of the circulatory system in live magelonids can be observed with relative ease (Fig. 4.2.3).

## Reproduction and development

### Reproduction

Relatively little is known about the reproductive biology of the group (Rouse 2001, Blake 2006). However, several references provide information on magelonid eggs and sperm, which are both easily observed within the abdominal

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cavity of magelonids when present. Egg sizes range from approximately 50 to 150 µm in diameter (Wilson 1982, Fiege *et al.* 2000, Mortimer and Mackie 2003, 2014, Mortimer 2010, Mortimer *et al.* 2012, Shakouri *et al.* 2017) (Fig. 4.2.17). Blake (2006) suggested that *Magelona* eggs possess a thin single layered envelope lacking ornamentation and cortical alveoli. Observations on the presence of eggs are given in a number of publications for several species: November–August in British waters (see McIntosh 1877, Wilson 1982, Fiege *et al.* 2000, Mortimer and Mackie 2014); April–October from east and west coasts of America and the Gulf of Mexico (Jones 1963, 1978), and March in the Seychelles (Mortimer and Mackie 2006). Further details on spawning season from a variety of European locations are provided by Mortimer and Mackie (2014). Blake (2006) suggested that British magelonid species exhibit seasonality in the maturation of gametes, based on results from Wilson (1982).

Rouse (1999) figured (Fig. 7 A) and described the sperm of an undescribed species of *Magelona*, suggesting that its morphology implied external fertilization. The sperm possessed conical nuclei with an apical invagination occupied by a spherical acrosome. Rouse (2006) suggested that magelonids may have ect-aquasperm, with Blake (2006) further suggesting that they are likely to be broadcast spawners. Fiege *et al.* (2000) recorded sperm masses in *M. mirabilis* from St Andrews, Scotland, in March.

Mortimer and Mackie (2014) observed lateral sinuous movements of the thorax outside of the burrow in *M. johnstoni* kept in laboratory tanks, suggesting a possible link with reproduction. This intermittent behavior often occurred for long periods and simultaneously in several animals. They postulated that this behavior may be related to gamete release, although no evidence to corroborate this was observed.

Fauchald (1983) considered *M. sacculata* to be an annual species, and preliminary observations on British magelonids by the current author would seem to support this theory. Although variations in longevity have been noted, animals kept in laboratory tanks appeared to live for approximately 2 years.

**Fig. 4.2.18:** Scanning electron microscope micrograph of 9-day-old *Magelona mirabilis* larvae (ventral view), showing asymmetrical larval tentacles. Conrad Helm (©Universitetet I Bergen).

### Life cycles

Planktotrophic and lecithotrophic larvae have been found within the Magelonidae (see Rouse 2006 based on the observations of Wilson 1982 and Johnson and Brink 1998). Rouse (2006) suggested that the possible mechanism for feeding in planktotrophic larvae was ciliary followed by encounter predation using palps once developed.

Most knowledge of magelonid larval development is provided by Wilson (1982), who studied both early and late larvae from southern British waters. Three species of magelonid larvae were detailed: *M. filiformis*, *M. alleni*, and *M. mirabilis*, all of which could be clearly distinguished from the other. The larval tentacles are derived from the prototroch and associated tissues and are replaced late on in development by the adult palps, at their bases. Larvae possess long larval chaetae, which are also shed at metamorphosis along with the larval tentacles. Early *M. mirabilis* larvae are unusual in possessing asymmetrical tentacles, the left being somewhat smaller and stump-like in comparison to the right (Fig. 4.2.18). Photographs of the larvae of two species (assumed to be *Magelona pitelkai* Hartman, 1944 and *M. sacculata*) are provided by Blake (2006).

### Regeneration

Little is known about regeneration in magelonids, although specimens showing posterior regeneration are not uncommon in samples. Mortimer and Mackie (2014) investigated palp regeneration in *M. johnstoni* observed

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in laboratory tanks. Palps were shown to regenerate in approximately 30 days, from which they could continue palpal feeding, although palps were thinner and shorter than those on intact animals.

## Biology and ecology

### Distribution

Magelonids are generally considered to be shallow-water species, at depths of less than 100 m (Rouse 2001), mainly distributed in coastal areas and on continental shelves (Hernández-Alcántara and Solís-Weiss, 2009). However, several species have been recorded from deeper waters (1,000 to over 4,000 m, see Hartman 1971, Aguirrezabalaga *et al.* 2001). Magelonidae has a worldwide distribution, although large gaps in our current knowledge exist (due to a lack of taxonomic work), particularly around Africa, Australasia, and in extreme northern and southern waters. This has been highlighted by preliminary results from studies of magelonids as part of the Marine Invertebrates of Western Africa project by the University Museum of Bergen and the current author, which have shown a high diversity of undescribed species within the region (>20 species). The presence of further undescribed magelonid species in Australian waters has also been suggested (Hutchings and Glasby, personal communication).

When they occur, a high diversity of magelonid species is often present. For example, Bolívar and Lana (1986) recorded six species from Brazilian waters; Uebelacker and Jones (1984), 13 from the Gulf of Mexico; Nateewathana and Hylleberg (1991), 10 from Thailand; Hernández-Alcántara and Solís-Weiss (2000), 7 from both coasts of Mexico; and Mortimer and Mackie (2003, 2006), 7 from the Seychelles. Further regional studies include those of: Blake (1996; California), Fiege *et al.* (2000; Europe), and Mortimer (2010), Mortimer *et al.* (2012), and Shakouri (2017; Arabian Sea).

### Behavior

Very little information about the biology and behavior of these worms exists. Jones (1968) made observations on an unnamed species of *Magelona* collected near Woods Hole, while Mortimer and Mackie (2014) observed the behavior of several British magelonids.

**Burrowing.** Several authors have described magelonids as good burrowers in mud and sands (Fauchald and Jumars 1979, Abd-Elnaby 2008), using their flattened prostomia and eversible burrowing organs (proboscis – see previous note on terminology) to move through the sediment. However, difficulty in penetrating sediment surfaces and differences in burrowing activity have been highlighted (Mortimer and Mackie 2014). When burrowing, the prostomium is moved laterally from side to side, aiding movement forward, while the everted burrowing organ acts as an anchor, allowing the body to be pulled towards the head.

**Feeding.** Fauchald and Jumars (1979) considered magelonids as motile surface deposit-feeders, primarily based on the observations of McMahon and Jones (1967) and Jones (1968). The distal tips of the papillated palps extend from the burrow into the water column and food particles are collected from the surface of the sediment and moved toward the mouth via manipulation of the papillae. However, suspension feeding and variability between feeding modes have additionally been suggested (Mortimer and Mackie 2014), with Jumars *et al.* (2015) implying a greater tendency toward carnivory and subsurface feeding. A "gulping" action aids in the consumption of food particles, although Jones (1968) suggested that a mucus string may be involved in the transport of particles to the mouth. The buccal region in several species, such as *M. mirabilis* and *M. fauchaldi*, has been observed to be more extendable (Mortimer *et al.* 2012, Mortimer and Mackie 2014). Detritus, diatoms, organic debris, algal cysts, spores, foraminiferans, tintinnids, the larvae of crustaceans, molluscs, worms, and sediment have been recorded in the diet of magelonids. However, Mortimer and Mackie (2014) suggested the probability of interspecific variation in diets across the group.

**Respiratory movements.** Magelonids have been observed to undergo lateral sinuous movements within the burrow; this may be connected to respiration as instances of this behavior occurred more frequently in animals lacking palps, which are believed to have an additional respiratory function (Mortimer and Mackie 2014). Magelonids in general move more or less continuously through the sediment; however, Mortimer and Mackie (2014) noted variability between species activity.

### Ecology

The ecology of magelonids is better understood: common in sands and muds in both the intertidal and subtidal regions. While some species span both regions, others such as *M. minuta* are distinct offshore species. Species show distinct sediment preferences; see Mackie *et al.* (2006), Meißner and Darr (2009), Mortimer *et al.* (2012), Mortimer and Mackie (2014), and Shakouri *et al.* (2017). Meißner and Darr (2009) additionally highlighted salinity and water depth as factors influencing species distributions.

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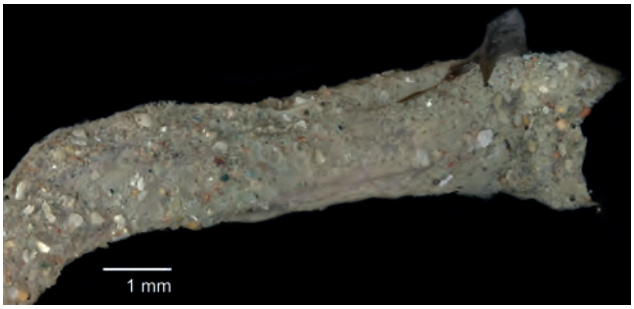


**Fig. 4.2.19:** Part of sediment tube of *Magelona alleni* from Morocco.

Hylleberg and Nateewathana (1991) investigated the temporal and spatial distribution of subtidal magelonids in Thailand, suggesting that monsoon-associated sediment disturbance plays an important role in the high diversity of species within the area. Uebelacker and Jones (1984) and Blake (1996) provide information on the biology and distributions of species in the Gulf of Mexico and California, respectively.

*Magelona mirabilis* individuals appear to occur in higher numbers in sediments around sea potato, *Echinocardium cordatum* (Pennant, 1777) burrows in South Wales as observed by the author. However, further investigations are warranted to look at this potential relationship.

Tube building has not been recorded for most magelonid species (Jumars *et al.* 2015); however, distinct tubes (Fig. 4.2.19) are known for species such as *M. polydentata*, *M. variolamellata*, *Magelona longicornis* Johnson, 1901 (see Jones 1971), *M. pitelkai* (see Jones 1978), *M. alleni* and *M. cincta* (see Mortimer and Mackie 2009), *M.* cf. *falcifera* and *M. symmetrica* (see Mortimer *et al.* 2012). Tubes may be mucose and covered in sand grains or more distinct parchment-like consisting of several layers. Those of *M. polydentata* were described as being yellow, membranous, to which foraminifera tests and other calcareous debris were attached (Jones 1963).

## Phylogeny and taxonomy

### Phylogeny

The group was elevated to the rank of family by Cunningham and Ramage in 1888 and they have long been regarded as part of the spioniform/Spiomorpha polychaetes along with taxa such as Chaetopteridae, Poecilochaetidae, and Trochochaetidae. Indeed, Rouse and Fauchald (1997, 1998) considered them to be part of Spionida within the Canalipalpata, based on morphological features. However, their unusual morphology has often led to debate about their placement within this group and Rouse (2001) stated that this unusual form has made it difficult to relate them to other polychaetes. Moreover, McIntosh (1911), although noting similarities with spionids, such as *Prionospio* and *Heterospio*, regarded them as being an "unusual" group within the Spionidae, particularly in regards to the division of the body and the nature of the "proboscis." Results from recent studies of annelid phylogeny based on molecular data suggest a placement of the Magelonidae as part of the basal radiation with Chaetopteridae, Sipuncula, and Oweniidae (Struck *et al.* 2014, Weigert *et al.* 2014, Helm *et al.* 2018). Struck *et al.* (2014) further noted the placement of the Myzostomida, Apistobranchidae within the basal part of the tree. However, Weigert *et al.* (2014) found the former group of the two to be deeply nested within the Annelida, as a sister group to Errantia in most analyses. This was further suggested by Weigert *et al.* (2016), including them within the Pleistoannelida. It has been suggested that the Magelonidae and Oweniidae (Palaeoannelida) represent the sister taxon of all other annelids. The relationship between the Magelonidae and Oweniidae has been further highlighted by cladistic analyses of morphological characters (Capa *et al.* 2012), based on the absence of nuchal organs, fusion of the prostomium and peristomium, presence of a ventral buccal organ, and monocilated epidermal cells. However, other phylogenetic analyses of the Annelida including fossil data did not find magelonids to be a sister group to the Owenidae (Parry *et al.* 2016).

Brasil (2003) examined the phylogeny of the Magelonidae based on external morphological features. The cladisitic analysis corroborated the monophyletic nature of the Magelonidae, based on two characters: the shovel-shaped flattened prostomium and the presence of ventrally inserted, papillated palps. The analysis further suggested that both *Meredithia* (now synonymized with *Magelona*) and *Octomagelona* are paraphyletic. However, the analysis suggested eight major clades within Magelonidae, Bremer support was low for most nodes. Further analyses are required to investigate the generic delinerations within the group. Brasil suggested that more thorough species descriptions including details on the division of the body and the position and shape of lateral lamellae are needed.

### Taxonomy

**Magelonidae Cunningham & Ramage, 1888**

**Type species:** *Magelona papillicornis* F. Müller, 1858 by monotypy

***Magelona* F. Müller, 1858 (Figs. 4.2.1–13 and 4.2.15–17)**

**Type species:** *Magelona papillicornis* F. Müller, 1858 by monotypy

67 species

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**Fig. 4.2.20:** Undescribed species of *Octomagelona* from West Africa.

**Diagnosis:** Body divided into the thoracic region with achaetous first segment and nine chaetigers, and abdominal region with numerous segments (up to and over 100). Prostomium dorso-ventrally flattened, with or without horns. Parapodia biramous with lateral lamellae, thoracic superior dorsal lobes present or absent. Branchiae absent. Thoracic capillary chaetae, those of the ninth chaetiger may be specialized, and an abdomen carrying hooded hooks, some of which may be enlarged in some species. Abdomen may carry anteriorly and posteriorly open pouches, just the latter, or may be absent. Pygidium with two cirri.

### *Octomagelona* Aguirrezabalaga, Ceberio & Fiege, 2001 (Fig. 4.2.20)

**Type species:** *Octomagelona bizkaiensis* Aguirrezabalaga, Ceberio & Fiege, 2001

Monotypic (although several other species are known to occur, see Brasil 2003: 10 and previous notes for example).

**Diagnosis:** Body divided into a thoracic region with achaetous first segment and eight chaetigers, and abdominal region with an unknown number of segments. Flattened prostomium with rudimentary frontal horns. Parapodia biramous, without superior dorsal lobes, lateral lamellae filiform. Branchiae absent. Thoracic chaetae long, limbate capillaries, abdominal chaetae hooded hooks. Posterior part unknown. Lateral pouches not described for the genus.

### Acknowledgments

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### Institutional abbreviations

BMNH – Natural History Museum, London
MNHN – Muséum National d'Histoire Naturelle, Paris
NMW – National Museum Wales
SMF – Senckenberg Museum Frankfurt

### References

Abd-Elnaby, F.A. (2008): New recorded species of Magelonidae and Maldanidae (Annelida: Polychaeta) from EL-Tina Bay, Mediterranean coast of Egypt. *Egyptian Journal of Aquatic Biology and Fisheries* 12: 119–141.

Aguado, M.T. & San Martín, G. (2003): A new species of *Magelona* Müller, 1858 (Polychaeta: Magelonidae). *Proceedings of the Biological Society of Washington* 116: 542–547.

Aguirrezabalaga, F., Ceberio, A. & Fiege, D. (2001): *Octomagelona bizkaiensis* (Polychaeta: Magelonidae) a new genus and species from the Capbreton Canyon (Bay of Biscay, north-east Atlantic). *Journal of the Marine Biological Association of the United Kingdom* 81: 221–224.

Benham, W.B. (1896): The blood of *Magelona*. *Journal of Cell Science* S2-39: 1–18.

Blake, J.A. (1996): Family Magelonidae Cunningham and Ramage, 1888. In: Blake, J.A., Hilbig, B. & Scott, P.H. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, Vol. 6: The Annelida. Part 3: Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara, CA: 252–261.

Blake, J.A. (2006): Chapter 13. Spionida. In: Rouse, G.W. & Pleijel, F. (eds). *Reproductive Biology and Phylogeny of Annelida*. Science Publishers Inc., Enfield, NH: 565–638.

Bleidorn, C., Helm, C., Weigert, A. & Aguado, M.T. (2015): Annelida. In: Wanninger, A. (ed.) *Evolutionary Developmental Biology of Invertebrates. Vol. 2. Lophotrochozoa (Spiralia)*. Springer-Verlag, Wien: 193–230.

Bolívar, G.A. & Lana, P.C. (1986): Magelonidae (Annelida: Polychaeta) do litoral sudeste do Brasil. *Neritica* 1: 131–147.

Brasil, A.C. dos S. (2003): *Filogenia de Magelonidae Cunningham & Ramage, 1888 (Annelida – Polychaeta) com base na morfologia externa*. Tese de Doutorado, Universidade Federal do Paraná: 1–113

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Capa, M., Parapar, J. & Hutchings, P. (2012): Phylogeny of Oweniidae (Polychaeta) based on morphological data and taxonomic revision of Australian fauna. *Zoological Journal of the Linnean Society* 166: 236–278.

Carrington, B. (1865): On the chaetopod annelides of the Southport sands. *Proceedings of the Literary and Philosophical Society of Manchester* 4: 176–188.

Clarke, D.T., Paterson, G.L.J., Florence, W.K. & Gibbons, M.J. (2010): A new species of *Magelona* (Polychaeta: Magelonidae) from southern Namibia. *African Natural History* 6: 77–82.

Cunningham, J.T. & Ramage G.A. (1888): The Polychaeta Sedentaria of the Firth of Forth. *Transactions of the Royal Society of Edinburgh* 33: 635–684.

Dales, R.P. (1962): The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proceedings of the Zoological Society of London*, 139(3): 389–428.

Dales, R.P. (1977): The polychaete stomodeum and phylogeny. In: Reish, D.J. & Fauchald, K. (eds). *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles: 525–546.

Ehlers, E. (1908): Die bodensässigen Anneliden aus dem Sammlungen der deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*. 16: 1–167.

Eliason, A. (1962): Undersökningar över Öresund. XXXXI. Weitere Untersuchungen über die Polychaetenfauna des Öresunds. *Acta Universitatis Lundensis, Avd. 2*, 58(9): 1–98.

Fauchald, K. (1983): Life diagram patterns in benthic polychaetes. *Proceedings of the Biological Society of Washington* 96(1): 160–177.

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

Fiege, D., Licher, F. & Mackie, A.S.Y. (2000): A partial review of the European Magelonidae (Annelida: Polychaeta): *Magelona mirabilis* redefined and *M. johnstoni* sp. nov. distinguished. *Journal of the Marine Biological Association of the United Kingdom* 80: 215–234.

Filippova, A., Purschke, G., Tzetlin, A.B. & Müller, M.C.M. (2005): Reconstruction of the musculature of *Magelona* cf. *mirabilis* (Magelonidae) and *Prionospio cirrifera* (Spionidae) (Polychaeta, Annelida) by phalloidin labeling and cLSM. *Zoomorphology* 124: 1–8.

Gallardo, V.A. (1968): Polychaeta from the Bay of Nha Trang, South Viet Nam. *Naga Report* 4(3): 35–279.

Gravier, C. (1905): Sur les annélides polychètes de la Mer Rouge (Cirratuliens, Spionidiens, Ariciens). *Bulletin du Muséum d'Histoire Naturelle* 11(1): 42–46.

Harmelin, J.G. (1964): Étude de l'endofaune des "mattes" d'herbiers de *Posidonia oceanica* Delile. *Recueil des Travaux de la Station Marine d'Endoume* 35(51): 43–105.

Hartman, O. (1944): Polychaetous annelids from California, including two new genera and nine new species. *Allan Hancock Pacific Expeditions* 10: 239–304.

Hartman, O. (1961): Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* 25: 1–226.

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

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

Hausen, H. (2001): *Untersuchungen zur Phylogenie "spiomorpher" Polychaeten (Annelida)*. Logos-Verlag, Berlin.

Hausen, H. (2007): Ultrastructure of presumptive light sensitive ciliary organs in larvae of Poecilochaetidae, Trochochaetidae, Spionidae, Magelonidae and its phylogenetic significance. *Zoomorphology* 126: 185–201.

Helm, C., Beckers, P., Bartolomaeus, T., Drukewitz, S.H., Kourtesis, I., Weigert, A., Purschke, G., Worsaae, K., Struck, T.H., Bleidorn, C. (2018): Convergent evolution of the ladder-like ventral nerve cord in Annelida. *Frontiers in Zoology* 15:36, 1–17.

Hernández-Alcántara, P. & Solís-Weiss, V. (2000): Magelonidae from the Mexican Pacific and northern Gulf of Mexico, with the description of a new genus (*Meridithia*) and four new species. In: Reish, D.J. & Lana, P. (eds) Proceedings of the 6th International Polychaete Conference, Curitiba, Brazil, 1998. *Bulletin of Marine Science* 67: 625–644.

Hernández-Alcántara, P. & Solís-Weiss, V. (2009): Magelonidae Cunningham & Ramage, 1888. In: León-González, J.A. de, Bastida-Zavala, J.R., Carrera-Parra, L.F., Garcia-Garza, M.E., Pena-Rivera, A., Salazar-Vallejo, S.I. & Solís-Weiss, V. (eds) *Poliquetos (Annelida: Poychaeta) de México y América Tropical*. Universidad Autónoma de Nuevo León, Mexico: 277–289.

Hylleberg, J. & Nateewathana, A. (1991): Temporal and spatial distribution of subtidal magelonid polychaetes at Phuket Island, Thailand, Andaman Sea. In: Petersen, M.E. & Kirkegaard, J.B. (eds). *Systematics, biology and morphology of world Polychaeta. Proceedings of the 2nd International Polychaete Conference, Copenhagen, 1986. Ophelia*, Supplement 5: 573–578.

Johnson, H. (1901): The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society of Natural History* 29: 381–437.

Johnson, K.B. & Brink, L.A. (1998): Predation on bivalve veligers by polychaete larvae. *Biological Bulletin* 194: 297–303.

Johnston, G. (1865): *A Catalogue of the British Non-parasitical Worms in the Collection of the British Museum*. Trustees of the British Museum, London.

Jones, M.L. (1963): Four new species of *Magelona* (Annelida, Polychaeta) and a redescription of *Magelona longicornis* Johnson. *American Museum Novitates* 2164: 1–31.

Jones, M.L. (1968): On the morphology, feeding, and behavior of *Magelona* sp. *Biological Bulletin* 134: 272–297.

Jones, M.L. (1971): *Magelona berkeleyi* n. sp. from Puget Sound (Annelida: Polychaeta) with a further redescription of *Magelona longicornis* Johnson and a consideration of recently described species of *Magelona*. *Journal of the Fisheries Research Board of Canada* 28: 1445–1454.

Jones, M.L. (1977): A redescription of *Magelona papillicornis* F. Müller. In: Reish, D.J. & Fauchald, K. (eds). *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles: 247–266.

Jones, M.L. (1978): Three new species of *Magelona* (Annelida, Polychaeta) and a redescription of *Magelona pitelkai* Hartman. *Proceedings of the Biological Society of Washington* 91: 336–363.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Jumars, P.A., Kelly, M.D. & Lindsay, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.

Mackie, A.S.Y., James, J.W.C., Rees, E.I.S., Darbyshire, T., Philpott, S.L., Mortimer, K., Jenkins, G.O. & Morando, A. (2006): The Outer Bristol Channel Marine Habitat Study. Studies in marine biodiversity and systematics from the National Museum of Wales. BIOMÔR Reports 4: 1–249 & A1–A227, + DVD-ROM (2007).

McIntosh, W.C. (1877): On the structure of *Magelona*. *Annals and Magazine of Natural History*, Ser. 4 20: 147–152.

McIntosh, W.C. (1878): Beiträge zur Anatomie von *Magelona*. *Zeitschrift für Wissenschaftliche Zoologie* 31: 401–472.

McIntosh, W.C. (1879): On the circulatory system of *Magelona*. *Journal of Anatomy and Physiology* 13(3): 331–345.

McIntosh, W.C. (1911): On the structure of *Magelona*. *Annals and Magazine of Natural History*, Series 8, 7: 417–457. [Translation of McIntosh, 1878].

McIntosh, W.C. (1915): A *monograph of the British marine annelids. Vol. III. Part I. Text. Polychaeta. Opheliidae to Ammocharidae*. The Ray Society: London.

McIntosh, W.C. (1916): *A monograph of the British marine annelids. Vol. III. Part II. Plates. Polychaeta. Opheliidae to Ammocharidae*. The Ray Society: London.

McMahon, R.F. & Jones, M.L. (1967): Observations on feeding in *Magelona* sp. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole* 133: 476.

Meißner, K. & Darr, A. (2009): Distribution of *Magelona* species (Polychaeta: Magelonidae) in the German Bight (North Sea): a modeling approach. *Zoosymposia* 2: 567–586.

Mohammad, M.-B.M. (1970): On two new polychaetous annelids from Kuwait. *Zoologischer Anzeiger* 185: 303–307.

Mohammad, M.-B.M. (1973): New species and records of polychaete annelids from Kuwait, Arabian Gulf. *Zoological Journal of the Linnaean Society* 52: 23–44.

Monro, C.C.A. (1933): The Polychaeta Sedentaria collected by Dr. C. Crossland at Colón, in the Panama region, and the Galapagos Islands during the expedition of the S.Y. 'St. George'. *Proceedings of the Zoological Society of London,* 1933: 1039–1092.

Mortimer, K. (2010): Magelonidae (Polychaeta) from the Arabian Peninsula: a review of known species, with notes on *Magelona tinae* from Thailand. *Zootaxa* 2628: 1–26.

Mortimer, K., Cassà, S., Martin, D. & Gil, J. (2012): New records and new species of Magelonidae (Polychaeta) from the Arabian Peninsula, with a re-description of *Magelona pacifica* and a discussion on the magelonid buccal region. *Zootaxa* 3331: 1–43.

Mortimer, K., Gil, J. & Fiege, D. (2011): Portuguese *Magelona* (Annelida: Magelonidae) with a description of a new species, a re-description of *Magelona wilsoni* Glémarec, and a key to adult Magelonidae from European waters. *Italian Journal of Zoology* 78 (Supplement 1): 124–139.

Mortimer, K. & Mackie, A.S.Y. (2003): The Magelonidae (Annelida: Polychaeta) from the Seychelles, with the description of three new species. In: Sigvaldadóttir, E., Mackie, A.S.Y., Helgason, G.V., Reish, D.J., Svavarsson, J., Steingrímsson, S.A. & Gudmundsson, G. (eds) *Advances in Polychaete Research*. *Hydrobiologia* 496(1–3): 163–173.

Mortimer, K. & Mackie, A.S.Y. (2006): The Magelonidae (Annelida: Polychaeta) from the Seychelles. 2. Description of four additional species, three new to science. In: Sardá, R., San Martín, G., López, E., Martin, D. & George, D. (eds). *Scientific Advances in Polychaete Research*. *Scientia Marina* 70(S3): 125–137.

Mortimer, K. & Mackie, A.S.Y. (2009): Magelonidae (Polychaeta) from Hong Kong, China; with discussions on related species and redescriptions of three species. In: Maciolek, N.J. & Blake, J.A. (eds). *Proceedings of the Ninth International Polychaete Conference. Zoosymposia* 2: 179–199.

Mortimer, K. & Mackie, A.S.Y. (2014): Morphology, feeding and behaviour of British *Magelona* (Annelida: Magelonidae), with discussions on the form and function of abdominal lateral pouches. *Memoirs of Museum Victoria* 71: 177–201.

Müller, F. (1858): Einiges über die Anneliden fauna der Insel Santa Catharina an der brasilianischen Küste. *Archiv für Naturgeschichte* 24: 211–220.

Nateewathana, A. & Hylleberg, J. (1991): Magelonid polychaetes from Thailand, the Andaman Sea, with descriptions of eight new species. In: Petersen, M.E. & Kirkegaard, J.B. (eds). *Systematics, Biology and Morphology of World Polychaeta. Proceedings of the 2nd International Polychaete Conference, Copenhagen, 1986*. *Ophelia* Supplement 5: 169–184.

Orrhage, L. (1973): Two fundamental requirements for phylogenetic scientific works as a background for an analysis for Dales (1962) and Webb (1969) theories. *Zeitschrift fur Zoologische Systematik und Evolutionsforschung* 11: 161–173.

Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D. & Vinther, J. (2016): The impact of fossil date on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society, Series B* 283: 20161378.

Pennant, T. (1777): *British Zoology, Vol. IV. Crustacea. Mollusca*. Testacea, London: 1–154, Plates 1–93.

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

Rouse, G.W. (1999): Polychaeta, including Pogonophora and Myzostomida. In: Jamieson, B.G.M. (ed.) *Reproductive Biology of Invertebrates, Vol. IXB. Progress in Male Gamete Ultrastructure and Phylogeny*. Oxford and IBH Publishing Co., New Delhi: 81–124.

Rouse, G.W. (2001): *Magelona* Müller, 1858. In: Rouse, G.W. & Pleijel, F. (authors). *Polychaetes*. Oxford University Press, Oxford: 261–263.

Rouse, G.W. (2006): Chapter 3. Annelid sperm and spermiogensis. In: Rouse, G.W. & Pleijel, F. (eds). *Reproductive Biology and Phylogeny of Annelida*. Science Publishers Inc., Enfield New Hampshire: 45–76.

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

Rouse, G.W. & Fauchald, K. (1998): Recent views on the status, delineation and classification of the Annelida. *American Zoologist* 38: 953–964.

Shakouri, A., Mortimer, K., & Dehani, E. (2017): A new species and new records of *Magelona* (Annelida: Magelonidae) from Chabahar Bay, Gulf of Oman, South-eastern Iran. *Journal of the Marine Biological Association of the United Kingdom*: 97(7), 1537–1552. doi: 10.1017/S002531541600076X.

Struck, T.H., Purschke, G., Dordel, J., Hösel, C., Nesnidal, M.P., Diersing, F., Bleidorn, C., Paul, C., Hill, N., Tiedemann, R., Selbig, J. & Hartmann, S. (2014): Phylogeny and evolution

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

of Annelida based on molecular data. In: Wägele, J.W. & Bartolomaeus, T. (eds) *Deep Metazoan Phylogeny: The Backbone of the Tree of Life. New insights from analyses of molecules, morphology, and theory of data analysis*. Walter De Gruyter GmbH, Berlin/Boston: 736 pp.

Uebelacker, J.M. & Jones, M.L. (1984): Family Magelonidae. In: Uebelacker, J.M. & Johnson, P.G. (eds). *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Final Report to the Minerals Management Service*, contract 14-12-001-29091. Barry A. Vittor and Associates, Mobile, AL: 7.1–7.29.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the Annelid tree using transcriptomics. *Molecular Biology and Evolution* 31(6): 1391–1401.

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

Wesenberg-Lund, E. (1949): Polychaetes of the Iranian Gulf. *Danish Scientific Investigations in Iran* 4: 247–400.

Wilson, D.P. (1958): The polychaete *Magelona alleni* n. sp. and a re-assessment of *Magelona cincta* Ehlers. *Journal of the Marine Biological Association of the United Kingdom* 37: 617–626.

Wilson, D.P. (1959): The polychaete *Magelona filiformis* sp. nov. and notes on other species of *Magelona*. *Journal of the Marine Biological Association of the United Kingdom* 38: 547–556.

Wilson, D.P. (1982): The larval development of three species of *Magelona* (Polychaeta) from localities near Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 62: 385–401.

Zhou, J. & Mortimer, K. (2013): A new species of *Magelona* (Polychaeta: Magelonidae) from Chinese coastal waters. *Journal of the Marine Biological Association of the United Kingdom* 93(6): 1503–1510.

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# 5 Chaetopterida

James A. Blake and Mônica A.V. Petti

## 5.1 Apistobranchidae Mesnil & Caullery, 1898

### Introduction

The Apistobranchidae Mesnil & Caullery, 1898 are elongate, soft-bodied polychaetes that inhabit fine sediments from low water to the continental shelf and slope to depths of 3,000 m or more. A single genus, *Apistobranchus* Levinsen, 1883 is currently recognized (Blake 1996, Petti *et al*. 2007). These worms superficially resemble spionids and trochochaetids but also share some characters of orbiniids and paraonids. A pair of grooved tentacular spionid-like palps is attached to a head composed of a prostomium fused with the peristomium. The entire head region is densely ciliated, with cilia continuing posteriorly from the mouth as a ventral ciliary band to near the pygidium. Parapodia are supported by internal aciculae, a feature that is unusual in sedentary, tubicolous polychaetes. Some postchaetal lamellae are fimbriated, superficially resembling similar structures in orbiniids. Another orbiniid structure, interramal cirri, is also present. Some chaetae are smooth, elongate capillaries; other chaetae are limbate and often splinter, superficially resembling compound chaetae. Posterior neuropodial spines have been observed in *Apistobranchus glacierae* Hartman, 1978 and are likely in other species.

The biology of apistobranchids is poorly known. They are believed to use their palps in feeding, but this has not been demonstrated. High densities of more than 135,000 individuals $m^{-2}$ of one species have been found using very fine sieves. Their reproductive biology is largely unknown. Egg and sperm morphologies suggest external fertilization and possible planktonic development, but such larvae have never been found; five-chaetiger juveniles found in the Antarctic species *A. glacierae* from benthic samples suggest direct development.

### Morphology

#### External morphology

Due to the fragile nature of their posterior body, apistobranchids are often fragmented when preserved, making accurate chaetiger counts rare. The largest number of segments recorded is 65 by Orrhage (1962) for *Apistobranchus tullbergi*, with the largest measured specimens recorded at 8 mm for 28 segments (Wesenberg-Lund 1951). The width (at the third chaetiger) has been recorded at more than 1 mm. Petti *et al*. (2007) recorded the largest specimens of *A. glacierae* from Antarctica at 57 chaetigers, 7 mm long and 0.9 mm wide at the third chaetiger. The same authors also discovered five-chaetiger juveniles measuring 0.4 mm long and 0.1 mm wide.

**Prostomium**. The prostomium is broadly rounded on the anterior margin and fused dorsally with the peristomium (Figs. 5.1.1 A, E and 5.1.4 A, C). Juveniles of *Apistobranchus tenuis* and *A. glacierae* may have a prostomium with a narrower anterior margin (Figs. 5.1.1 A and 5.1.3 B). The entire head is covered with cilia that merge ventrally and form a band of cilia that extends from the mouth along the entire ventral length of the body (Fig. 5.1.1 C, D). A pair of grooved, thickened spionid-like palps arise from the junction of prostomium and chaetiger 1 (Figs. 5.1.1 A and E and 5.1.3 A, B); these palps contract greatly during preservation (Orrhage 1962) and are often lost due to rough handling during the preservation process. Palps will be retained if handled gently, as Petti *et al*. (2007) found using meiofaunal collection techniques. Paired, ciliated nuchal organs occur laterally and posteriorly at the bases of the palps (Fig. 5.1.1 A, E). The mouth is ventral, with a ridged lower lip, from which a small, saclike proboscis may emerge.

**Parapodia**. Parapodia are subbiramous, with notopodia reduced to clavate, erect ciliated structures that are either continuous along the body from chaetiger 2 or absent from chaetigers 6–11, 7–10, or 8–11. These ciliated notopodia probably function as branchiae but are supported by internal aciculae (Figs. 5.1.1 E and 5.1.2 C) that do not protrude externally. Juvenile specimens of *A. tenuis* have been noted to lack the notopodia in chaetigers 6–11, with these being replaced by a "lateral organ," visible in thin sections (Orrhage 1962). The missing notopodia develop with growth in *A. tullbergi* but apparently do not develop in *A. tenuis*, *Apistobranchus typicus*, and *Apistobranchus ornatus*. An interramal cirrus is present between the notopodium and neuropodium of some anterior chaetigers (Figs. 5.1.1 A, E, 5.1.2 A–E, and 5.1.4 C). The neuropodia of the first 11–12 chaetigers are specialized. The first seven neuropodia are enlarged and bear numerous chaetae (Fig. 5.1.2 A–E). These chaetae are gradually

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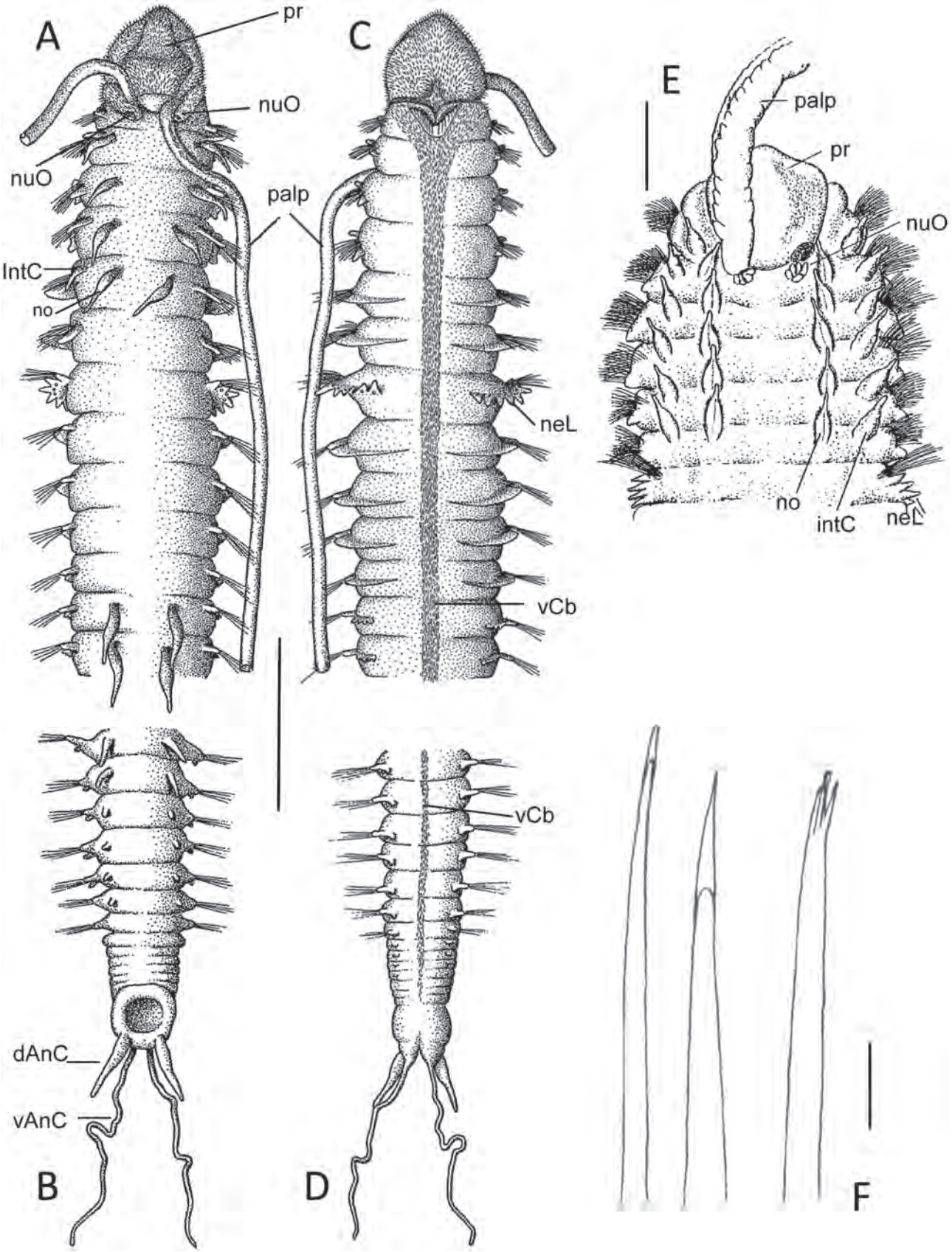


**Fig. 5.1.1:** *Apistobranchus tenuis* in dorsal (A–B) and ventral (C–D) views. E, *Apistobranchus ornatus, anterior end,* dorsal view. F, Neurochaetae in different forms of wear. dAnC, dorsal anal cirrus; intC, interramal cirrus; neL, neuropodial lamella; no, notopodium; nuO, nuchal organ; pr, prostomium; vAnC, ventral anal cirrus; vCb, ventral ciliary band. Scale bars: A–E, 500 µm; F, 10 µm. A–D, after Orrhage (1962); E–F, after Blake (1996).

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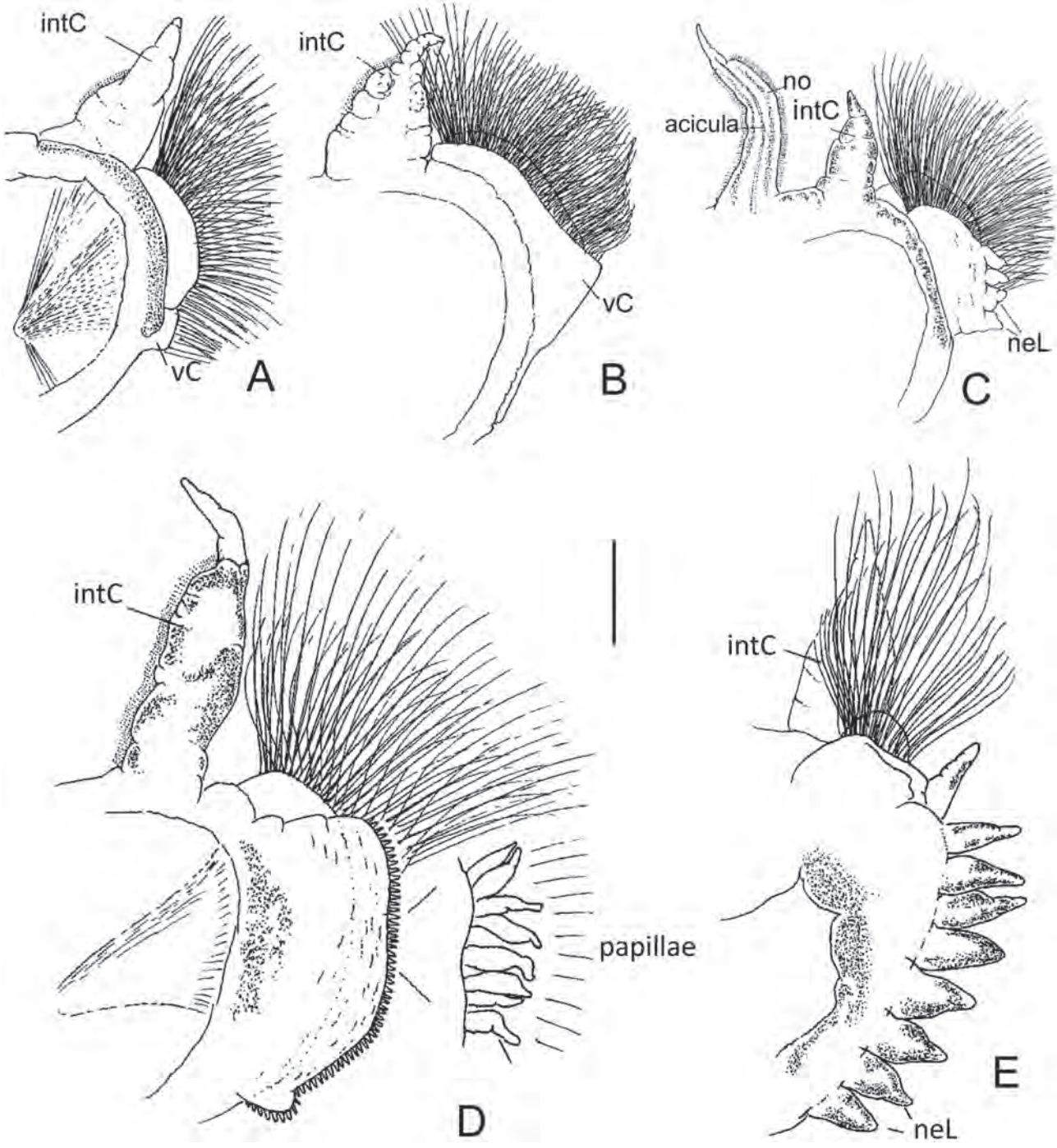


**Fig. 5.1.2:** *Apistobranchus ornatus,* anterior views of parapodia. A, Chaetiger 1; B, chaetiger 3; C, chaetiger 4; D, chaetiger 5; E, chaetiger 7. intC, interramal cirrus; neL, neuropodial lamella; no, notopodium; vc, ventral cirrus. Scale bars: A–E, 200 µm. All after Blake (1996).

reduced in number, so that from chaetiger 8, the neuropodium is a small cylindrical structure bearing few chaetae. The neuropodial postchaetal lamellae are specialized in anterior chaetigers, with those of chaetigers 1–3 bearing a short digitate ventral lobe; chaetiger 4 may be simple or with several lobes. Chaetigers 5–6 have broad ventral lamellae with minute papillae along one edge (Fig. 5.1.2 D). The ventral lamellae of chaetiger 7 are highly modified and divided into about 10 large vacuolated lobes (Figs. 5.1.2 E and 5.1.4 D); the number of lobes is size dependent (Orrhage 1962). The ventral lamellae of chaetigers 8–11 (or 12) are broad and bear minute papillae, resembling those of chaetigers 5–6. From chaetiger 13, the neuropodial lamellae are reduced to a few papillae or to single cirrus.

Apart from an internal acicula, notochaetae are lacking (Fig. 5.1.2 C). An acicula or supporting chaeta is also

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present in the neuropodia, but unlike the notopodia, in *A. typicus*, this chaeta is visible externally, usually ventral to the main fascicle of neurochaetae (Hausen 2005). In *A. glacierae*, neuropodia are supported by two strong aciculae, one acuminate and the other with a rounded or spoon-shaped tip (Petti *et al.* 2007; Fig. 5.1.2 F). In *A. ornatus*, smooth, blunt-tipped protruding aciculae are observed (Blake unpublished). The neurochaetae of chaetigers 1–7 are short and robust, usually golden in color and arranged in dense fascicles of numerous chaetae. The neurochaetae of subsequent segments are fewer in number and consist of (1) long capillary chaetae, with some having mucronate tips (Fig. 5.1.1 F) (Pettibone 1963, Imajima 1974, Blake unpublished); however, the tip of the chaeta is surrounded by a

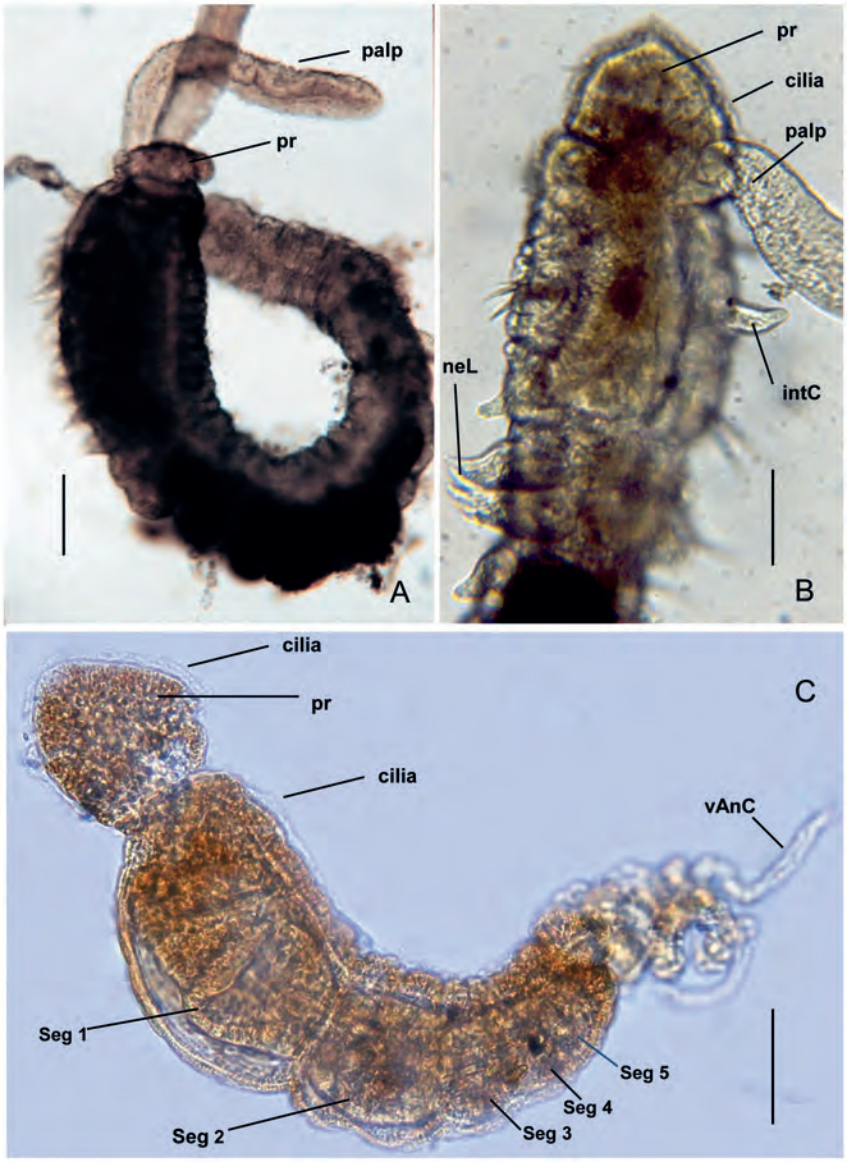


**Fig. 5.1.3:** *Apistobranchus glacierae,* photographs of living specimens from Antarctica. A, Entire animal from Weddell Sea. B, Anterior end of juvenile from Weddell Sea. C, Five-chaetiger benthic juvenile from King George Island. intC, interramal cirrus; pr, prostomium; Ch, chaetiger; vAnC, ventral anal cirrus. Scale bars: A, B, 200 µm; C, 60 µm. A, B, Originals by J.A. Blake; C, after Petti *et al.* (2007).

▸ **Fig. 5.1.4:** *Apistobranchus glacierae,* scanning electron micrographs (SEMs) and photomicrographs of specimens from King George Island, Antarctica. A, Entire animal in right lateral view. B, Posterior end of same. C, Anterior-ventral view of another specimen. D, Details of chaetigers 5–7, left lateral view. E, Details of chaetigers 5–6 of specimen in C. F, Scanning electron microscopy image of short limbate and long capillaries. G, Photomicrograph of splintered limbate chaetae. H, Posterior serrated spine. intC, interramal cirrus; neL, neuropodial lamella; per, peristomium; pr, prostomium; vAnC, ventral anal cirrus; vCb, ventral ciliary band; ves, vestibule (mouth). Scale bars: A–C, 100 µm; D-F, 30 µm; G, 50 µm; H, 10 µm. A, C, D, F, G, after Petti *et al.* (2007); B, E, H, originals.

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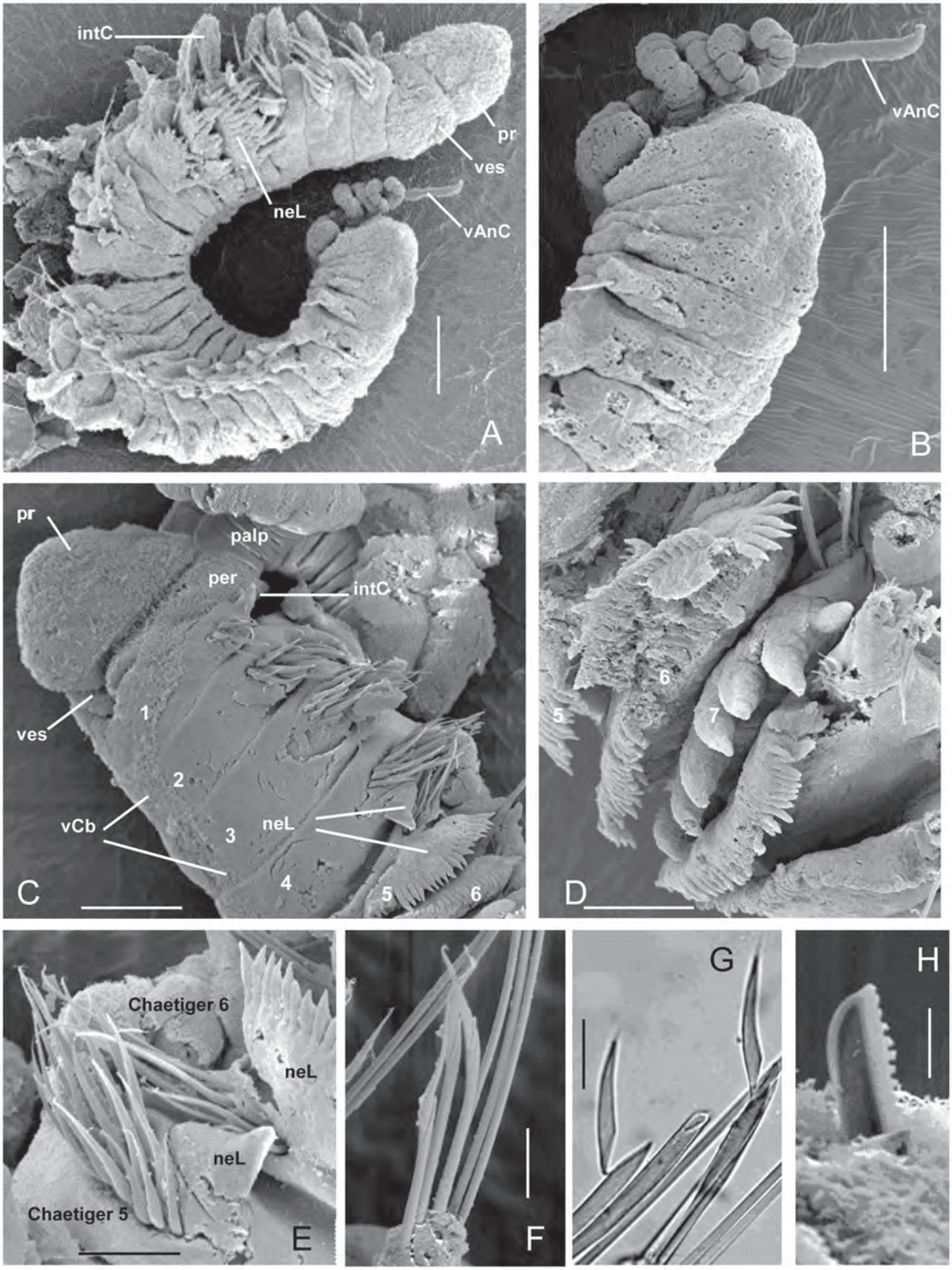


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sheath of fibrils or numerous points; (2) limbate chaetae that are moderately long, with blades often splintered, sometimes resembling a compound chaeta (Fig. 5.1.4 F, G). The compound chaetae reported for the Antarctic species *Apistobranchus gudrunae* by Hartmann-Schröder and Rosenfeld (1988) were in fact found to be normal limbate chaetae that had splintered (Petti *et al.* 2007). This species was therefore synonymized with *A. glacierae* by these same authors. One very strong serrated falcate chaeta is present on the posterior chaetigers of *A. glacierae* (see Petti *et al.* 2007; Fig. 5.1.4 H); thick, curved spines or protruding aciculae are present in *A. ornatus* (Blake unpublished).

**Pygidium.** The anus is dorsal on the pygidium, which bears two short dorsolateral digitiform cirri and two ventral elongate filiform cirri (Fig. 5.1.1 B). In most descriptions, however, the elongate filiform cirri have not been reported and it is likely that they have been lost. Petti *et al.* (2007) reported that the dorsal pair of pygidial cirri was shorter and inconspicuous, while the longer ventral pair was conspicuous (Fig. 5.1.4 A, B).

### Anatomy

The only account of internal anatomy is by Orrhage (1974), who investigated anatomy and histology in an effort to establish the systematic position of apistobranchids among other polychaete families. He found close anatomical similarities between apistobranchids, spionids, and trochochaetids, but little similarity with paraonids and orbiniids.

### Reproduction and development

Orrhage (1974) found ripe eggs and sperm in specimens of *A. tenuis* in various months from January to October, suggesting a long period of reproduction. The eggs had a diameter of 70–80 µm. Sperm were of the short-headed type that have been termed primitive by Franzén (1956) and ect-aquasperm by Rouse and Jamieson (1987). The presence of relatively small eggs and primitive sperm suggested to Blake (1996) that the gametes are dispersed into the water column, where fertilization and subsequent embryonic development take place, thus possibly producing planktic larvae. However, planktic larvae of *Apistobranchus* have never been identified. In contrast Petti *et al.* (2007) found small, five-chaetiger juveniles of the Antarctic species *A. glacierae*, suggesting direct development. An illustration of one of these individuals is shown in Fig. 5.1.3 C. The prostomium/peristomium is fused and heavily ciliated, with the first segment being unusually large; the following segments are sequentially smaller. The pygidium consists of two very long, tangled anal cirri.

### Biology and ecology

Virtually nothing is known concerning the biology of apistobranchids. They have been collected from a wide variety of sediment types, including sands, mixed sands, and fine silty muds. They range from shallow continental shelf depths to the deep sea and from the Arctic to the Antarctic.

According to Fauchald (1977), apistobranchids feed from loosely constructed burrows, which they may leave. The large, spionid-like palps suggest a surface deposit feeding mode, but this has not been confirmed, although Fauchald and Jumars (1979) assigned apistobranchids to their SDT feeding guild (surface deposit-feeding, discretely motile, tentaculate). The carbon and nitrogen isotopic signatures of *A. glacierae* in Antarctica were closely related to that of the sediment and microphytobenthos associated with their habitat and represents additional evidence that they are deposit feeders (Petti unpublished). Jumars *et al.* (2015) predict strong selection for high-quality food items such as benthic diatoms. Kędra *et al.* (2012) reported $\delta^{15}N$ and $\delta^{13}C$ values for *A. tullbergi* from Kongsfjorden, Svalbard, collected in 15 m of water, consistent with values observed in other deposit feeder (Jumars *et al.* 2015).

Petti *et al.* (2007) reported high densities of 135,714 individuals $m^{-2}$ *A. glacierae* in Martel Inlet, Admiralty Bay, King George Island, Antarctica, in 18 m of water depth. These samples were processed using meiofaunal sieving methods; coarser macrofaunal sieves yielded densities of 17,800 individuals $m^{-2}$. Apistobranchids were most abundant in finer sediments composed of mud and sand. High densities of the same species had earlier been reported by Lowry (1975) (1,110 individuals $m^{-2}$) and Richardson and Hedgpeth (1977) (6,000 individuals $m^{-2}$) from 18–43 m depth along the Antarctic Peninsula. Population densities of up to 3,440 individuals $m^{-2}$ of *A. ornatus* from shallow-water sediments off Prince Rupert, British Columbia, Canada, separated with 500 µm sieves were obtained as part of a benthic reconnaissance (Blake unpublished). Recent results in an Arctic fjord showed densities around 3,300 individuals $m^{-2}$ of *A. tullbergi*, representing more than 40% of the total macrofauna at 15 m depth in winter (Kędra *et al.* 2011).

A recent histological analysis of the gonads of 40 specimens of *A. glacierae* (1.1–8.2 mm total length) recorded 14 females, 20 males, and 4 individuals with both oocytes and spermatids, indicating simultaneous hermaphroditism. The sex of two small individuals was not identified due to the absence of reproductive tissue. The diameters of mature megalecithal oocytes were 180–190 µm, and oocyte development was asynchronous. In male gonads,

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only spermatids were found. Larvae and/or fertilized eggs were not identified (Petti *et al*. 2016). Fauchald (1977) reported that *Apistobranchus* is thought to be tubicolous, but no tubes were observed by Orrhage (1962) and Webster and Benedict (1887). Probably, they are so fragile and thin that they are destroyed or lost during sieving and fixation.

### Distribution

Apistobranchids are global in distribution, ranging from very shallow depths to continental slope depths. The distribution of the five known species is summarized here:

1 *Apistobranchus tullbergi* (Théel, 1879) (includes *Skardaria fragmentata* Wesenberg-Lund, 1951): Widespread in European waters from the Arctic to the Mediterranean; reported from NE North America and NE Pacific, shallow water to continental shelf depths.
2 *Apistobranchus tenuis* Orrhage, 1962: Northern Europe, Skagerrak, Kattegat, shallow water.
3 *Apistobranchus typicus* (Webster and Benedict, 1887): Northeastern North America, shallow water to continental slope depths; Southwestern Atlantic, Brazilian waters in slope depths (Paiva and Barroso 2010).
4 *Apistobranchus ornatus* Hartman, 1965: Northeastern Pacific, Southern California to British Columbia, shallow subtidal to continental slope depths.
5 *Apistobranchus glacierae* Hartman, 1978 (includes *A. gudrunae* Hartmann-Schröder & Rosenfeldt, 1988): Antarctic Peninsula, Ross Sea, and Weddell Sea, shallow subtidal to continental slope depths.

## Phylogeny and taxonomy

### Phylogeny

**Morphological studies.** The phylogenetic position of *Apistobranchus* within Annelida is somewhat of an enigma at the present time. Morphologically, apistobranchids exhibit an unusual combination of characters that over the years have resulted in comparisons with Orbiniidae and more typically with the spioniform families. Indeed, the paired palps were a key character that Rouse and Fauchald (1997) used to include *Apistobranchus* within their Canalipalpata. Apistobranchidae were originally considered part of the Orbiniidae due to the presence of numerous postchaetal lamellae on some neuropodia and the presence of interramal cirri. In his study of internal anatomy, Orrhage (1974) found close anatomical similarities between Apistobranchidae, Spionidae, and especially Trochochaetidae, but little similarity with Paraonidae and Orbiniidae. As part of a cladistic analysis of Spionidae and related families, Blake and Arnofsky (1999) found that *Apistobranchus* behaved more as an out-group than an in-group taxon.

One character that has been entirely overlooked and that may help define the morphological relationships of *Apistobranchus* to other polychaetes is the presence of a ventral ciliary band that extends posteriorly from the mouth along the length of the body to the posterior end. This was first reported by Orrhage (1962) for *A. tenuis* (Fig. 7.2.2.1 C–D) but is also present in *A. glacierae* (Fig. 7.2.2.4 C). A close inspection of specimens of *A. ornatus* from the eastern Pacific reveals that the same cilia are present in that species as well. Worsaae *et al*. (2004) and Mackie *et al*. (2005) demonstrated that two groups of polychaetes having this same structure and previously thought be unrelated, Nerillidae and *Aberranta*, were in fact closely related. The presence of a similar ciliary band in *Apistobranchus* provides another avenue to explore for placement of this enigmatic genus.

**Molecular studies.** To date, molecular efforts to identify the relationships of *Apistobranchus* with other polychaetes have been inconclusive and with results that are intuitively unlikely. The earliest paper to address the possible affinities of *Apistobranchus* was by Bleidorn *et al*. (2003) using 18S rRNA sequence data for 70 species. A strict consensus of 33 most parsimonious trees showed a sister relationship between *A. typicus* and *Owenia fusiformis*. However, this clade was of insufficient significance when clade significance values and decay indices were calculated. In the same paper; these authors presented a maximum likelihood (ML) tree based on Bayesian analysis of the TrNef + É + Γ model of sequence evolution. From this tree, *A. typicus* and *O. fusiformis* were again most closely related to one another, but also to the oyster, *Ostrea edulis*. Given that such a relationship is unlikely, the authors did note that Bayesian a posteriori probabilities are not easy to interpret. Bleidorn (2009) updated his analysis and presented a new ML dataset analysis of 18S rRNA using the GTR + I + Γ model. In this tree, *A. typicus*, *Chaetoderma nitidulum*, an aplacophoran mollusc, and two oweniids, *O. fusiformis* and *Myriochele* sp., formed a clade that when bootstrap was applied was not strongly supported.

Rousset *et al*. (2007) presented a molecular phylogeny of annelids using two nuclear ribosomal genes, 18s rDNA, and the D1 region of 28S rDNA, one nuclear protein coding-gene, Histone H3, and one mitochondrial ribosomal gene, 16S rDNA. A total of 217 taxa were used. The results from a strict consensus of 144 trees resulted in one clade, where *Apistobranchus* and two nemerteans were a sister group to *Owenia, Myriochele*, and three molluscs. This

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result was poorly supported. Another strict consensus using a more restricted data set resulted in a distinct basal clade for *Apistobranchus* without the oweniids, nemerteans, molluscs, albeit these taxa were in adjacent clades.

Struck *et al*. (2008) presented a new analysis of 18S rRNA and of 28S rRNA sequences. This study was aimed at addressing the problem of multiple substitutions in nucleotide positions that tend to obliterate signal, a situation called saturation. In the first ML tree where the possibility of saturation was excluded, *A. typicus* was once again part of a clade with *O. fusiformis*, but also with *Cerebratulus lacteus*, a nemertean. This clade had no nodal support in the analysis. The second ML cladogram, not excluding saturation, yielded another clade with *A. typicus, O. fusiformis, C. lacteus*, and two brachiopods, *Terebratalia transversa* and *Glottidia pyramidata*. The only comments made about these results by Struck *et al*. (2008) was that *Apistobranchus* was a sister to *Owenia* in both analyses, ignoring the perceived genetic link to nemerteans and brachiopods. In our opinion, this analysis and others where *Apistobranchus* and Oweniidae are joined in a clade with other unrelated invertebrates (nemerteans, molluscs, and brachiopods) is seriously flawed and requires some explanation before such results can be used in any classification or phylogenetic scheme.

The most recent effort that contributes to an understanding of where *Apistobranchus* might reside in the phylogeny of polychaetes was presented by Zrzavý *et al*. (2009), who attempted to combine morphological and molecular data as part of a "total evidence" analysis. In this analysis, *Apistobranchus* grouped more or less consistently with or as a sister to a clade that included Orbiniidae and Parergodrilidae, what the authors termed the OPC clade. There was no evidence of a close relationship with Oweniidae as in the strictly molecular analyses.

**Phylogenetic conclusions.** Given the wide range of results with molecular phylogeny to date and how unlikely some of the relationships with nemerteans, molluscs, and brachiopods represent, we suggest that no definitive phylogeny of *Apistobranchus* to other polychaetes has been demonstrated. It is evident, however, that *Apistobranchus* is not part of the Spionida. This was more or less demonstrated by Blake and Arnofsky (1999) when the genus behaved as an out-group rather than an in-group within the larger spioniform analysis performed by these authors. Hausen (2005) showed that chaetal development in *A. typicus* was entirely different from that of spioniforms. Instead of chaetae that develop and become arranged into distinct rows dorsal to ventral, newly formed chaetae of *Apistobranchus* are formed in the posterior part of the fascicle and move anteriorly with development forming an irregular arrangement of chaetae, never in distinct rows. However, our observations of *A. glacierae* suggest that chaetae are sometimes arranged in rows in smaller specimens (Fig. 7.2.2.4 C, E). None of the molecular approaches have demonstrated any grouping of *Apistobranchus* with other spioniform genera or families. In a later paper, Hoffmann and Hausen (2007) found that orbiniid chaetae developed in the same manner as spioniforms.

The potential link to Orbiniidae identified by Zrzavý *et al*. (2009) in the combined morphology/molecular analysis is interesting because the first apistobranchid to be described, A. *tullbergi*, was described as an orbiniid (Théel 1879). In fact, there are several shared characters with Orbiniidae, including aciculae supporting the notopodia and the recent discovery of aciculae supporting the neuropodia (Hausen 2005, Petti *et al*. 2007), the presence of numerous postchaetal lamellae on some anterior neuropodia, and the presence of interramal cirri. As noted earlier, however, chaetal development in orbiniids (and spioniforms) differs from that of *Apistobranchus*, and orbiniids do not have grooved palps or the ventral ciliary band. The latter character is present in *Aberranta* and Nerillidae, and an analysis of *Apistobranchus* relationships with those taxa should be explored. These latter taxa were not included in the majority of molecular studies conducted to date. Either way, a link to Oweniidae suggested in some of the molecular studies should be viewed with caution. We cannot think of a single morphological similarity between *Apistobranchus* and *Owenia* that makes any sense or that supports such a relationship.

**Taxonomy**

The taxonomic history of *Apistobranchus* was reviewed by Blake (1996), who demonstrated past errors and misconceptions that were introduced by Wesenberg-Lund (1951) and perpetuated by others, resulting in a very confused literature. A total of seven species have been described, some of which were by authors who were either unaware of previous works or misconstrued the earlier descriptions. Five species are now considered valid (Blake 1996, Petti *et al*. 2007).

The first apistobranchid to be described was *A. tullbergi* by Théel (1879) as an orbiniid in the genus *Aricia*. *Apistobranchus* was subsequently established for the species by Levinsen (1883). The family Apistobranchidae was established by Mesnil and Caullery (1898). The type species, *A. tullbergi* has been widely reported from Europe (Eliason 1916, 1962, Hartmann-Schröder 1971, 1996), the Gulf of Mexico (Gathof 1984), the Pacific Northwest (Banse 1972, Hobson and Banse 1981), Japan (Imajima 1974), and

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the Arctic (Reish 1965). However, some non-European records may refer to other species.

The second species to be described was *Ethocles typicus* by Webster and Benedict (1887) from Maine in New England, USA. These authors referred the species to the Chaetopteridae and were unaware of the earlier papers and the genus *Apistobranchus*. Mesnil and Caullery (1898), Eisig (1914), and Pettibone (1963) all synonymized *A. typicus* with *A. tullbergi*. However, Hartman (1965) referred specimens of *Apistobranchus* from the Atlantic continental slope to *A. typicus*. This species has been observed elsewhere in the northeastern United States (Blake unpublished), and the *A. typicus* specimens used for the molecular analyses mentioned previously were collected from Greenland.

Wesenberg-Lund (1951) described *Skardaria fragmentata* from Iceland, but according to Blake (1996), she apparently mistranslated Théel's original description and misconstrued perceived differences between her specimens and *A. tullbergi*. Wesenberg-Lund also assumed that the absence of palps on *A. tullbergi* was of taxonomic significance, even though Eliason (1916) had already demonstrated that specimens from the Baltic had them. Blake (1996) documented that these errors and others were passed unquestioned through several papers and reviews (e.g., Hartman 1965). The synonymy of *A. tullbergi* and *S. fragmentata* is now widely supported (Eliason 1962, Pettibone 1963, Hartmann-Schröder 1971, 1996, Fauchald 1977, Blake 1996).

*Apistobranchus tenuis*, described by Orrhage (1962), may represent either a small species or possibly a neotenous phase of *A. tullbergi* because the interramal cirri of some anterior chaetigers are missing. Hartmann-Schröder (1971, 1996) considers *A. tenuis* to be a synonym of *A. tullbergi*.

The name *Apistobranchus ornatus* was introduced by Hartman (1965) to name the records of *Apistobranchus* from California she had previously and erroneously referred to *S. fragmentata*. Illustrations were introduced by Hartman (1969), but these contained errors as noted by Blake (1996), who accurately described and illustrated the species for the first time. The species was reported from the NE Pacific by Banse and Hobson (1968) and Hobson and Banse (1981) and has been found in high densities in shallow waters of British Columbia (Blake unpublished).

The most recent species to be described was *A. glacierae* Hartman, 1978 (Hartman 1978) from the Antarctic Peninsula. The status of this species was reviewed by Blake (1996) and more recently by Petti *et al.* (2007), who synonymized *A. gudrunae* Hartmann-Schröder & Rosenfeldt, 1988 with *A. glacierae*.

There appear to be five valid species of *Apistobranchus* (*A. glacierae, A. ornatus. A. tenuis, A. tullbergi*, and *A. typicus)*, with very few characters available to separate them. These species are separated by characters presented in the key below.

***Apistobranchus* Levinsen, 1883.**

**Type species:** *Aricia tullbergi* Théel, 1879.

**Synonyms:** *Ethocles* Webster & Benedict, 1887; type species: *Ethocles typicus* Webster & Benedict, 1887.

*Skardaria* Wesenberg-Lund, 1951; type species: *S. fragmentata* Wesenberg-Lund, 1951.

**Diagnosis:** Prostomium rounded to somewhat pointed anteriorly, wider posteriorly, with two nuchal folds and a pair of long, contractile palps (often deciduous, missing, or regenerating); eyes absent; peristomium narrow, typically merged with prostomium and indistinguishable. Entire head region densely covered with cilia; ventrally, extending posteriorly from the mouth as a narrow ciliated band to near the posterior end. Anterior body region with modified neuropodia, including some chaetigers with subpodial fringed lobes. Notopodia reduced to simple cirrus supported by internal acicula. Interramal cirri present from chaetiger 1. Chaetae all simple, including long, curved capillaries and shorter limbate capillaries; the latter sometimes with mucronate or splintered tips; falcate posterior neurochaetae or spines reported for some species; thin non-emergent aciculae present in notopodia of all species; thin, emergent aciculae present in posterior neuropodia in *A. typicus*, *A. glacierae*, and *A. ornatus*, with thicker emergent aciculae sometimes with rounded tips. Pygidium with two short dorsal and two long ventral anal cirri.

**Key to the Known Species of *Apistobranchus* (Modified from Blake 1996)**

| | | |
|---|---|---|
| 1. | Notopodia present on all segments from chaetiger 2 except last few | 2 |
| | Notopodia present from chaetiger 2, then absent on several anterior segments from chaetiger 6–7, then continuing to near posterior end | 3 |
| 2. | Neuropodia of chaetiger 4 with a single lobe; neuropodial spines absent | *Apistobranchus tullbergi* |
| | Neuropodia of chaetiger 4 multilobed; far posterior neuropodia with serrated spine | *Apistobranchus glacierae* |
| 3. | Neuropodia of chaetiger 4 with a single lobe; notopodia absent on chaetigers (6)7–11; methyl green staining as transverse strip posterior to anterior notopodia | *Apistobranchus tenuis* |
| | Neuropodia of chaetiger 4 multilobed | 4 |

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| | | |
|---|---|---|
| 4. | Methyl green stain: (1), concentrating on posterior face of neuropodial lamellae from chaetiger 5; (2) papillae of chaetiger 7 staining internally; (3) a paired line of stain extends posteriorly along the ventral midline of body from about chaetiger 7–8; and (5) interramal "glands" of chaetigers 8–10 stain darkly; neuropodial aciculae large, smooth, rounded or curved apically, associated with chaetal fascicle; posterior neuropodia with protruding blunt-tipped spines | *Apistobranchus ornatus* |
| | Methyl green stain limited to pale reaction on swollen dorsal glandular areas; neuropodial aciculae thin, emergent ventral to chaetal fascicle | *Apistobranchus typicus* |

## References


Banse, K. (1972): On some species of Phyllodocidae, Syllidae, Nephtyidae, Goniadidae, Apistobranchidae, and Spionidae (Polychaeta). *Pacific Science* 26: 191–222.

Banse, K. & Hobson, K.D. (1968): Benthic polychaetes from Puget Sound, Washington, with remarks on four other species. *Proceedings of the United States National Museum* 125(3667): 1–53.

Blake, J.A. (1996): Chapter 3. Family Apistobranchidae. In: Blake, J.A. Hilbig, B. & Scott, P.H. (eds.). *Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel, Vol. 6. Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara: 71–79.

Blake, J.A. & Arnofsky, P.A. (1999): Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. In: Dorresteijn, A.W.C. & Westheide, W. (eds.) Reproductive Strategies and Developmental Patterns in Annelids. *Hydrobiologia* 402: 57–106.

Bleidorn, C. (2009): Chapter 2. Annelid phylogeny – molecular analysis with an emphasis on model animals. In: Shain, D.H. (ed.) *Annelids in Modern Biology*. Wiley-Blackwell, New York: 13–30.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003): A contribution to sedentary polychaete phylogeny using 18S rRNA data. *Journal of Zoological Systematics and Evolutionary Research* 41: 186–195.

Eliason, A. (1916): Biologisch-faunistische Untersuchungen aus dem Öresund. Zwei für unsere Fauna neue Polychaeten, *Sphaerodorum philippi* Fauvel und *Apistobranchus tullbergi* Théel. *Lunds Universitets Årsskrift New Series* 12(10): 1–10.

Eliason, A. (1962): Die Polychaeten der Skagerak-Expedition 1933. *Zoologiska Bidrag från Uppsala* 33: 207–293.

Eisig, H. (1914): Zur Systematik, Anatomie und Morphologie der Ariciiden nebst Beiträgen zur generellen Systematik. *Mitteilungen der Zoologischen Station zu Neapel* 21: 153–600.

Fauchald, K. (1977): The polychaete worms: definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–190.

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

Franzén, Å. (1956): On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zoologiska Bidrag från Uppsala* 31: 355–480.

Gathof, J.M. (1984): Family Apistobranchidae Mesnil and Caullery, 1898. In: Uebelacker, J.M. and Johnson, P.G. (eds.). *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Vol. 5*. Barry A. Vittor & Associates, Inc., Mobile, AL: 5-1–5-3.

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

Hartman, O. (1969): *Atlas of the Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles: 812.

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

Hartmann-Schröder, G. (1971): Annelida, Borstenwürmer, Polychaeta. In: Dahl, M. & Peus, F. (eds.) *Die Tierwelt Deutschlands 58*. Gustav Fischer, Jena: 1–594.

Hartmann-Schröder, G. (1996): Annelida, Borstenwürmer, Polychaeta. In: Dahl, M. & Peus, F. (eds.) *Die Tierwelt Deutschlands 58*. 2nd ed. Gustav Fischer, Jena: 1–648.

Hartmann-Schröder, G. & Rosenfeldt, P. (1988): Die Polychaeten der "Polarstern"-Reise ANT III/2 in die Antarktis 1984. Teil 1: Euphrosinidae bis Chaetopteridae. *Mitteilungen des Hamburgischen Zoologischen Museums und Instituts, Supplement* 85: 5–72.

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

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

Hoffmann, S. & Hausen, H. (2007): Chaetal arrangement in Orbiniidae (Annelida, Polychaeta) and its significance for systematics. *Zoomorphology* 126(4): 215–227.

Imajima, M. (1974): Occurrence of species of three families, Eulepethidae, Apistobranchidae, and Heterospionidae (Polychaeta) from Japan. *Bulletin of the National Science Museum, Tokyo* 17: 57–64.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520 [+ Supplemental Appendix A. Family-by-Family Updates: A1–A350 + Supplemental Table of Guild Characteristics: 1–14].

Kędra, M., Kuliński, K., Walkusz, W. & Legeżyńska, J. (2012): The shallow benthic food web structure in the high Arctic does not follow seasonal changes in the surrounding environment. *Estuarine and Coastal Shelf Science* 114: 183–191.

Kędra, M., Legeżyńska, J. & Walkusz, W. (2011): Shallow winter and summer macrofauna in a high Arctic fjord (79° N, Spitsbergen). *Marine Biodiversity* 41: 425–439.

Levinsen, G.M.R. (1883): Systematisk-geografisk oversigt over de nordiske annulata, gephyrea, chaetognathi og balanoglossi. *Videnskabelige Meddelelser fra den naturhistoriske Forening Copenhagen* 2: 93–350.

Lowry, J.K. (1975): Soft bottom macrobenthic community of Arthur Harbor, Antarctica. *Antarctic Research Series* 23: 1–19.


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Mackie, A.S.Y., Pleijel, F. & Rouse, G.W. (2005): Revision of *Aberranta* Hartman, 1965 (Aberrantidae: Annelida), with descriptions of new species from the Mediterranean and Hong Kong. *Marine Ecology* 26: 197–208.
Mesnil, F. & Caullery, M. (1898): Étude de morphologie externe chez les annélides. La famille nouvelle des levinséniens. Révision des ariciens. Affinités des deux families. Les apistobranchiens. *Bulletin Biologique de la France et de la Belgique* 31: 126–150.
Orrhage, L. (1962). Über die äussere Morphologie der Familie Apistobranchidae Mesnil und Caullery (Polychaeta Sedentaria). *Zoologiska Bidrag från Uppsala* 33: 42–446.
Orrhage, L. (1974): Über die Anatomie, Histologie und Verwandtschaft der Apistobranchidae (Polychaeta Sedentaria) nebst Bemerkungen über die systematische Stellung der Archianneliden. *Zeitschrit für Morphologie der Tiere* 79: 1–45.
Paiva, P.C. & Barroso, R. (2010): Polychaeta. In: Lavrado, H.P. & Brasil, A.C.S. (eds.) *Biodiversidade da região oceânica profunda da Bacia de Campos. Macrofauna*. SAG Serv., Rio de Janeiro: 97–171.
Petti, M.A.V., Nonato, E.F., Bromberg, S., Gheller, P.F., Paiva, P.C. & Corbisier, T.N. (2007): On the taxonomy of *Apistobranchus* species (Polychaeta: Apistobranchidae) from the Antarctica. *Zootaxa* 1440: 51–59.
Petti, M.A.V., Rouefski, F.A.C., Dias, J.F., Silbiger, H.L.N. & Lavrado, H.P. (2016): Hermaphroditism in the Antarctic polychaete *Apistobranchus glacierae Hartman*, 1978 (Apistobranchidae). In: 12th International Polychaete Conference, Cardiff. Abstracts: National Museum Wales, p. 82. https://museum.wales/media/38943/IPC2016_publication_22_08_16.pdf
Pettibone, M.H. (1963): Marine polychaete worms of the New England Region 1. Families Aphroditidae through Trochochaetidae. *Bulletin of the United States National Museum* 227(1): 1–356.
Reish, D.J. (1965): Benthic polychaetous annelids from Bering, Chukchi, and Beaufort Seas. *Proceedings of the United States National Museum* 117(3511): 131–158.
Richardson, M.D. & Hedgpeth, J.W. (1977): Antarctic soft-bottom, macrobenthic community adaptations to a cold, stable, highly productive, glacially affected environment. In: Llano, G.A. (ed.) *Adaptations Within Antarctic Ecosystems*. Proceedings of the 3rd SCAR Symposium on Antarctic Biology. Smithsonian Institution, Washington, DC: 181–196.
Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.
Rouse, G.W. & Jamieson, B.G.M. (1987): An ultrastructural study of the spermatozoa of the polychaetes *Eurythoe complanata* (Amphinomidae), *Clymenella* sp. and *Micromaldane* sp. (Maldanidae), with definition of sperm types in relation to reproductive biology. *Journal of Submicroscopical Cytology* 19: 573–584.
Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.
Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–545.
Théel, H.J. (1879): Les annélides polychètes des mers de la Nouvelle-Zemble. Konglika Svenska Vetenskaps-Akademiens *Hanlingar* 16(3): 1–75.
Webster, H.E. & Benedict, J.E. (1887): The Annelida Chaetopoda from Eastport, Maine. *Reports of the U.S. Fish Commission for 1885*, 707–755.
Wesenberg-Lund, E. (1951): Polychaeta. *The Zoology of Iceland* 2(19): 1–182.
Worsaae, K., Nygren, A., Rouse, G.W., Giribet, G., Persson, J., Sundberg, P. & Pleijel, F. (2004): Phylogenetic position of Nerillidae and *Aberranta* (Polychaeta, Annelida), analyzed by direct optimization of combined molecular and morphological data. *Zoologica Scripta* 34: 313–328.
Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189. https://doi.org/10.1186/1471-2148-9-189.

Katrine Worsaae

# 5.2 Psammodrilidae Swedmark, 1952

## Introduction

Psammodrilidae is a small family of eight described small-sized to microscopic species, 1–8 mm long, 0.06–0.2 mm wide. They all belong to the genus *Psammodrilus* Swedmark, 1952 and are all described from shallow, medium-coarse sand bottoms of the Atlantic. Yet, several undescribed species have been reported from, e.g., the Red Sea and the Pacific (Worsaae *et al*. 2018).

The nearly completely ciliated body is divided into a prostomium lacking appendages, an elongated peristomium, a muscular collar region with nonciliated "warty" epidermal cells, a six-segmented thorax with long motile, dorsal cirri (with internal flexible aciculae), and an abdomen with hooked chaetae (uncini) protruding directly from the body wall (parapodia absent) (Figs. 5.2.1–5.2.6). Whereas the larger semisessile species, *Psammodrilus balanoglossoides* Swedmark, 1952, *P. aedificator* Kristensen & Nørrevang, 1982, and *P. norenburgi* Worsaae & Martínez, 2018 build tubes or pyramidal "houses" using small sand particles (Swedmark 1952, 1958, Kristensen and Nørrevang 1982, Worsaae and Sterrer 2006, Worsaae *et al*. 2015), the smaller species, *P. fauveli* (Swedmark, 1958), *P. swedmarki* Worsaae & Sterrer, 2006, *P. moebjergi* Worsaae & Sterrer, 2006, *P. curinigallettii* Worsaae, Kvindebjerg & Martínez, 2015, and *P. didomenicoi* Worsaae & Martínez, 2018, represent minute and free-living, interstitial forms (Fig. 5.2.7). The tube-building species possess a distinct nonciliated collar region with polygonal, mucus-secreting cells (Kristensen and Nørrevang 1982), as well as a unique muscular pumping apparatus of short

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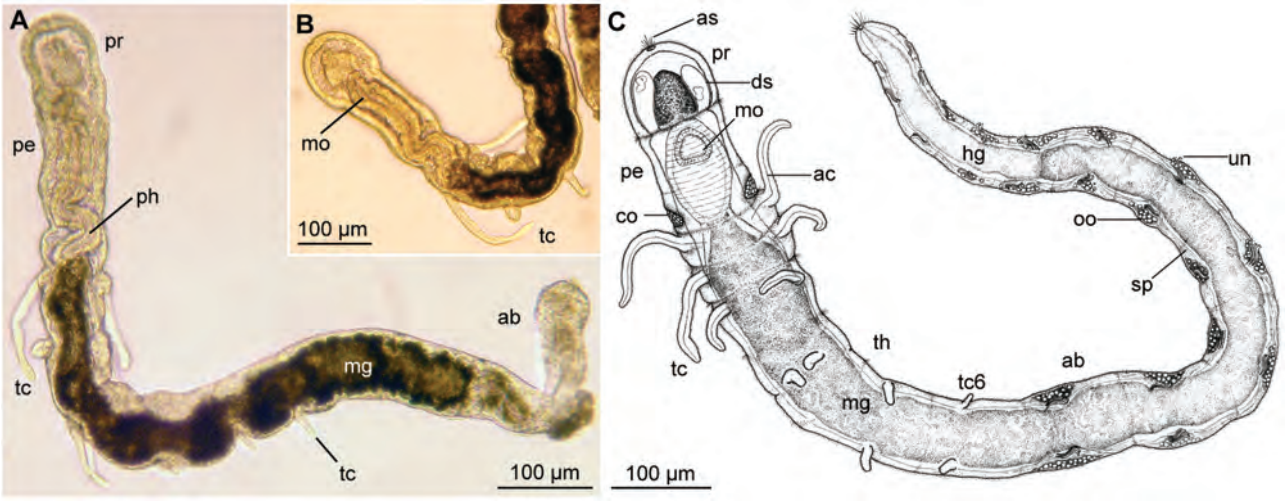


**Fig. 5.2.1:** Habitus of *Psammodrilus moebjergi* Worsaae & Sterrer, 2005 from Bermuda. A, B, Light micrographs. C, Slightly schematic representation. ab, abdomen; ac, acicula; as, anterior sensory cilia; co, collar; ds, prostomial diaphragm sac; hg, hindgut; mg, midgut; mo, mouth opening; oo, oocyte; pe, peristomium; ph, pharynx; pr, prostomium; sp, sperm; tc, thoracic cirrus; tc6, sixth thoracic cirrus; th, thorax; un, uncinus.

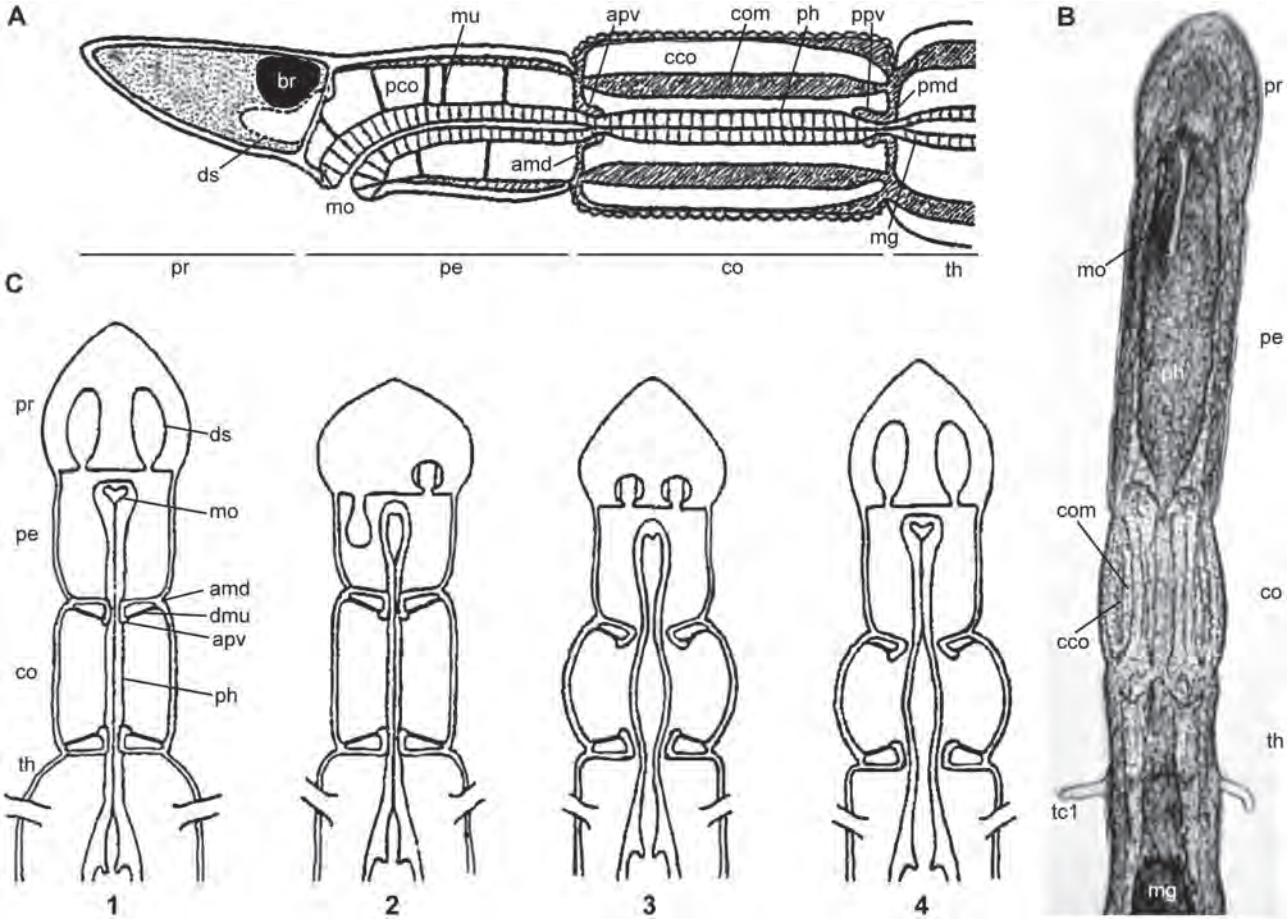


**Fig. 5.2.2:** *Psammodrilus balanoglossoides* Swedmark, 1952. A, B, Schematic drawings. A, Midsagittal view of anterior end. B, Series showing pharyngeal pumping movement generated by muscles and diaphragms. C, Light micrograph. ab, abdomen; amd, anterior muscle diaphragm; apv, anterior pharyngeal valve; co, collar; cco, coelom of collar muscles; com, longitudinal collar muscles; dmu, dilator muscle of valve; ds, prostomial diaphragm sac; hg, hindgut; mg, midgut; mo, mouth opening; mu, muscle; oo, oocyte; pe, peristomium; ph, pharynx; pmd, posterior muscle diaphragm; ppv, posterior pharyngeal valve; pr, prostomium; sp, sperm; tc, thoracic cirrus; tc1, first thoracic cirrus; th, thorax. A, B, modified from Swedmark 1955; C, from Worsaae and Sterrer (2006).

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longitudinal muscles surrounding the posterior pharynx and an anterior and a posterior transverse muscular diaphragm (called *diaphragme musculaire antérieur* and *postérieur* by Swedmark 1955); two prostomial sacs that by infolding allow for expansion of mouth and pharynx in the peristomium aid in the pumping action (Fig. 5.2.2). These characters are generally reduced or absent in the interstitial species (Swedmark 1958, Kristensen and Nørrevang 1982, Worsaae and Sterrer 2006). Psammodrilids can be gonochoric or simultaneous hermaphrodites with direct development.

The presence of uncini with barbules and the semisessile lifestyle in several species indicated that Psammodrilidae may have evolved from a macrofaunal, tube-dwelling ancestor, such as Maldanidae or Arenicolidae, which show similarity in structure and development of the uncini (Swedmark 1958, Meyer and Bartolomaeus 1997). However, a new phylogenomic study of Annelida for the first time included Psammodrilidae and found that it positioned outside Pleistoannelida, instead nesting with Apistobranchidae and Chaetopteridae (Helm *et al*. 2018), hereby dismissing a close relationship to Maldanidae and a common origin of their uncini. Still, their position in Chaetopteriformia does support that the family originated from a larger, tube-building, macrofaunal ancestor with a well-developed collar. This has sometimes been questioned due to the several minute members of Psammodrilidae belonging to the meiofauna and that with their conspicuous gliding by ciliary motion and vagile lifestyle are highly adapted to the interstitial environment among sand grains (Worsaae and Kristensen 2005). But finally, a phylogenetic study of Psammodrilidae established that regressive evolution has taken place several times within the family, since the smallest species are nested deep within the two major clades of the family, and the larger species branch off more basally (Worsaae *et al*. 2018) (Fig. 5.2.7).

## Morphology

### External morphology

**Body shape and regions.** Psammodrilids are almost fully ciliated, microscopic animals except for a middorsal nonciliated region as well as a nonciliated collar region in the larger species. The characteristic collar region comprises rows of nonciliated "warty" polygonal cells (sometimes described as hexagonal or pentagonal), with each wart measuring from a few to almost 20 µm in diameter (Figs. 5.2.3 and 5.2.4). Animals are whitish-hyaline, but the gut has a characteristic green-brownish color, caused by a combination of a pigmented endoderm cells and gut content. Their 1–8-mm-long, 0.06–0.2-mm-wide bodies are divided into a prostomium, peristomium, collar region, thorax, and abdomen. It is still unclear how many segments exactly are contained in the peristomium and collar region, whereas the thorax is always described with six segments (with dorsal cirri) and the abdominal segments, although varying in number, can easily be counted by the presence of uncini. Westheide (2008) argues that the development of *P. balanoglossoides* (see Swedmark 1955) in combination with the lack of a collar ganglion support that the collar region should be regarded a posterior part of the peristomium and not a separate segment. Yet, the seemingly presence of an additional ganglion in the collar region (Fig. 5.2.5), may indicate otherwise, and further examination employing confocal laser scanning microscopy (CLSM) are warranted.

**Ciliation** (Figs. 5.2.3–5.2.6). A uniform ciliation covers the entire body, including the cirri, except for the mid-dorsal furrow and collar region, which is devoid of cilia. Such a dense ciliation is found only in one other annelid group, Lobatocerebridae Rieger, 1980 (Rieger 1980, Kerbl *et al*. 2015). Circumventing bands of longer cilia are found between pro- and peristomium (Fig. 5.2.3 G) and on each of the segments behind the collar. These ciliary bands are interrupted in the ventral midline. The total surface of *Psammodrilus* is provided with microvilli that in, e.g., the collar region form a real brush border and, among their bases, a fibrillar material is present (Fig. 5.2.6, Kristensen and Nørrevang 1982).

Possibly due to the uniform multiciliated nature of the epidermal cells, the integument of *P. aedificator* and *P. balanoglossoides* is totally devoid of a cuticular lining, the collagenous fiber grids. This unique lack of cuticle also makes the animals highly fragile, and the animals easily break or implode during handling, even just by getting caught in the surface water tension of a Petri dish. Animals may even rip themselves apart if they get stuck between grains in a Petri dish, which is why the posterior end is often not found in marine samples.

**Glands** (Figs. 5.2.3, 5.2.4, and 5.2.6). The epidermis possesses a wealth of glands, used for, e.g., adhesion, locomotion, and tube building, most of which are unicellular. The exact nature and position of the adhesive glands have not been described in detail, but since larger adhesive field or glandular complexes are not observed, most are regarded to be unicellular (e.g., Kristensen and Nørrevang 1982, Worsaae and Sterrer 2006). Adhesive glands are used for adhering to the sediment and not getting swept away in the current. They are especially numerous in the abdominal region and thoracic cirri,

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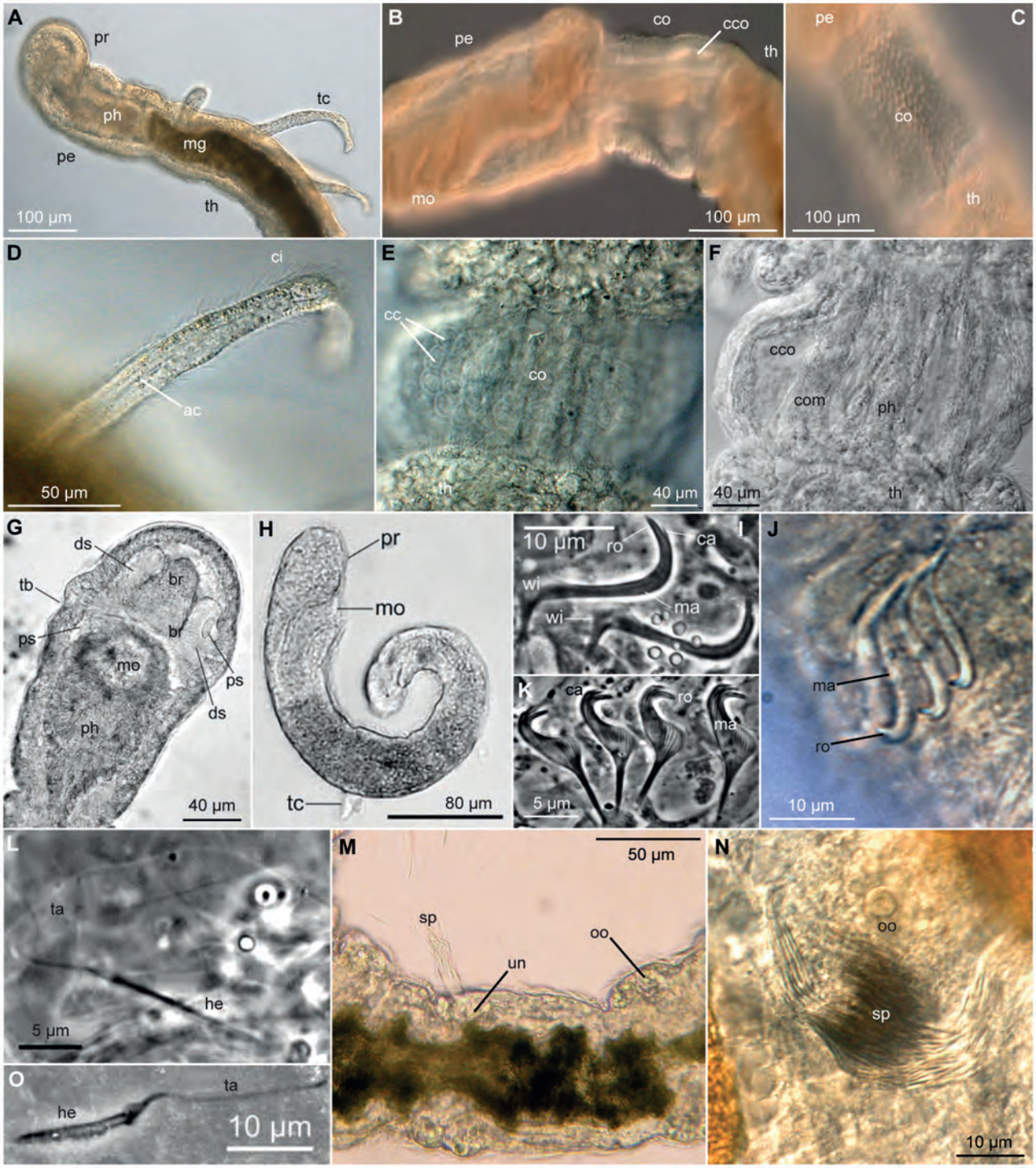


**Fig. 5.2.3:** Light micrographs of *Psammodrilus* spp. A, D, *Psammodrilus fauveli* Swedmark, 1958. A, Anterior end without collar region. D, Close-up of thoracic cirrus. B, C, *Psammodrilus norenburgi* Worsaae & Martínez, 2018. Anterior end with collar. E, F, *Psammodrilus didomenicoi* Worsaae & Martínez, 2018. Collar region. G, H, L, M, *Psammodrilus moebjergi* Worsaae & Sterrer 2006. Head, juvenile, sperm, oocyte, uncinus. I, O, *Psammodrilus swedmarki* Worsaae & Sterrer, 2006. Uncini and sperm. K, Uncini of *Psammodrilus balanoglossoides* from Florida. J, N, *Psammodrilus curinigalletti* Worsaae, Kvindebjerg & Martínez, 2015. Uncini, sperm, and oocytes. ab, abdomen; ac, acicula; br, brain; cc, "warty" collar cells; co, collar; cco, coelom of collar muscles; ci, cilia; ca, capitium; com, longitudinal collar muscles; ds, prostomial diaphragm sac; he, head of sperm; ma, manubrium; mg, midgut; mo, mouth opening; mu, muscle; oo, oocyte; pe, peristomium; ph, pharynx; pr, prostomium; ro, rostrum; sp, sperm; ta, tail of sperm; tb, transverse band of cilia; tc, thoracic cirrus; th, thorax; un, uncinus; wi, wings. From Worsaae and Sterrer (2006), Worsaae *et al*. (2015, 2018).

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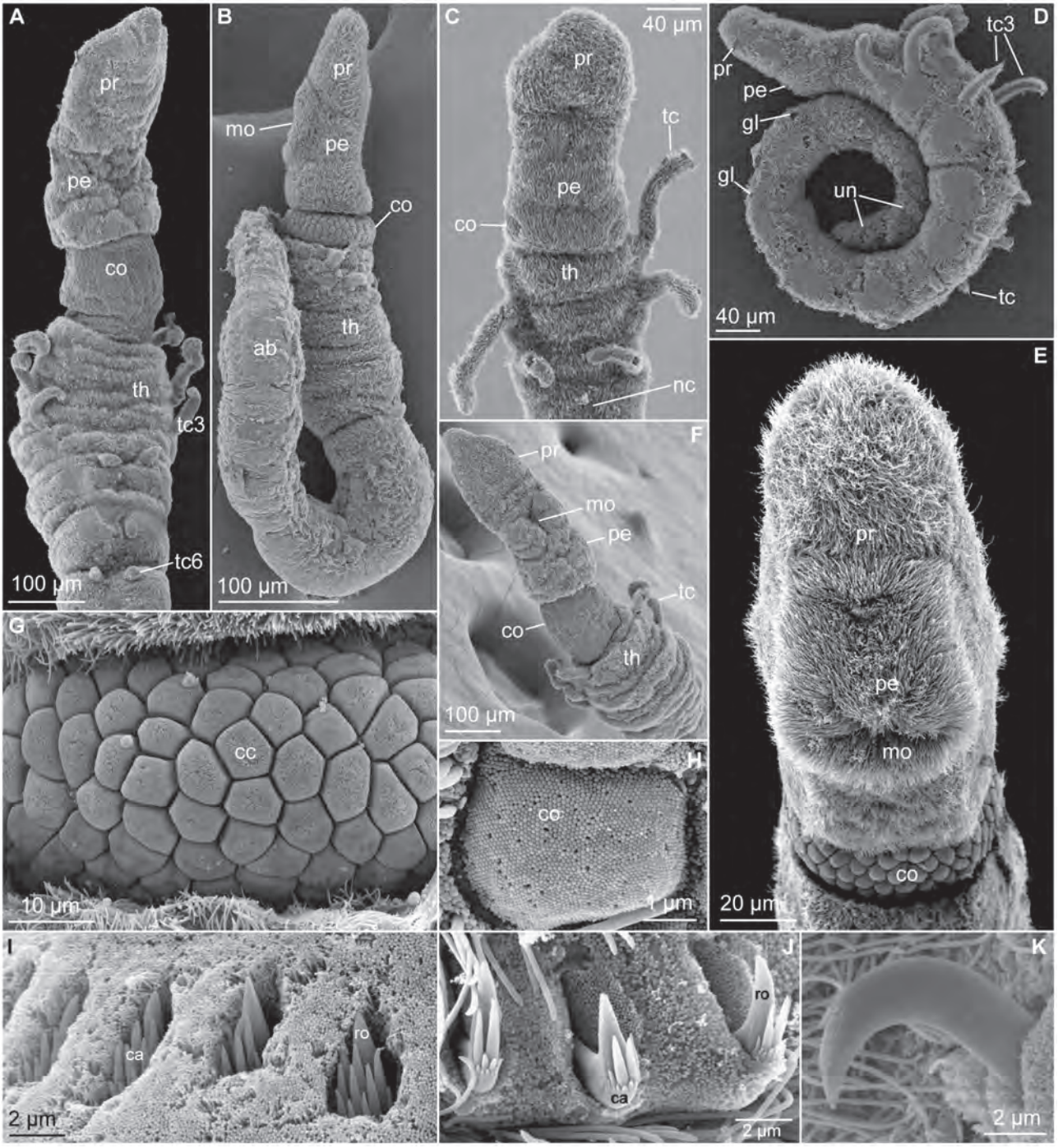


**Fig. 5.2.4:** Scanning electron micrographs of *Psammodrilus* spp. A, F, I, *Psammodrilus balanoglossoides* Swedmark, 1952 from Denmark. A, Anterior end, dorsal view. F, Anterior end, ventral view. I, Unicini. B, G, *Psammodrilus didomenico* Worsaae & Martínez, 2018. B, Entire animal, lateral view. G, Close-up of collar cells. C, H, J, *Psammodrilus moebjergi* Worsaae & Sterrer, 2006. C, Anterior end in dorsal view. H, Close-up of collar cell. J, Unicini. D, K, *Psammodrilus curinigalletti* Worsaae, Kvindebjerg & Martínez, 2015. D, Entire animal with no collar. K, Uncinus. E, *Psammodrilus norenburgi* Worsaae & Martínez, 2018, anterior end in ventral view. ab, abdomen; cc, "warty" collar cells; co, collar; ca, capitium; gl, gland; ma, manubrium; mo, mouth opening; pe, peristomium; pr, prostomium; ro, rostrum; sp, sperm; ta, tail of sperm; tb, transverse band of cilia; tc, thoracic cirrus; tc3, tc6, third and sixth thoracic cirrus; th, thorax; un, uncinus; wi, wings. A, F, I, Unpublished micrographs from Alejandro Martínez.

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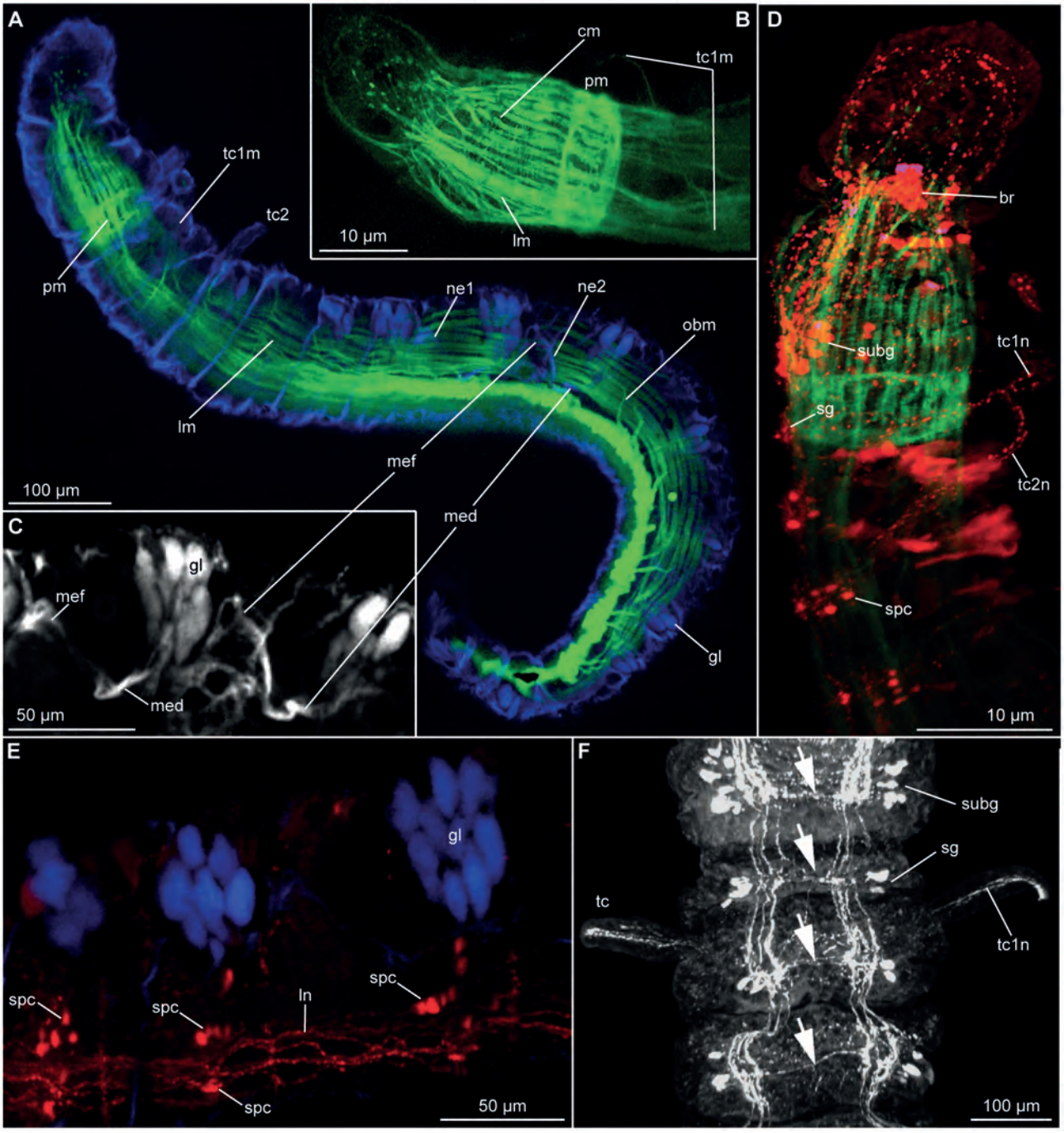


**Fig. 5.2.5:** *Psammodrilus curinigalletti* Worsaae, Kvindebjerg & Martínez, 2015 from Sardinia, Italy. Maximal projection of Z-stack of scans obtained with confocal laser scanning microscopy of immunostained specimens. A, Entire animal, muscles (green, phalloidin stain) and cilia (antiacetylated α-tubulin immunoreactivity [IR]). B–E, Close-ups of A. B, Muscles of the head and first thoracic cirrus. C, Metanephridia and glands of segment six and seven, maximal projection of two optical sections. D, Muscles (green) and anti-serotonin-like IR nerves of anterior end (red). E, Glands (blue) and anti-serotonin-like IR nerves of nerve cord in anterior abdomen (red). F, Anti-serotonin-like IR in ventral cords of collar and anterior thorax, arrows point to segmental commissural bundles. br, brain; cm, circular muscle; gl, rhombe-shaped gland; lm, longitudinal muscle; med, metanephridial duct; mef, metanephridial funnel; ne1, 2, metanephridia 1,2; obm, oblique muscle; tc, thoracic cirrus; tc2, second thoracic cirrus; tc1m, muscle of first thoracic cirrus; tc1n, tc2n, nerve of first and second thoracic cirri; sg, segmental ganglion; spc, serotonergic perikaryon of transverse commissure; subg, subesophageal ganglion. A–E, From Worsaae *et al*. (2015); F, courtesy of C. Helm.

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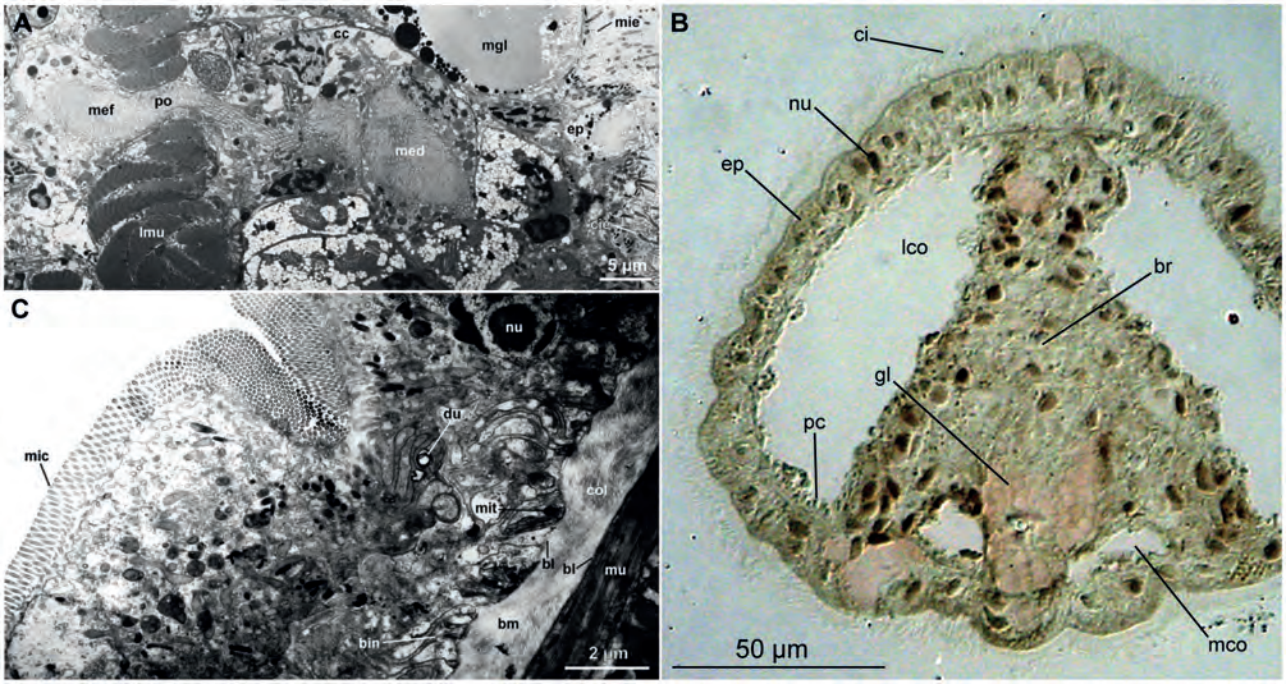


**Fig. 5.2.6:** *Psammodrilus balanoglossoides* Swedmark, 1952 from Helsingør, Denmark. A, Oblique section through thorax region showing metanephridial system, with ciliated and microvillar funnel (mef) and metanephridial duct (med) passing through longitudinal muscles (lmu) as a pore (po). Transmission electron micrograph. B, Anterior end with brain and lateral coelomic cavities. Light micrograph of semithin cross-section (1 µm), toluidine blue, coronal view. C, Collar region. Two basal laminae form a true basement membrane (bm) with collagen fibers (col). The basal infoldings of the epidermal cells (bin) form a labyrinth with ducts (du). Transmission electron micrograph, parasagittal. bl, basal lamina; br, brain; cc, coelomocyte; ci, cilia covering the entire surface of the prostomium; cie, cilia of epidermis; ep, epidermis; gl, gland in close contact with the brain; lco, lateral coelom of prostomium; lmu, longitudinal muscle; mco, median coelom of prostomium; mgl, mucous gland of epidermis; mic, microvilli of collar epidermis; mie, microvilli of thorax epidermis; mit, mitochondrion; mu, muscle; nu, nucleus; pc, peritoneal cell. From Worsaae and Kristensen (2005).

which possess so great adhesive forces that the animals easily get stuck to particles in the Petri dish and, due to the lack of cuticle, may break themselves apart and the posterior end is often lost during sampling (e.g., Worsaae and Sterrer 2006). Mucus-secreting glands facilitating ciliary gliding, mostly unicellular, are found along the entire body, but most numerous on the head and along the ventral side of the thorax (Swedmark 1958). A special type of paired multicellular, segmented, diamond-shaped glands with separate dorsal openings are found dorsolaterally in the thorax and abdomen of *P. curinigalletti* (Fig. 5.2.5), the function of which is not known (Worsaae *et al*. 2015). None of these epidermal glands are present in the collar region, where each polygonal epidermis cell instead may be regarded as glandular due to their form and well-developed Golgi complexes (Fig. 5.2.6). Each of these "warty" cells interdigitate and forms ducts in the intercellular space, along which secreted material are suggested to pass and spread over the surface (Fig. 5.2.6, Kristensen and Nørrevang 1982).

**Chaetae** (Figs. 5.2.3–5.2.4). The six thoracic segments may contain more or less well-developed dorsal cirri. Each cirrus is internally supported by muscles, nerves, and a long chaeta. This uniquely flexible acicula is bendable along the free and moveable part of the cirrus but stiff basally, anchoring the cirrus to the ventral midline. Its special characteristics cast doubts on its homology with aciculae found in Errantia (Swedmark 1958, Worsaae and Kristensen 2005).

Each abdominal segment has one group of hooked chaetae (uncini) on each lateral side with 1–16 uncini per ramus, which project directly from the epidermis without parapodia. Their development has been described in detail for *P. balanoglossoides* (Bartolomaeus 1995, Bartolomaeus and Meyer 1997). Similar types of uncini (sometimes with wings or barbules) are found in several burrowing or tube-dwelling annelids such as Maldanidae, although following recent phylogenomic results, they are most likely not of common origin (Helm *et al*. 2018).

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## Anatomy

**Musculature** (Figs. 5.2.2, 5.2.3, and 5.2.5). The body wall musculature in psammodrilids is relatively simple and consists of longitudinal muscles, outer circular muscles, and oblique muscles (Figs. 5.2.2 and 5.2.5). Yet, psammodrilids possess a unique muscular suction pharynx with two pharyngeal muscular diaphragms (Figs. 5.2.2, 5.2.3, and 5.2.5). Moreover, a combination of muscles and coelomic cavities helps shape the prostomium for burrowing and generally supports an enormous flexibility of the prostomial shape (from anchor shaped to pointed) (Figs. 5.2.2 and 5.2.6; Swedmark 1958, Worsaae and Sterrer 2006).

Striated mesodermal muscles have been examined both with histology (Swedmark 1952, 1955, 1958, Helm *et al*. 2018), transmission electron microscopy (TEM) (Kristensen and Nørrevang 1982, Worsaae and Kristensen 2005), and confocal laser scanning microscopy (CLSM) (Worsaae *et al*. 2015, Helm *et al*. 2018). CLSM data on *P. curinigallettii* (Fig. 5.2.5; Worsaae *et al*. 2015) show four discrete bundles of longitudinal muscles (resembling *P. fauveli* and *P. aedificator*; Swedmark 1958, Kristensen and Nørrevang 1982), each with two to three fibers, originating at the prostomial edge with the number of fibers increasing at the peristomium to form a uniform dense layer of totally ca. 50 fibers around the mid-body (spaced 1–5 µm apart, ca. 1–3 µm in diameter). In the larger *P. balanoglossoides*, longitudinal muscles are divided in two dorsolateral and two ventrolateral bundles along the entire body length but are more poorly developed in the abdomen (Swedmark 1955).

Using CLSM, each thoracic, dorsal cirrus in *P. curinigalletti* was found supported along the entire length, not only by a flexible internal acicula but also by two to four muscle fibers (less in the posterior-most underdeveloped cirri) branching off from the ventral longitudinal muscles, aiding to motility of the cirrus (Fig. 5.2.5) (Worsaae *et al*. 2015). In *P. aedificator*, several muscle cells were found surrounding and attaching to the base of the acicula, and additional fibers were found attaching more distally to the chaetoblast cup (Kristensen and Nørrevang 1982), but these tiny muscles were never found to extend along the entire length of the cirrus. Thoracic cirri muscles were not found with histology of *P. balanoglossoides* and *P. fauveli* (Swedmark 1955, 1958). Although parapodia are lacking in psammodrilids, the uncini of *P. curinigalletti* are clearly shown to be supplied by an oblique muscle bundle (a muscular fascicle) in all abdominal segments (Worsaae *et al*. 2015). These muscles are probably responsible for the retraction and extension of the uncini. Similar oblique muscles are present in *P. aedificator* but not are reported for *P. balanoglossoides* and *P. fauveli* (Swedmark 1955, 1958, Kristensen and Nørrevang 1982).

In *P. curinigalletti*, outer circular muscle fibers are arranged as transverse rings, spaced ca. 5 µm apart, around the longitudinal muscles along the thorax and abdomen. Around the peristomium, the circular muscles form two layers extending diagonally in opposite directions (cm, Fig. 5.2.5 B, Worsaae *et al*. 2015), a pattern possibly also present in *P. aedificator* (Fig. 8A in Worsaae and Kristensen 2005). Oblique muscles are arranged in lateral pairs on each abdominal segment, originating midlaterally (Fig. 5.2.5) and extending ventrally to supply the uncini. Circular muscles have not been found in the semisessile *P. aedificator* (Kristensen and Nørrevang 1982) or in the small-sized *P. fauveli* (also lacking oblique muscles, Swedmark 1958); however, these tiny muscular structures can be easily overlooked in histological sections and were actually found in the minute *P. curinigalletti* (Worsaae *et al*. 2015). In contrast, circular muscles are well developed in *P. balanoglossoides* and distinguishable with histology, probably due to the larger size and semisessile, lifestyle exhibited by this species (Swedmark 1955).

**Digestive system** (Figs. 5.2.1–5.2.3 and 5.2.5). The first psammodrilid described, *P. balanoglossoides*, was found to possess a unique muscular pumping apparatus used for suction of detritus and diatoms in the interstitial environment (Swedmark 1952, 1955). In the larger psammodrilids, this structure is easily distinguishable in compound microscope as a barrel-shaped set of short longitudinal musculature filling up the interior of the collar region, the muscle tissue arranged as a swollen sac on each side of the pharynx, each surrounding a coelomic cavity (Fig. 5.2.2). The entire apparatus is delineated by an anterior and a posterior transverse muscular diaphragm (called *diaphragme musculaire antérieur* and *postérieur* by Swedmark 1955) that forms muscular valves, interconnected by the short longitudinal muscles (Fig. 5.2.2 A). Contraction of these longitudinal muscles moves the transverse anterior and posterior muscular diaphragms closer, increasing the volume of the mouth cavity and opening the valves. The pumping mechanism is aided by contraction of the prostomial musculature, which creates a positional shift of the nonmuscular prostomial sacs into the peristomial lumen. After this, a contraction of the longitudinal muscles and muscular diaphragms surrounding the pharynx follows, which again expands the posterior pharyngeal lumen (Fig. 5.2.2 C). Coordinated movements hereby create a negative pressure for suction of detritus and diatoms into the mouth and pharynx. Relaxation

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of the prostomium and the return of sacs into the prostomial cavity close the anterior pharyngeal lumen aid in the further peristaltic movement of food particles into the gut (Swedmark 1955). Prostomial sacs are absent or very reduced in the small-sized psammodrilids that may also have a further reduced muscular pharynx. It is noteworthy that CLSM analyses of F-actin in *P. curinigallettii* actually revealed most of the muscle sets, although the transverse muscular diaphragms are thinner and they are interconnected by only about 16 bundles of short longitudinal muscles, which do not seem to form hollow coelomic sacs as seen in the larger species (Worsaae *et al*. 2015, 2018).

The alimentary canal is surrounded by a regular grid of thin longitudinal and circular muscles, which extend from the mouth opening along the entire gut (Worsaae *et al*. 2015).

The entire alimentary canal is ciliated and comprises a triangular mouth opening, an elongated pharynx and esophagus, followed by a green-brownish straight gut, terminating in a dorsal anus. In *P. aedificator* a special condition is found where the large endodermal gut cells fill up most of the abdomen and may have a chordoid function. The thin middorsal area of the epidermis contains many small vacuoles, and the endoderm is almost in contact with the environment, suggesting that a kind of pinocytosis may take place (Kristensen and Nørrevang 1982).

**Body cavities** (Figs. 5.2.1–5.2.3). The different species exhibit different body cavity conditions, which also change along the body: In *P. balanoglossoides*, the longitudinal muscles of the thorax form true coelomic cavities, lined by a continuous mesodermal epithelium. On the contrary, giant endoderm gut cells and coelenchyme cells fill up most of the thorax and abdomen in *P. aedificator*, and a body cavity lined by a continuous mesodermal epithelium is missing (Kristensen and Nørrevang 1982). Smaller vagile species are lesser studied, but for an undescribed small species from the US East coast, Fransen (1980) described a similar compactness and acoelemate condition of the trunk, although generated here by large coelenchyme cells and not by endoderm cells. However, lateral coelomic cavities (lined with peritoneal cells) are observed in the prostomium of most species as well as medio-ventral smaller prostomial cavities of uncertain nature (Worsaae and Kristensen 2005). The peristomium in most species likewise contains a coelomic cavity surrounding the pharynx.

**Blood vascular system** (Figs. 5.2.5 and 5.2.6). The blood vascular system is largely reduced in all species (Swedmark 1952) and is not readily distinguished even with TEM studies (Worsaae and Kristensen 2005), yet, in all examined species, the nephridia are of the metanephridial type, warranting proof of existence of a blood vascular system.

**Excretory system** (Figs. 5.2.5 and 5.2.6). Metanephridia are observed in *P. balanoglossoides*, *P. aedificator*, and an undescribed small species of the US East coast, with the former having well-developed heavily ciliated nephridia with a microvillar funnel opening into a true coelom and a metanephridial duct passing through the longitudinal muscles to the external nephridiopore (Figs. 5.2.5 and 5.2.6). The metanephridia of *P. aedificator* and the small undescribed species comprise less than 10 cilia and the whole metanephridial system seems to be weakly developed.

**Nervous system** (Fig. 5.2.5). The nervous system has been investigated with varying methodologies and degrees of detail in psammodrilids; however, not a single study has yet described the entire nervous system in detail of any of the psammodrilid species, nor compared subparts of the nervous system across species using the same technique. Hence, the different observations generated and little immediate overlap across species may not reflect actual variations.

The central nervous system is intraepidermal, situated between the bases of the epidermal cells, and composed of a relatively large brain and two ventro-lateral longitudinal nerve cords.

The brain can easily be distinguished in compound microscope with its dorso-posterior position and triangular, slightly bilobed and condensed shape; it is flanked by two lateral and two medio-ventral prostomial coelomic cavities as well as a ventro-posterior glandular area (Worsaae and Kristensen 2005, Worsaae and Sterrer 2006).

In *P. fauveli* and *P. balanoglossoides*, several nerves are found to extend from the brain (Swedmark 1958). From the lateral brain, the two major circumesophageal connectives extend ventro-posteriorly around the mouth opening and immediately posterior to this connect in the large paired subesophageal ganglia and continue into the paired ventro-lateral cords. Besides, two minor short nerves extend laterally from the posterior brain (Swedmark 1955, 1958), innervating the septum separating the prostomial coelomic cavities from the peristomial cavities and which may extend as so-called peristomial diaphragmal sacs into the prostomial cavities (see earlier in the chapter) during burrowing or feeding behavior. In *P. balanoglossoides* two anterior nerves are further described, not recognized in *P. fauveli* (see Swedmark 1958).

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The ventro-lateral nerve cords are widely separated and connected by segmentally repeated commissures with associated clusters of somata (ganglia), in between which the cords are nearly somata-free (Fig. 5.2.5; Swedmark 1958, Kristensen and Nørrevang 1982, Helm *et al*. 2018). *Psammodrilus balanoglossoides* was originally described as having tetraneural cords in the thorax (Swedmark 1955) as well as an unpaired midline neuropil (Orrhage 1964), whereas *P. fauveli* was described with two cords only (Swedmark 1958). However, CLSM and histology studies of *P. curinigalletti* (see Worsaae *et al*. 2018) and *P. balanoglossoides* (see Helm *et al*. 2018) found only two ventrolateral cords but showed how these are very loosely organized with the median-most neurites sometimes branching toward the ventral midline, which may point to previous misinterpretations of the cords in *P. balanoglossoides*. Yet, some of the differing observations may also reflect actual variation between small- and larger-sized species or life stages as discussed by Swedmark (1958). Further analyses of the CLSM data of the anterior nerve cords and position of segmental commissures may help understand the patterns of the cords and the exact number of segments contained in the head and collar region (Fig. 5.2.5; Helm *et al*. 2018). The new data here presented on *P. curinigalletti* (Fig. 5.2.5) actually points toward the collar region containing an additional ganglion (sg, in Fig. 5.2.5) posterior of the subesophageal ganglion and the collar perhaps therefore should be regarded a separate segment from the peristomium.

Furthermore, peripheral nerves innervating the muscles of the dorsal cirri (most pronounced in the first three pairs) and the muscular diaphragms of the collar seems to branch off from the ventral cords (Swedmark 1958, Helm *et al*. 2018). In addition, two smaller longitudinal nerves are found dorsally in *P. aedificator* (see Kristensen and Nørrevang 1982). A similar stomatogastric nervous system is reported for *P. balanoglossoides* and *P. fauveli* (see Swedmark 1958) consisting of paired nerves extending dorso-anteriorly along the esophagus from two ventral stomatogastric ganglia posterior to the mouth and an unpaired dorso-median nerve extending posteriorly.

**Sensory organs** (Fig. 5.2.5). A ciliated anterior sensory organ is found on the prostomium of *P. moebjergi* and *P. swedmarki*. Long compound cilia (sensoria) or ciliary tufts are found in high density around the anus of several species (Swedmark 1952, 1955, 1958, Kristensen and Nørrevang 1982, Worsaae and Sterrer 2006).

In the larger sized species *P. balanoglossoides* and in *P. aedificator*, a pair of round depressions are found on the posterior peristomium, which Kristensen and Nørrevang (1982) described as two sulci containing many sensory cells of the choanocyte type. They furthermore described for *P. aedificator* two lateral phaosomes and sensory organs (Fig. 5.2.5). On either side of the anterior prostomium, which have not been found in any other psammodrilids and still only in few annelids (Purschke 2016).

### Reproduction and development

All psammodrilids are gonochoristic, except for *P. curinigalletti* and *P. moebjergi*, seemingly being hermaphroditic possessing both sperm and oocytes (Worsaae and Sterrer 2006, Worsaae *et al*. 2015); only females have been described for *P. aedificator*. Nothing is known about the fertilization, and although the lack of copulatory organs indicates external fertilization, spermathecae were found in *P. swedmarki*, which suggests that copulatory behavior may exist in some species.

No oviducts are found in any species, and Swedmark (1955) proposed that the eggs may be shed by rupture of the body wall. Oocytes are found in each abdominal segment, often concentrated around the uncini and varying in size and number relative to the species; in *P. aedificator*, the oocytes are located close to the basal membrane of the gut with developing oocytes even sunken in between the endodermal cells (Swedmark 1958, Kristensen and Nørrevang 1982, Worsaae *et al*. 2015).

Sperm varies in shape among the species with an ellipsoidal short head and four spherical mitochondria at base in *P. balanoglossoides* and filamentous spermatozoa with slender to oval heads and no clear separation of acrosome, midpiece, and mitochondria in *P. aedificator*, *P. moebjergi*, *P. curinigalletti*, and *P. swedmarki*, all species having long sperm flagellate tails (Fig. 5.2.3; Swedmark 1955, Worsaae and Sterrer 2006, Worsaae *et al*. 2015).

The life cycle of *P. balanoglossoides* is similar to several other interstitial annelids, showing a 1-year life span with an extended breeding time during the spring/summer period (Kristensen and Nørrevang 1982, Westheide 2008).

Development is direct. Despite these apparent differences among the adults, the smaller vagile psammodrilids resemble the juveniles of the tube-building species, which is why a progenetic origin of the smaller species from a juvenile ancestor of a larger species has been suggested since Swedmark (1958) described *P. fauveli*. Swedmark (1955) had previously studied the development of *P. balanoglossoides* and found that the collar region is not developed until the late juvenile stages of the dorsal thoracic cirri and the number of uncini likewise increases progressively during development. A recent phylogenetic

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study placed the smaller species as derived within the tree of Psammodrilidae, hereby confirming their regressive evolution, and found that progenesis might even have happened several times during the diversification of Psammodrilidae (Worsaae *et al*. 2018).

## Biology and ecology

Psammodrilids are found in shallow subtidal sandy bottoms from 0 to 55 m depth, preferring coarse, well-sorted sand or shell gravel. Most species are described and reported from the North, East, and West Atlantic, as well as Mediterranean Sea (Swedmark 1952, 1955, 1958, Boaden 1961, 1963, 1976, von Salvini-Plawen 1968, Fransen 1980, Kristensen and Nørrevang 1982, Worsaae and Sterrer 2006, Curini-Galletti *et al*. 2012, Worsaae *et al*. 2015, 2018). However, undescribed species are found in the White Sea, Red Sea, and the West Pacific (New Zealand, Australia) (Riser 1984, Tzetlin and Saphonov 2002, Mastepanova 2004, Worsaae *et al*. 2018). Due to their fragile nature and low abundance, the biodiversity of psammodrilids is generally understudied (Worsaae *et al*. 2018).

Psammodrilids are regarded deposit feeders, which suck up deposited particles and diatoms among the sand grains using their muscular pumping pharynx; a similar diet is reported for all species. Epidermal cilia surrounding the mouth opening may, especially in the smaller species with less developed pharyngeal musculature, aid in guiding food particles to the mouth opening and further on into the digestive system (Worsaae *et al*. 2018).

Smaller psammodrilids move freely in the pore spaces between the sand grains, in both forward and backward directions, propelled by the continuous beating of the kinocilia covering the body surface. Ciliary locomotion also dominates in the larger species but may be aided by peristaltic contractions of body wall musculature. The prostomium has a highly variable shape from broad and flat to acorn shaped and pointed, useful for burrowing and generated by contraction in musculature. Sideways movements of the head and changes in direction are produced by contraction of the longitudinal muscles in one of the lateral sides (Worsaae and Sterrer 2006). The first three pairs of longer thoracic cirri move actively in all directions supported by several muscle fibers, whereas the three shorter posterior ones are less motile. Larger species may build straight mucus tubes (*P. balanoglossoides*) or small pyramidal houses (*P. aedificator*) and live a semisessile or sessile life, mainly collecting their food particles around their temporary houses (Kristensen and Nørrevang 1982).

## Phylogeny and taxonomy

**Phylogeny** (Fig. 5.2.7)

A recent phylogenomic study (Helm *et al*. 2018) for the first time included transcriptomic data of Psammodrilidae and found it nesting with Apistobranchidae and Chaetopteridae among the basally branching lineages and not within Sedentaria such as previous morphological analyses had suggested (Rouse and Pleijel 2001, Parry *et al*. 2016). Psammodrilidae, Apistobranchidae, and Chaetopteridae together constitute the clade Chaetopteriformia, which is the second lineage to branch off after Oweniidae + Magelonidae, occupying a maximally supported position as sister group of (Sipuncula + Amphinomida) + (Errantia + Sedentaria).

A comprehensive combined phylogenetic study of all eight described and four undescribed species of Psammodrilidae included three molecular markers and 20 morphological characters (Worsaae *et al*. 2018). Despite the close resemblance of the smaller vagile species to the juvenile stages of the larger tube-building species, the lack of a phylogenetic framework for Psammodrilidae has, for a long period, hindered a more detailed explanation of their putative progenetic origin and a settlement on whether the family originated from a large-sized or a small-sized psammodrilid form.

With the new phylogeny of Psammodrilidae, the family was shown to be monophyletic and rumor two major clades (A and B), none of which was supported morphologically. Clade A includes *P. moebjergi, P. curinigallettii, P. fauveli, P. balanoglossoides, P. aedificator,* and *Psammodrilus* sp. 4 from Italy, whereas clade B includes *P. swedmarki*, *P. didomenicoi*, *P. norenburgi*, *Psammodrilus* sp. 1 from Spain, *Psammodrilus* sp. 2 from Australia, and *Psammodrilus* sp. 3 from Egypt.

Parsimonious character reconstruction supports a large semisessile ancestor for Psammodrilidae with pharyngeal muscular diaphragms and longitudinal muscle bundles, prostomial sacs, nonciliated polygonal collar cells, and large dorsal cirri on segments 5–6. These exclusive features of Psammodrilidae most likely evolved once in the root of Psammodrilidae, with several subsequent losses within the family.

Smaller vagile psammodrilids were nested within two respective subclades, indicating two independent progenetic origins of these more specialized interstitial species of the family. The diversification of Psammodrilidae through multiple regressive adaptations indicates that the development and morphology of Psammodrilidae is genetically susceptible to progenesis.

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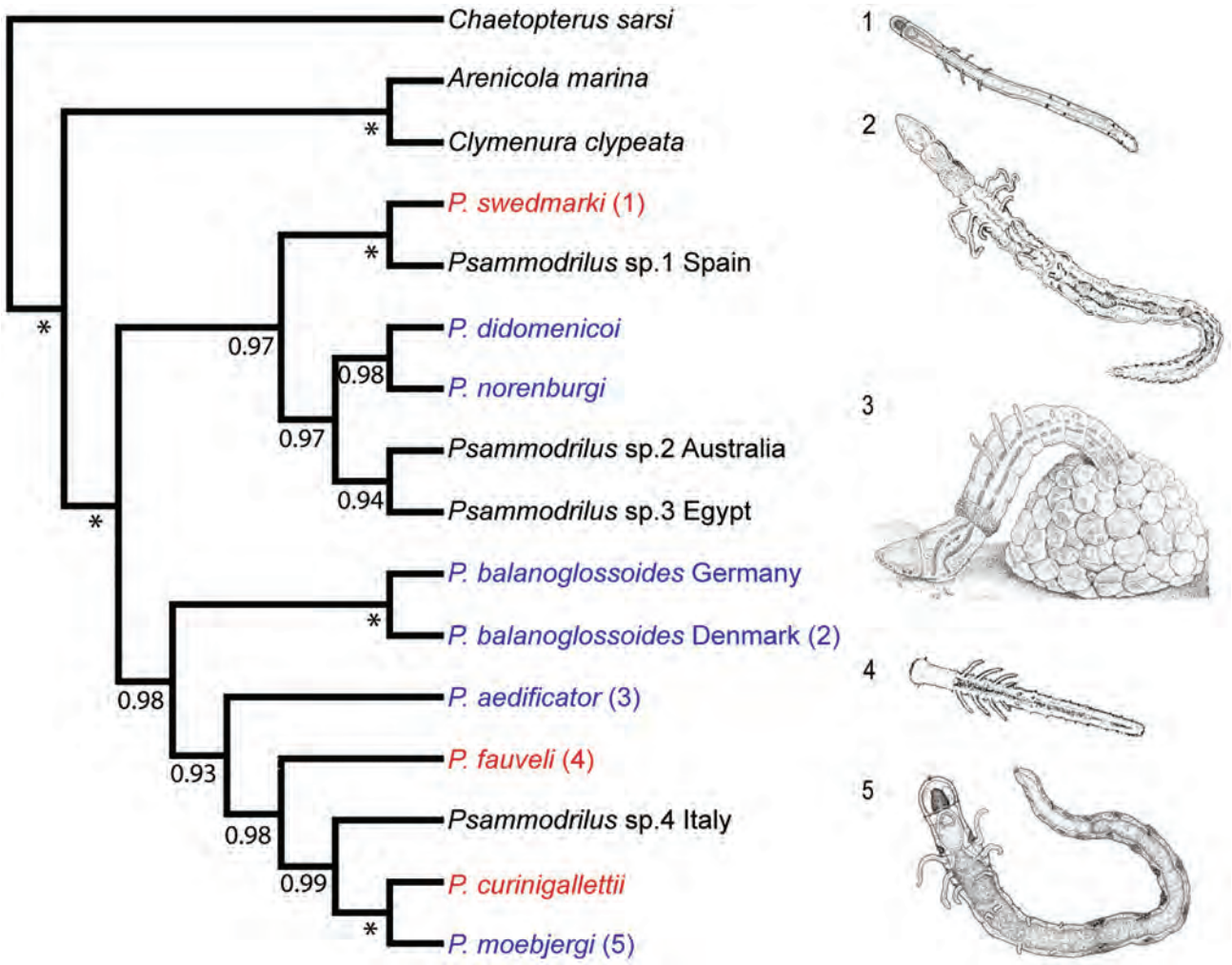


**Fig. 5.2.7:** Phylogenetic tree based on direct optimization parsimony analyses of combined molecular and morphological data (Worsaae *et al*. 2018). Numbers at nodes indicate jackknife support values, calculated for the analysis under parameter set 3211 (3008 weighted steps), asterisk = maximum support. Psammodrilid taxa in blue color are of larger size, taxa in red of smaller size, and black unknown.

Multiple losses of features during the evolution of Psammodrilidae have resulted in interstitial species of *Psammodrilus* having a highly similar (but convergent) morphology, making taxonomy challenging. Most of the small species are in fact diagnosed by different combinations of absent features and variation in number and length of structures rather than by the presence of species-specific autapomorphies.

## Taxonomy

### Family Psammodrilidae Swedmark, 1952

### *Psammodrilus* Swedmark, 1952

**Diagnosis** (from Worsaae and Sterrer 2006): Ciliated annelids with three cylindrical body regions. (1) Head region, comprising the prostomium and peristomium. Prostomium: appendages and eyes lacking; apical sensory organ with compound cilia; coeloms with prostomial diaphragm sacs, more or less developed. Peristomium: anterior mouth and posterior simple or complex pharyngeal apparatus; complex suctorial pharynx comprising muscular diaphragms within a ring of nonciliated epidermal collar cells; simple pharynx with nonciliated collar region limited to two lateral areas of polygonal collar cells, or completely absent. (2) Thorax: three to six pairs of dorsal cirri with internal pliable aciculae. (3) Abdomen: 1 to 16 lateroventral sigmoid uncini per parapodium; pygidium with a dorsal to terminal anus and compound sensory cilia. Metanephridia well developed, reduced or absent. Gonochoristic or hermaphroditic, direct development. Epidermis completely ciliated except for collar region and dorsal midline of thorax and abdomen; segmental rings of longer cilia on head and thorax.

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**Type species:** *Psammodrilus balanoglossoides* Swedmark, 1952
**Distribution and habitat:** *Psammodrilus* contains eight described species and four undescribed species, reported from the East and West Atlantic as well as the Red Sea and Pacific Ocean.

***Psammodrilus balanoglossoides* Swedmark, 1952**
**Type locality:** Intertidal beach sand, Roscoff, France, East Atlantic. Also reported from the East and West North Atlantic; White Sea; New Zealand, intertidal and subtidal depths. Cryptic species may exist.
**Habitat:** well-sorted medium fine sand.

***Psammodrilus fauveli* (Swedmark, 1958)**
**Type locality:** subtidal, 15–50 m depth, Bloscon (near Trezen à Skoden), Roscoff, France, East Atlantic.
**Habitat:** coarse calcareous shell gravel. Additional reports from the European North-East Atlantic.

***Psammodrilus aedificator* Kristensen & Nørrevang, 1982**
**Type locality:** subtidal, 1–2 m depth, Flakkerhuk, Disko Island, W. Greenland.
**Habitat:** medium-fine to medium coarse quartz sand.

***Psammodrilus curinigallettii* Worsaae, Kvindebjerg, & Martínez, 2015**
**Type locality:** subtidal, 33–37 m depth, Buddelli Island, Sardinia, Italy.
**Habitat:** Medium-fine carbonate sand from a *Posidonia* meadow.

***Psammodrilus didomenicoi* Worsaae & Martínez, 2018**
**Type locality:** subtidal, 20 m depth, Punta Campanella, Campagna, Italy.
**Habitat:** coarse sand in a *Posidonia oceanica* meadow.

***Psammodrilus moebjergi* Worsaae & Sterrer, 2006**
**Type locality:** subtidal, 17 m depth, near the wreck Marie Celeste, Bermuda.
**Habitat:** medium-coarse calcareous sand.

***Psammodrilus norenburgi* Worsaae & Martínez, 2018**
**Type locality:** Subtidal, 15 m depth, Bocas del Toro, E. Panama.
**Habitat:** medium coarse sand, sand bottom with ripple marks.

***Psammodrilus swedmarki* Worsaae & Sterrer, 2006**
**Type locality:** subtidal, 6–8 m depth, Windsor Beach, Bermuda.
**Habitat:** medium-coarse calcareous sand.
**Remarks:** Four undescribed species mentioned in Worsaae *et al*. (2018) from Lanzarote (Canary Islands), Lizard Island, NE Australia, Dahab, Egypt, and Campagna, Italy, respectively, further extend the distribution of *Psammodrilus*. The smaller species are generally difficult to distinguish from juveniles of larger species. Molecular data on *P. balanoglossoides* from Helgoland, North Sea, and Baltic Sea, Denmark, showed surprising differences in 18S rRNA, and cryptic species may be discovered limiting the current distribution of *P. balanoglossoides* and *P. fauveli*.

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## References

Bartolomaeus, T. (1995): Zur Ultrastruktur von *Psammodrilus balanoglossoides*: Hypothesen zur Stellung der Psammodrilida innerhalb der Annelida. *Microfauna Marina* 10: 295–303.
Bartolomaeus, T. & Meyer, K. (1997): Morphogenesis and phylogenetic significance of hooked setae in Arenicolidae (Polychaeta, Annelida). *Invertebrate Biology* 116: 227–242.
Boaden, P.J.S. (1961): Littoral interstitial species from Anglesey representing three families new to Britain. *Nature* 191: 512.
Boaden, P.J.S. (1963): The interstitial fauna of some North Wales beaches. *Journal of the Marine Biological Association of the United Kingdom* 43: 79–96.
Boaden, P.J.S. (1976): Soft meiofauna of sand from the delta region of the Rhine, Meuse and Scheldt. *Netherlands Journal of Sea Research* 10: 461–471.
Curini-Galletti, M., Artois, T., Delogu, V., De Smet, W. H., Fontaneto, D., Jondelius, U., Leasi, F., Martínez, A., Meyer-Wachsmuth, I., Nilsson, K. S., Tongiorgi, P., Worsaae, K., & Todaro, M. (2012): Patterns of diversity in soft-bodied meiofauna: dispersal ability and body size matter. *Plos One* 7: e33801.
Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphologie* 95: 235–249.
Helm, C., Beckers, P., Bartolomaeus, T., Drukewitz, S. H., Kourtesis, I., Weigert, A., Purschke, G., Worsaae, K., Struck, T.H., & Bleidorn, C. (2018): Convergent evolution of the ladder-like ventral nerve cord in Annelida. Frontiers in Zoology 15: 36. DOI: 10.1186/s12983-018-0280-y
Kerbl, A., Bekkouche, N., Sterrer, W., & Worsaae, K. (2015): Detailed reconstruction of the nervous and muscular system

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of Lobatocerebridae with an evaluation of its annelid affinity. *BMC Evolutionary Biology* 15: 1.
Kristensen, M.R. & Nørrevang, A. (1982): Description of *Psammodrilus aedificator* sp. n. (Polychaeta), with notes on the Arctic interstitial fauna of Disko Island, W. Greenland. *Zoologica Scripta* 11: 265–279.
Mastepanova, E.A. (2004): The interstitial Polychaeta of Russian seas. *Invertebrate Zoology* 1: 59–64.
Meyer, R. & Bartolomaeus, T. (1997): Ultrastruktur und Morphogenese der Hakenborsten bei *Psammodrilus balanoglossoides* – Bedeutung für die Stellung der *Psammodrilus* (Annelida). *Microfauna Marina* 11: 87–113.
Orrhage, L. (1964): Über die Anatomie des zentralen Nervensystems der sedentären Polychäten. *Arkiv für Zoologie* 19: 99–133.
Parry, L.A., Edgecombe, G.D, Eibye-Jacobsen, D., & Vinther, J. (2016): The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society Series B* 283: 20161378.
Purschke, G. (2016): Annelida: basal groups and Pleistoannelida. In: Schmidt-Rhaesa, A., Harzsch, S., & Purschke, G. (eds.) *Structure and Evolution of Invertebrate Nervous Systems, Oxford University Press, Oxford*: 254–312.
Rieger, R.M. (1980): A new group of interstitial worms, Lobatocerebridae nov. fam. (Annelida) and its significance for metazoan phylogeny. *Zoomorphologie* 95: 41–84.
Riser, N.W. (1984): General observations on the intertidal interstitial fauna of New Zealand. *Tane* 30: 239–250.
Rouse, G.W. & Pleijel, F. (2001): *'Polychaetes'*. Oxford University Press, Oxford, UK.
von Salvini-Plawen, L. (1968): Zur Kenntnis des Mesopsammales der Nord Adria I: Die für den Meeresteil neuen Gruppen und Arten. *Thalassia Jugoslavica* 4: 11–17.
Swedmark, B. (1952): Note préliminaire sur un polychète sédentaire aberrant, *Psammodrilus balanoglossoides* n. g. n. sp. *Arkiv für Zoologie* 4: 159–162.
Swedmark, B. (1955): Recherches sur la morphologie le developpement et la biologie de *Psammodrilus balanoglossoides,* polychète sédentaire de la microfaune des sables. *Arch Zool Exp Gén* 92: 141–220.
Swedmark, B. (1958): *Psammodriloides fauveli* n. gen. n. sp. et la famille des Psammodrilidae (Polychaeta Sedentaria). *Arkiv für Zoologie Séries* 2 (12): 55–65.
Tzetlin, A.B. and Saphonov, M.V. (2002): Interstitial polychaetes (Annelida) from the Kandalaksha Bay of the White Sea. *Zoologicheskii Zhurnal* 81: 899–908.
Westheide, W. (2008): Polychaetes: Interstitial Families. 2nd ed. The Linnean Society of London (Field Studies Council Shrewsbury), London.
Worsaae, K. & Kristensen, R.M. (2005): Evolution of interstitial Polychaeta (Annelida). *Hydrobiologia* 535/536: 319–340.
Worsaae, K., Kvindebjerg, K., & Martínez, A. (2015): Morphology of a new interstitial *Psammodrilus* (Psammodrilidae, Annelida) from Sardinia, Italy. *Zoologischer Anzeiger* 259: 13–21.
Worsaae, K. & Sterrer, W. (2006): Description of two new interstitial species of Psammodrilidae (Annelida) from Bermuda. *Marine Biological Research* 2: 431–445.
Worsaae, K., Giribet, G., & Martínez, A. (2018): The role of progenesis in the diversification of the interstitial annelid lineage Psammodrilidae. *Invertebrate Systematics* 32(4) 774–793 https://doi.org/10.1071/IS17063.

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# 5.3 Chaetopteridae Audouin & Milne Edwards, 1833

## Introduction

The Chaetopteridae Audouin and Milne Edwards, 1833 constitutes a monophyletic clade with an unclear position within the Annelida and Polychaeta hierarchy (Rouse and Fauchald 1997, Struck *et al*. 2011). They are characterized by one pair of long, grooved, ciliated, peristomial palps and a body divided in three parts, namely, the A (anterior-most), B (mid-body), and C (posterior-most) regions (Figs. 5.3.1 A and 5.3.3 A–D). Parapodia in region A and in regions B and C are uniramous and biramous, respectively. The most characteristic chaetae include cutting chaetae[1] in chaetiger A4 (Figs. 5.3.8 C, 5.3.9 E, F, 5.3.10 B, and 5.3.11 B), which are considered as a robust taxonomic character (e.g., Bhaud *et al*. 2006 and references herein), and pectiniform uncini in posterior chaetigers (Figs. 5.3.8 D, F–H, 5.3.9 B, 5.3.10 C, and 5.3.11 C). The presence of grooved palps has traditionally been the reason to place the family within spioniform taxa (Rouse and Fauchald 1997), while their uncini resemble those of some Sabellida and Terebellida. In turn, recent molecular approaches tend to place chaetopterids as a basal group within Annelida (Weigert *et al*. 2014).

The species of the family may occur everywhere in the World Ocean (Pettibone 1982). They are generally considered to be active suspension- or deposit-feeders (Barnes 1965, Jumars *et al*. 2015) and tend to inhabit mainly shallow water, with some species reaching abyssal bottoms (e.g., Fabri *et al*. 2010, Nishi and Rouse 2014). Nearly all chaetopterids are benthic organisms building parchment-like tubes often incrusted with sand, which are either embedded in soft sediments or attached to hard substrates (Barnes 1964, 1965, Sendall *et al*. 1995). There

**1** Modified chaetae of chaetiger 4 are employed by the worms to cut tubes and/or to make holes in the tube transverse partitions present in some species in the posterior sections or in the tube section closing the posterior end. These chaetae have been named as "modified," "specialized," "tear-drop," "cutting," "modified cutting," "modified acicular," or "thick" chaetae, as well as "spines" or "stout black spines," among others. As their function in most species seems to be clearly related with cutting, we decided to adopt "cutting chaetae" to consistently refer to these chaetae along this chapter.

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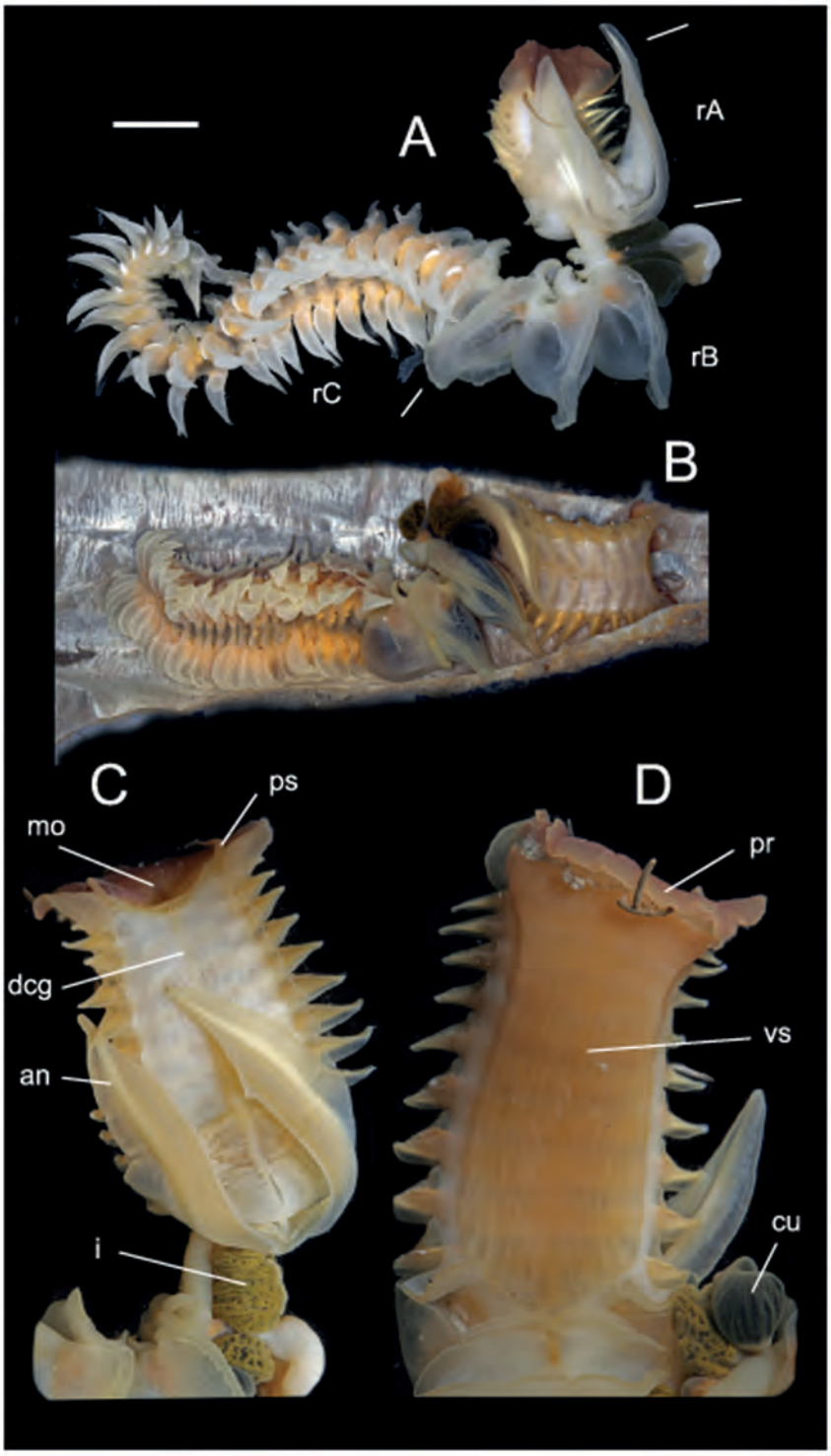


**Fig. 5.3.1:** Living specimen of *Chaetopterus cf. appendiculatus* collected in Nhathrang (Vietnam), courtesy of E.S. Mekhova. A, Whole body. B, The worm inside its tube (dissected). C, Region A and first segment of region B in dorsal view. D, Same, ventral view. rA, region A; rB, region B; rC, region C; an, aliform notopodia; cu, cupule; dcg, dorsal ciliary groove; mo, mouth opening; pr, peristomium; ps, palps; vs, ventral shield or plastron. Scale bar is 10 mm for A, 15 mm for B, and 5 mm for C and D.

is one planktonic species known from bathyal depths (Osborn *et al*. 2007).

Within Chaetopteridae, 73 nominal species are currently accepted as valid: 16 within *Chaetopterus* Cuvier, 1830, 16 within *Mesochaetopterus* Potts, 1914, 24 within *Phyllochaetopterus* Grube, 1863, and 17 within *Spiochaetopterus* M. Sars, 1856.

## Morphology

### External morphology

**Color.** The body of living worms is overall pale whitish or yellowish (Fig. 5.3.1). The heads sometimes have dark red pigments (e.g., reddish melanoid pigments in *Chaetopterus*) (Kennedy and Nicol 1959). Palps are uniformly

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colored or have stripped transversal bands, greenish to dark brown, and dark reddish longitudinal pigmentation (e.g., in *Mesochaetopterus*, Fig. 5.3.2), often species specific (Martin *et al*. 2008). Palps and parapodial lobes from region A sometimes produce bluish bioluminescence, e.g., in *Chaetopterus* (see Nishi *et al*. 2000 and references herein) and *Mesochaetopterus* (Fujiwara 1935, D. Martin, laboratory personal observations). The gut is often dark green (Fig. 5.3.1 C) due to chaetopterin (a pigment mixture of phaeophorbides a and b and chlorophyll a and b derivates) occurring inside small green spherules in its epithelial cells (Kennedy and Nicol 1959). The ventral surface of region A has different combinations of color, usually pale whitish or yellowish at plastron (e.g., in *Chaetopterus*, Fig. 5.3.1 D), with a dark brown, crescent-like structure followed by one or two bright whitish crescent like structures in the last segments of region A (e.g., in *Spiochaetopterus*). The chaetae are most often pale brown or yellowish and translucent, except for black cutting chaetae (Fig. 5.3.2 D). Color in preserved specimens is usually uniformly grayish or yellowish, probably depending on species, fixative fluid, and exposure. Original pigmentation is best preserved on palps and crescent like structures of region A.

**Body shape.** Except for the neotenous *Chaetopterus pugaporcinus* Osborn, Rouse, Goffredi & Robison, 2007, which is roughly spherical and measures 1–2 cm long (Fig. 5.3.2 A, B) (Osborn *et al*. 2007), chaetopterids are elongate and fragile polychaetes having numerous segments. They can reach considerable lengths, even more than 60 cm (Petersen and Fanta 1969) and may be easily recognized by a body divided into three very characteristic, distinct regions, together with one pair of long, grooved, ciliated, peristomial palps and the presence of cutting chaetae in chaetiger 4 (Figs. 5.3.1 C and 5.3.13 A–D).

**Prostomium and Peristomium.** The prostomium is a small lobe, surrounded by a broad collar (i.e., peristomium) projecting forward and laterally (Fig. 5.3.1 D). There is one pair of prostomial eyes in *Chaetopterus*, sometimes absent in other genera, as small, rudimentary, reddish to blackish spots, without crystalline lens (Martin and Anctil 1984). Nuchal organs are lacking in *Chaetopterus*, but ciliated epidermal sensory cells (responsible of bioluminescence) are often present (Anctil 1979, Martin and Anctil 1984). Nuchal organs in *Spiochaetopterus* and *Mesochaetopterus* are located laterally, on the posterior prostomial border (Gravier 1904). There is one pair of peristomial grooved palps, shorter in *Chaetopterus*, intermediate in *Mesochaetopterus*, and very long in *Phyllochaetopterus* and *Spiochaetopterus* (Fig. 5.3.3 A–D). A second pair of "antennae", i.e., elongated notopodia from segment A1, is present in *Phyllochaetopterus* (Fig. 5.3.3 C) (Bhaud *et al*. 1994).

**Body regions.** The body is divided into three distinct regions: referred to as A, B, and C (Figs. 5.3.1 A and 5.3.3 A). Region A begins at segment 1 and has from 9 to less than 20 segments that are short, broad, flattened, and uniramous, except for the last segment in *Chaetopterus* (Fig. 5.3.1 C, D). There is a ciliated groove reaching the mouth dorsally and a thick, ventral, glandular field, i.e., plastron, regularly pierced with pores responsible for mucus production for tube construction (Bhaud 1998a). The chaetae of region A are lancet shaped to oar, sickle, or spoon like (Figs. 5.3.8 B, 5.3.9 B–D, 5.3.10 B, and 5.3.11 D), except on chaetiger A4. A4 cutting chaetae are stout spines, 1–2 in *Spiochaetopterus* and *Phyllochaetopterus* and more than 20 in *Mesochaetopterus* and *Chaetopterus* (Figs. 5.3.5, 5.3.8 C, 5.3.9 E, F, 5.3.10 D, and 5.3.11 B).

Region B has from 2 to more than 30 segments, which are more elongated than A segments and highly specialized (Barnes 1964, 1965, Nishi and Arai 1996). *Chaetopterus* and some *Mesochaetopterus* have segments responsible for water pumping along the tube (i.e., piston-like), with aliform notopodia and cup-shaped feeding organs (i.e., cupules) producing food bolus from filtration bags (Figs. 5.3.1 A, C and 5.3.3 A, B). In *Phyllochaetopterus* and *Spiochaetopterus*, the segments responsible for water pumping along the tube and supporting filtration bags are simpler and uniform, foliaceous, elongated, and lined with cilia (Fig. 5.3.3 C–E). Filtration bags and cupules range from one (e.g., in *Chaetopterus*) to eight (e.g., in *Mesochaetopterus*) or more (e.g., in *Phyllochaetopterus* and *Spiochaetopterus)*. The segments of region B are biramous, having or not notoacicula and notochaetae and a series of neuropodial uncini arranged in a row.

Region C has more segments than regions A and B, which are short, biramous, and similar to each other (Figs. 5.3.1 A and 5.3.8 A). Notochaetae are often internal. Neuropodia are bilobed (with or without symmetrical lobes) or unilobed and have low ridges bearing rows of characteristic D-shaped uncini with more or less numerous curved teeth on one side (Figs. 5.3.8 D, H, 5.3.9 H, and 5.3.11 C). Except in *Chaetopterus*, C segments are highly contractile, allowing a quick retraction into tube at least in *Mesochaetotperus* (Martin *et al*. 2008). The pygidium is a simple lobe, and the anus is terminal.

**Tube morphology.** The tube is parchment or paper like, as in *Chaetopterus* (sometimes incorporating mud, sand, and shell particles; Figs. 5.3.1 B, 5.3.4 B, D, and 5.3.7 E) and *Mesochaetopterus* (sometimes incorporating sand and shell fragments; Fig. 5.3.2 C) or translucent and chitin

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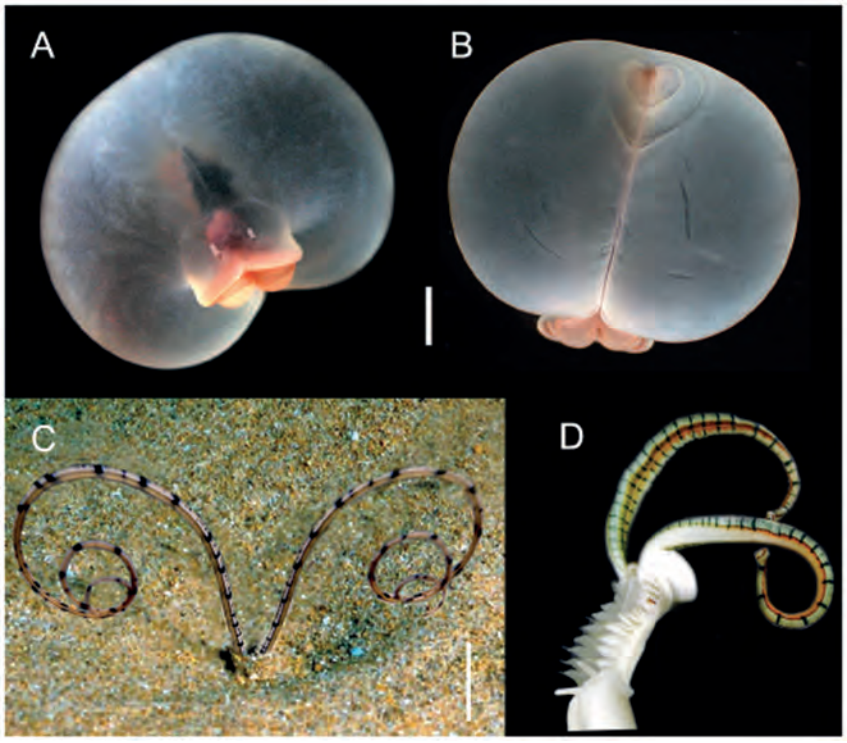


**Fig. 5.3.2:** Living specimens of *Chaetopterus pugaporcinus*, courtesy of Dr. K. Osborn. A, Anteroventral view showing palps, peristomium, and prostomium. B, Dorsal view showing the posterior segments, the inflated B region, and a peak of the peristomium and prostomium. Color of palps in *Mesochaetopterus rogeri*. C, Living specimen. D, Recently preserved specimen. Scale bars are 4 mm (A, B), 15 mm (C), and 10 mm (D).

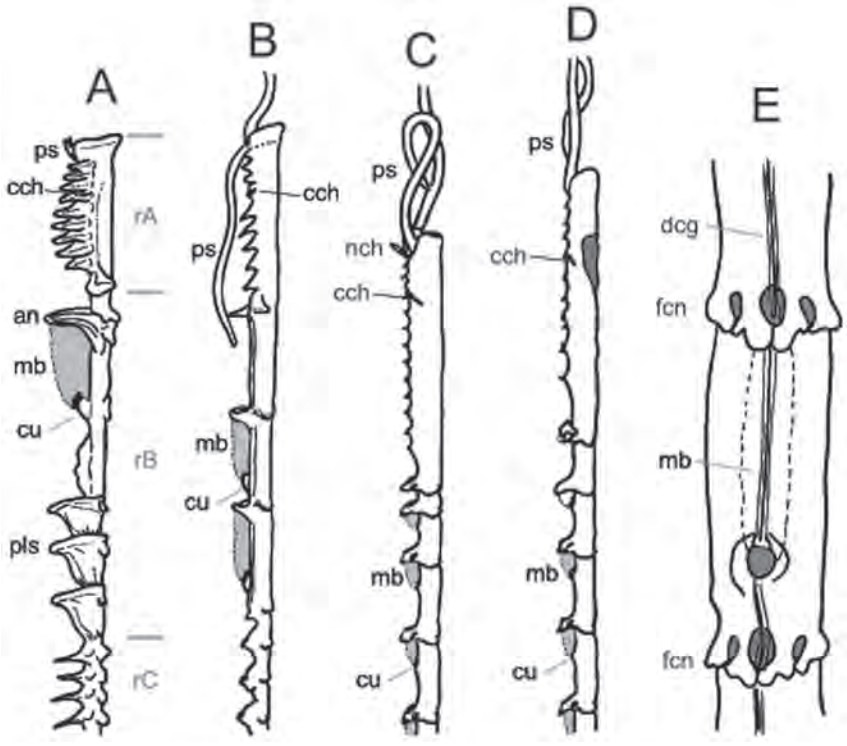


**Fig. 5.3.3:** Schematic drawings of anterior and middle body regions of representatives of each of four genera, redrawn from Barnes (1965). A, *Chaetopterus*. B, *Mesochaetopterus*. C, *Phyllochaetopterus*. D, *Spiochaetopterus*. rA, region A; rB, region B; rC, region C; an, aliform notopodia; cch, cutting chaetae of chaetiger 4; cu, cupules; dcg, dorsal ciliary groove; fcn, foliaceous ciliated notopodia; mb, mucous bag; nch, notopodia of chaetiger 1 ("antenna"); pls, piston-like segments; ps, palps.

like, as in *Phyllochaetopterus* (Fig. 5.3.10 D) and *Spiochaetopterus* (Fig. 5.3.11 E, F). The tube wall in *Chaetopterus* consists of alternating layers of aligned protein fibers, embedded in an unstructured matrix. Protein fibers range from 50 to 400 nm in diameter (Brown and McGee-Russell 1971) and are oriented at 0°, ±45°, and ±60°, this producing biocomposite tubes extremely resistant to mechanical and thermal impacts (Shah *et al.* 2014). Typical

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*Chaetopterus* tubes are roughly U shaped (Fig. 5.3.4), with several openings, among which only the two most recent are functional (Enders 1908). Tubes in *Mesochaetopterus* are straight, L or J shaped; one end protrudes from the bottom surface and the other is more or less deeply embedded into the sediment, e.g., from 20 cm to more than 2.5 m (Rullier 1976, Sendall *et al*. 1995, Nishi 1999, Martin *et al*. 2008). Tubes in *Phyllochaetopterus* and *Spiochaetopterus* are most often straight, sometimes branching (Fig. 5.3.10 D) and often have external annulations associated to internal perforated transverse partitions (Barnes 1965) (Fig. 5.3.10 E). The lower tube ends in some species of *Mesochaetopterus*, *Phyllochaetopterus*, and *Spiochaetopterus* are closed, sometimes showing characteristic perforations in *Mesochaetopterus* (Nishi 1999).

### Anatomy

Information on the anatomy of chaetopterids is mostly based on *Chaetopterus* (see Rouse and Pleijel 2001 and references herein). The prostomium has a terminal mouth. The pharynx is simple and noneversible. The gut is straight, sometimes pouching at the region B level. The ventral plastron of region A has numerous, specialized secretory glands, responsible for tube building (Enders 1908, Barnes 1964, 1965).

The circulatory system is closed, with a major dorsal vessel in region A, ending in a heart at the beginning of region B. A large blood sinus is placed around the gut and behind the heart, extending almost along whole regions B and C. The ventral vessel is large, extending along the whole body (Enders 1909, Probst 1929).

**Nervous system and sensory organs.** The anatomy of prostomial eyes and nuchal organs is not described. The anterior-most nervous system has two dorsolateral cerebral ganglia in *Chaetopterus*. Nerve cords are lateral, converging at the segment B1 level and forming a ventro-median nerve cord with repetitive segmental ganglia. Numerous short commissures and three segmental nerves course toward the dorsal and ventral regions of parapodia and toward neuropodia, emerging from segmental ganglia (Martin and Anctil 1984).

**Nephridia.** Segmental organs are absent in region A, have an excretory function in region B (sometimes containing gametes at least in *Spiochaetopterus*), and are used to expel gametes in region C (Rouse and Pleijel 2001).

### Reproduction and development

Chaetopterids have separate sexes and spawn directly into the water column, where gamete fertilization takes place.

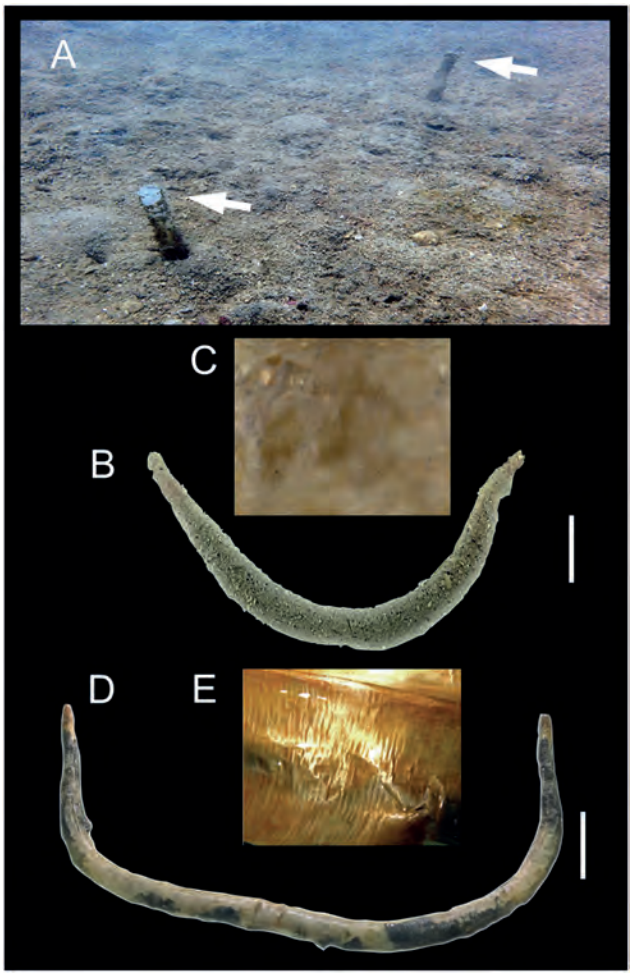


**Fig. 5.3.4:** A, Underwater view of the siphons (white arrows) of a soft bottom species of *Chaetopterus* protruding from the sediment surface. B–E, External and internal aspect of the tubes of two syntopic species of *Chaetopterus* inhabiting shallow Vietnamese soft bottoms. *Chaetopterus* sp.: B, paper-like tube, covered by sand and coral and shell fragments; C, whitish to light brown, semitransparent inner lining. *Chaetoperus cf. appendiculatus*: D, parchment-like tube, covered by silt; E, silver to golden, striated, iridescent inner lining. Scale bars are 5 cm.

Embryology and early development were first studied in *Chaetopterus* by Wilson (1883) and Enders (1909), while natural reproduction is poorly known for the whole family. Mature adults seem to be distinguishable by the color of the posterior parapodia, which are whitish in males and yellowish in females, at least in *Chaetopterus*, whose gametes, fertilized eggs, and larvae seem to be easy to obtain in laboratory conditions (Loeb 1901, Costello and Henley 1971).

Gamete formation, early development, and embryology were subjects of different studies, all them focusing on *Chaeropterus* (Eckberg and Kang 1981, Eckberg 1981a,b, Anderson and Eckberg 1983, Polk *et al*. 1987, Eckberg *et al*.

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1986, Eckberg and Hill 1996, Eckberg and Anderson 1997), while larval development and metamorphosis are well known for many species of the four chaetopterid genera, in most cases based on larvae directly collected from the plankton (Werner 1953, Cazaux 1965, Bhaud 1966, 1978, 2003, Mileikovsky 1967, Scheltema 1974, Sveshnikov 1978, Bhaud and Cazaux 1987, Gaikwad 1988, Irvine *et al*. 1999, Bhaud and Fernandez-Alamo 2000). Chaetopterid larvae have relatively large, spherical, or oval bodies, more or less clearly divided into three regions (Irvine *et al*. 1999); as development progresses, the posterior region becomes more elongated, which seems to be related with metamorphosis and settlement (Fig. 5.3.5). The larvae have a well-developed ciliation, including two or three ciliary bands, a fine ciliation on the anterior end and oral opening, and some additional sensory cilia along the body (Fig. 5.3.5). They also have palps and chaetae (including the cutting chaetae of chaetiger 4), which are similar to those in adults, thus allowing to their identification even to species level.

Most chaetopterid larvae have extended periods of planktonic life (Scheltema 1974), while the corresponding adult distributions appear to be more local than expected likely because larval dispersal (as well as gamete production and development, spawning and settlement) is limited by environmental constraints (Bhaud 1975, 1998b, 2003, Bhaud and Fernandez-Alamo 2000, Bhaud *et al*. 2002b). Chaetopterid larvae are regular components of the meroplankton in most seas of the world. In all cases, they became active filter feeders even before losing all yolk remains. Larvae recently collected from the plankton show the final portion of the digestive tract full of pellets, which often contain the skeletons of small crustaceans (Enders 1909). In laboratory conditions, they perfectly survive feeding on mixed diatom and chlorophycean planktonic algae (Bhaud 1966), but they have been observed to capture preys that may reach half their own size (Enders 1909). The presence of chaetopterid larvae in the plankton is often coupled with seasonal phytoplankton blooms (Thompson and Schaffner 2001), and the exact period of the year in which they occur is often species specific (Bhaud 1966). In *Mesochaetopterus rogeri*, Martin, Gil, Carreras-Carbonell & Bhaud, 2008 there seemed to be two annual peaks of density, but only the spring one responded to a recruitment event. The second one was caused by the return to the bottom surface of the adults that were deeply hidden into the sediment to survive the autumn storms typical of the region (Martin *et al*. 2008).

*Chaetopterus pugaporcinus* (Fig. 5.3.2 A, B), the first pelagic Chaetopteridae, can be particularly highlighted within a reproductive context as the specimens resemble

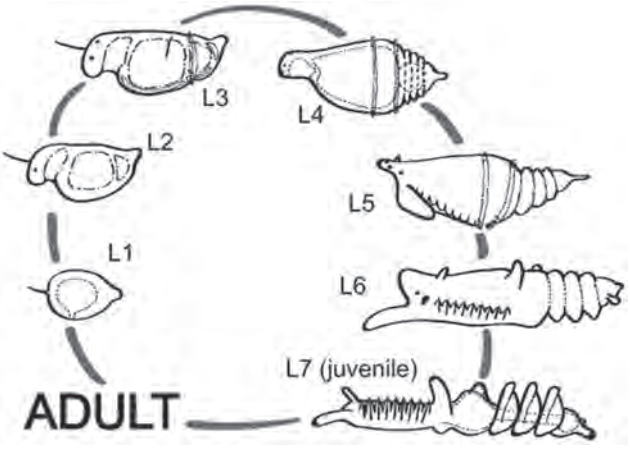


**Fig. 5.3.5:** Scheme of the planktonic larval phases of *Chaetopterus*. Redrawn from Irvine *et al*. (1999).

L5 stage (competent to metamorphose) larvae according to Irvine *et al*. (1999). However, due to the absence of reproductive individuals, it was not possible to determine whether the specimens were gigantic larvae that have yet to metamorphose and settle. Therefore, the species was described as an adult that combined larval and adult features with an extended use of the planktonic habitat within the deep mesopelagic waters (Osborn *et al*. 2007).

Settlement and first tube building were well described for *Chaetopterus* by Enders (1909). Settlement occurs after the larvae became large bodied. They first approach the bottom using mucus parachutes (Werner 1953) and become attached by the holdfast, an adhesive area located in the anal region that may also be used by the young settled worms to move over the bottom. Juveniles start then to creep, first leaving a slight mucus trail, but quickly starting to build mucus coated tunnels that also agglutinate sediments. One of these tunnels may reach several times the juvenile length, and from this mucous gallery, the worms start to build a small version of the typical U-shaped tube. However, at least the larvae of *Chaetopterus* reared in laboratory conditions are able to reverse from recently settled long-bodied forms to oval planktonic forms if the sediment is not adequate for them to settle. This process can be repeated several times until they find an adequate habitat (D. Martin and M. Bhaud, personal laboratory observations). If occurring in natural conditions, this mechanism, in addition to the contribution to increase the possibilities of settlement success, implies also a secondary return to the plankton and, thus, higher dispersal, higher risk of predation, and more possibilities of a successful colonization. No other detailed descriptions of the first phases of settlement are known to date for species of the other genus of the family.

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Asexual reproduction has been reported at least for *Phyllochaetopterus* and *Spiochaetopterus* (Claparède 1870, Potts 1914, Nishi 1996a). *Phyllochaetopterus socialis* Claparède, 1869 and *Phyllochaetopterus prolifica* Potts, 1914 have branched and crooked tubes, which may be inhabited by several worms (Claparède 1870, Potts 1914). In this case, the worms are smaller than normal adults, lack some of the most characteristic morphological features (e.g., the cutting chaetae of chaetiger 4), and belong to the same sex. These individuals originate from asexual reproduction (i.e., fragmentation) in which a fragment of an individual containing segments of the regions B and C may fully regenerate the anterior region A and fragments containing segments from regions A and B may regenerate region C. Region A is re-formed much more quickly than the posterior regions. Accordingly, only the segments from region B are able to regenerate the remaining ones, and in all cases, they first regenerate the segments of the other regions before completing those of the own B one. This way, some species are able to quickly form large colonies in a given area after a successful colonization by planktonic larvae generated by sexual reproduction.

*Spiochaetopterus* apparently has a fragmentation/regeneration mechanism similar to that described for *Phyllochaetopterus* (Nishi 1996a). However, an alternative view was proposed in which fragmentation is not interpreted as a way to reproduce asexually, but as a complement of sexual reproduction by facilitating the availability of energy to region B, which is the responsible for bringing the products of the sexual organs to maturity (Bhaud 1998c). The final result is, however, that several small individuals of *Spiochaetopterus* may share the same tube, which, in this case, is not branched. Whether this fragmentation/regeneration mechanism could represent a real asexual reproduction or a mechanism increasing the success of sexual reproduction is still an open question.

Both in *Phyllochaetopterus* and *Spiochaetopterus*, the worms sharing a tube are able to move quickly inside. They can even turn around and pass each other. Thus, all of them have access to the tube opening (or openings, if several are available).

Regeneration of posterior segments from a fragment containing anterior ones has been reported for *Chaetopterus* and *Mesochaetopterus*, as a normal result of breaking for any reason, including induced autotomy (Gravier 1909a,b, Martin *et al*. 2008). Moreover, these authors reported rebuilding of anterior segments from fragments containing middle and posterior segments. In these cases, the rebuilt section can be easily distinguished in the early stages of reconstruction due to the smaller size of the components relative to those of a normal adult (Fig. 5.3.9 I). In all cases, however, the regeneration has been attributed to breaking after accidental events (for instance predation) and not to asexual reproduction.

## Biology and ecology

### Distribution

Chaetopterids are widely distributed in marine waters from the Arctic to the Antarctic (Pettibone 1982). Most species inhabit shallow shelf depths (Nishi and Bhaud 2000, Nishi *et al*. 2009), while some *Phyllochaetopterus* and *Spiochaetopterus* species extend to abyssal hydrothermal vent sites (Nishi *et al*. 1999, Nishi and Rouse 2007, Nishi 2008, Fabri *et al*. 2010, Morineaux *et al*. 2010). Nearly all known species have benthic, tubiculous adults, except for the neotenic *C. pugaporcinus*, a planktonic species from bathyal depths (Osborn *et al*. 2007) (Figs. 5.3.2 A and 5.3.2 B). Benthic chaetopterids construct permanent tubes most often buried into the sediment (Fig. 5.3.4), where some live solitary and some may form colonies and/or dense aggregates reaching densities higher than 14,000 individuals per square meter (Bailey-Brock 1976, Bhaud *et al*. 1994, Nishi 1996a, 1996b). Some species, however, may attach the tubes to hard substrates in close vicinity of soft bottoms (Barnes 1964, 1965), where they may also form aggregates. For instance, the coverage by dense aggregates of *Chaetopterus* has been reported to smother colonies of scleractinian corals, being the second cause of major mortality among them (Smith and Harriott 1998, Harriott and Smith 2000).

Despite this, the functional role of chaetopterids in the marine ecosystems is poorly known. They may reach high density and biomass, becoming the dominant organisms in benthic communities (e.g., Bhaud *et al*. 1994, Smith and Harriott 1998, Britayev *et al*. 2010) and thus being an important food source for fish and crustaceans. Despite evidence that they suffer from the attacks of predators (Bailey-Brock 1976, Martin *et al*. 2008), the available information on their role in the trophic network is often indirect and obscure (e.g., Enders, 1909, Nishi and Rouse, 2014). Chaetopterids may also play a relevant role in structuring sedimentary bottoms (Bailey-Brock 1976). The irrigation of their tubes buried into the sediment drives oxygen-rich water into deeper sediment layers (which otherwise would have been anoxic), facilitating the growth of aerobic organisms such as bacteria that are found clustering around the tubes (Martin *et al*. 2008). Also, it has been suggested that the numerous fragments of long-lasting empty tubes formed a dense palisade that is a major contributor to stabilize the upper layer of sediments after storms (Martin *et al*. 2008). On

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the other hand, chaetopterids may harbor highly diverse epifaunal organisms (Nalesso *et al*. 1995), and the characteristic dense aggregates formed by some species may provide shelter to a highly diverse associated fauna, which represents an important contribution to the local biodiversity (Smith and Harriot 1998). In turn, an additional contribution of the family to increase the complexity and biodiversity of marine ecosystems dealt with the fact that many of their species are well-known hosts for many different species of symbiotic organisms (Martin and Britayev 1998).

**Behavior**

The behavior of chaetopterids has often been subject of study, likely because some species are big and easy to be reared in captivity. Accordingly, most of these studies focus on *Chaetopterus* and are related with feeding, food recognition, tube building, tube cleaning and irrigation, and water pumping (MacGinitie 1939, Wells and Dales 1951, Barnes 1965, Brown 1977, Brown and Rosen 1978, Sumida and Case 1983), while the few dealing with the species of the other genera mostly refer to feeding and tube building (Barnes 1964, 1965, Sendall *et al*. 1995, Nishi and Rouse 2014).

Chaetopterids are generally active suspension feeders (Barnes 1964, 1965, Jumars *et al*. 2015) using either complex mucus-net based mechanisms (e.g., *Chaetopterus)* or the palps (e.g., *Mesochaetopterus*). These palps, which may be very long (except in *Chaetopterus*), may play an accessory role in deposit and passive suspension feeding, for instance, in *Spiochaetopterus* and *Phyllochaetopterus* (Barnes 1964, 1965).

The most remarkable behavioral feature of chaetopterids is certainly the use of mucous nets or bags for filtering food particles (Enders 1909, Barnes 1965, Brown 1975), which were first described by MacGinitie (1939). Accordingly, the bag is produced from mucus threads secreted by the inner walls of the aliform notopodia of region B. The cilia on the inner surface of these notopodia drives the mucus across the opening between notopodia, from their distal end to the body surface, thus forming the filtration net. The net is carried back by the dorsal ciliated groove, forming a bag that reached the cupule, whose inner concave surface contains the closed end of the net. The result is an elongated mucus net extending from the aliform notopodia to the dorsal cupule. Mucus is continuously secreted at the anterior end of the net, and, at the same rate, the posterior end is rolled into a ball inside the cupule. The final purpose of this net is to remove from the water the solid particles that constitute the food of *Chaetopterus*. From time to time, the anterior end of the net is cut off from the notopodia, and the cupule continues to rotate the ball of mucus with food inside until the whole bag is rolled up. Then, the cupule expels the food ball toward the posterior end of the dorsal ciliated groove, whose cilia carry forward the bolus to the mouth, where it is enveloped by the lips, swallowed, and finally ingested (MacGinitie, 1939). This feeding mode is also employed by other chaetopterids, with minor variations (Barnes 1964, 1965). For instance, the number of filtration bags used varies from one in *Chaetopterus* and some species of *Mesochaetopterus* and *Spiochaetopterus* to eight or more in some *Phyllochaetopterus* and *Spiochaetopterus* (Fig. 5.3.3 A–D).

Filtration currents are generated by peristaltic contractions of the piston-like segments of region B, in *Chaetopterus* and in some species of *Mesochaetopterus* (Figs. 5.3.1 A and 5.3.3 A, B), or by the beating of cilia lining the ring-like openings created by the foliaceous notopodia of region B in *Phyllochaetopterus* and *Spiochaetopterus* (Barnes 1964, 1965) (Fig. 5.3.3 C–E). The planktonic species *C. pugaporcinus* also filters by means of a mucous net that is ingested when filled. Filtration is achieved by more or less continuous spinning rather than the generation of feeding currents (Osborn *et al*. 2007). In turn, some species of *Spiochaetopterus* (e.g., *S. oculatus* Webster, 1879) are able to use their large, grooved, ciliated palps for suspension and deposit feeding depending on the available food source, the former when food is driven by horizontal flows, the latter when bottom deposits are presented (Turner and Miller 1991). This dual suspension- and deposit-feeding ability has also been reported for *Mesochaetopterus taylori* Potts, 1914 (Busby and Plante 2007). Passive suspension feeding in *Spiochaetopterus* seems to be related with a helical coiling of the palps (Turner and Miller 1991), a peculiar arrangement that has also been recently reported for *M. rogeri* (see Martin *et al*. 2008) (Fig. 5.3.2 C).

Tubes are an intrinsic part of the filtration mechanism aside their function as housing. Particularly, the tubes of *Chaetopterus* appear to be very well designed to channel the powerful pumping of the three specialized segments of region B, as both ends progressive narrow to increase current speed (Fig. 5.3.4). Also, *Chaetopterus* are almost unique within the family in having both ends of the U-shaped tubes opening at the ground surface and being used alternately for inhalation or excretion, as the worms are able to turn 180° inside the tubes (Brown 1977). Hence, the worms are not able to enlarge the tubes through the siphons, but instead, they must cut an additional opening or rupture in the tube wall using the cutting chaetae of chaetiger 4 and form a new tube extension from this point (Enders 1908).

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Species incorporating sediment particles into the tube (e.g., in *Mesochaetopterus*) use the large ventral lip for molding the outer sand layer. To enlarge the tube, the worms protrude out their anterior end, adhere sediment particles to the mucus on the lip surface, and press them to the rim of the tube at the same time as the inner secreted lining is being produced (Barnes 1965). This building mechanism is not only used to adapt the tube length while the worms are growing but may also be part of an intrinsic adaptive mechanism of some species to the peculiarities of the surrounding environment. The native habitat of *M. rogeri* consists of highly motile sediments, in which upper centimeters are frequently displaced by the storms habitually affecting the area. During these episodes, the worms remain deeply retracted inside their tubes, while upper tube sections are lost so that the presence of the species cannot be perceived when looking on the seafloor from above. As soon as the upper sediment layer stabilizes again, the upper tube sections are rebuilt up, so that the presence of the worms becomes again detectable (Martin *et al*. 2008). These authors also suggested that the ability of fast retraction toward the deep inner sections of the tube can also be an escape mechanism from predators, although it is not fast enough to protect them against all attacks, as the presence of individuals with regenerating anterior ends (Fig. 5.3.9 I) appears to be common.

**Bioluminiescence**

Chaetopterids are known to be bioluminescent, as reported for *Chaetopterus* (see Nishi *et al*. 2000 and references therein) and *Mesochaetopterus* (Fujiwara 1935, D. Martin, personal laboratory observations). *Chaetopterus* species produce a bright luminescent mucus that is generated in abundance from various parts of the body, particularly the aliform notopodia and parapodial flaps. The mucus is produced by epithelial eosinophilic cells (i.e., the photocites), which may be scattered singly or massed together, forming dense aggregations named luminous organs (Nicol 1952a). There are numerous photogenic glands, the largest being located on the dorso-median surface of segments 10 to 12 (Martin and Anctil 1984), whose secretions are under the control of the peripheral nervous system (Nicol 1952b).

Luminescence is an extracellular phenomenon (Nicol 1952c). The photocytes produce a luminescent protein that emits light when secreted without concomitant consumption of oxygen (Shimomura and Johnson 1968, Deheyn *et al*. 2013). Light is produced as a long glow in the blue range, which is an unusual color for a shallow water benthic invertebrate (Deheyn *et al*. 2013), and its function has been a subject of debate for a long time. The luminous mucus has been suggested to be a tool used to trap food, to attract small living organisms (MacGinitie 1939, Nicol 1957, Flood and Médioni 1982), or to deter organisms from settling in the tube (Morin 1983). However, the bioluminescent properties seemed to be more likely related with a defense from predators' attack. It has been observed that disturbing an individual of *Chaetopterus* triggers the emission of a bioluminescent mucus cloud through one tube end while the worm moves to the other end (Martin and Anctil 1984). These authors also suggested that the dispersal of the cloud in the water would confuse the potential attacker and hide the exact location of its prey. However, the real functions, as well as the chemical structure of the photoprotein, are still unresolved.

**Symbiotic associations**

Chaetopterid tubes offer a "comfortable" habitat for diverse symbiotic species, due to well-protected shelter and continuous water flow, likely bringing easily accessible food particles. Known inhabitants include crustaceans, polychaetes, mollusks, and fish (Pearse 1913, Petersen and Britayev 1997, Britayev *et al*. 2017). Polynoid scaleworms dominate among symbiotic polychaetes living inside chaetopterid tubes (13 out of 16 species), but they are greatly outnumbered by pinnotherid and porcellanid crabs (25 species, 24 of which are symbionts of *Chaetopterus* spp.). As the species of *Chaetopterus* are those with the largest tubes, it is not surprising that crabs predominate among their symbionts, whereas those of chaetopterids with more close-fitting, slender tubes are generally inhabited by polychaetes. The species of *Chaetopterus* harbor the most diverse symbiotic fauna. These worms are large, inhabit parchment-like tubes that may reach more than 1 m long and 2.5 cm in diameter (e.g., *Chaetopterus cautus* Marenzeller, 1879 from the Sea of Japan; T. A. Britayev, personal observations), have two equifunctional ends that open at the ground surface, and have a very powerful system of tube ventilation (Fig. 5.3.4). The combination of all these characteristics appears to favor the presence of symbionts by facilitating the process of entering the host tubes at different stages of the symbionts' life cycles. Moreover, they generate powerful water currents that seem to supply enough oxygen and food particles not only to support the host itself but also to maintain several coexisting symbiotic individuals often belonging to species from different taxonomic groups as well. In fact, this co-occurrence of symbiotic species sharing the same host seems to be rather common and may include not only relatively large animals, such as polychaetes, mollusks, pinnotherid or porcellanid crabs

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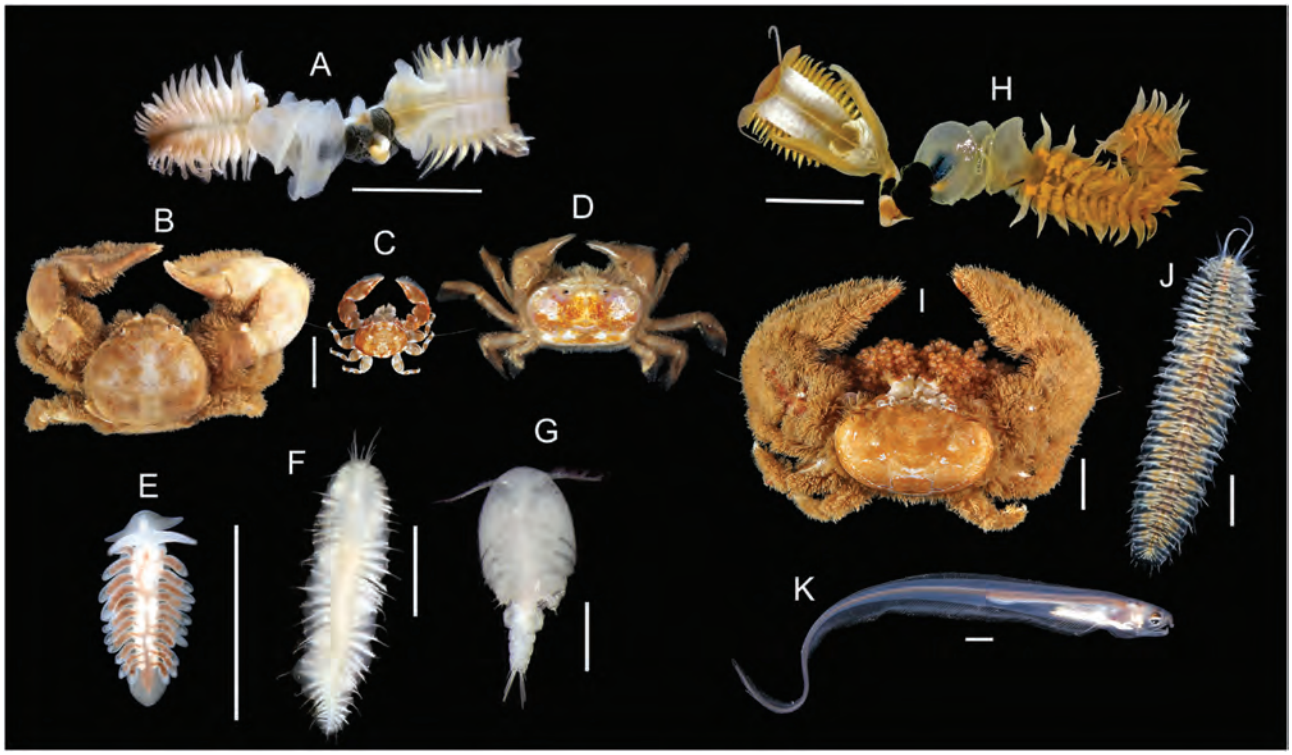


**Fig. 5.3.6:** Symbiotic communities associated with two syntopic species of *Chaetopterus* inhabiting shallow Vietnamese soft bottoms. A–G, *Chaetopterus* sp. and its symbionts: A, undescribed species of *Chaetopterus* without tube; B, female of the porcellanid crab *Polyonyx hoek* Osawa & Ng, 2016; C, female of the porcellanid crab *Polyonyx* sp.; D, female of the pinnotherid crab *Tetrias* sp.; E, nudibranch gastropod *Tenellia chaetopterana* Ekimova, Deart & Schepetov, 2017; F, polynoid polychaete *Hololepidella* sp.; unidentified poecilostomatoid copepod. H–K, *Chaetopterus* cf. *appendiculatus* and its symbionts: H, *Chaetopterus* cf. *appendiculatus* without tube; I, female of the porcellanid crab *Eulenaios cometes* (Walker, 1887); J, polynoid polychaete *Ophthalmonoe pettiboneae* Petersen & Britayev, 1997; K, carapid fish *Onuxodon fowleri* (Smith, 1964). Scale bars are 0.5 cm except for A and B (2.5 cm) and G (0.5 mm).

and carapid fish, but also small poecilostomatoid copepods (Fig. 5.3.6; Pearse 1913, Britayev 1993, Petersen and Britayev 1997, Britayev and Martin 2005, Britayev *et al*. 2017). When these complex symbiotic communities associated with species of *Chaetopterus* occur, it has been suggested that species richness, intensity, and dominance are determined by interspecific interactions, while intensity and abundance are driven by intraspecific interactions (Britayev *et al*. 2017).

In contrast, chaetopterids are poorly known as symbionts of other animals. Probably, the only known case refers to an unknown species of *Spiochaetopterus* that infest some colonies of *Montipora* spp. and induces more than 10-cm-long, finger-like, skeletal modifications in the coral (Bergsma 2009). These fingers were frequently found detached from the parent colony, which evidences that symbionts may reduce the ability of *Montipora* spp. to withstand physical disturbances. However, detached coral fingers are able to survive and reattach to form new colonies, which can help coral dispersal, thus enhancing the reproductive potential and competitive ability of *Montipora* spp.

## Phylogeny and taxonomy

### Phylogeny

The morphological and molecular support for the phylogenetic position of chaetopterids within the Annelida and Polychaeta remained unclear for a long time. An essential morphological aspect regarding their placement within the polychaetes is that their uncini resemble those of some Sabellida and Terebellida, while they have a pair of grooved palps, a character that has traditionally been the reason why the family has been usually placed within spioniform taxa. Therefore, both morphological characters only appear as indicative of their placement within Sedentaria.

As the position of Chaetopteridae in the polychaete tree strongly depends on the taxa included in the phylogenetic analysis, as well as on the character coding and weighting, they may be part of a basal polytomy (Rouse and Fauchald 1997, Rouse 1999, 2000). By considering larval characters together with those based on adults in Rouse and Fauchald (1997), Rouse (1999) placed the Chaetopteridae within the Sabellida (including Siboglinidae), with the Oweniidae as

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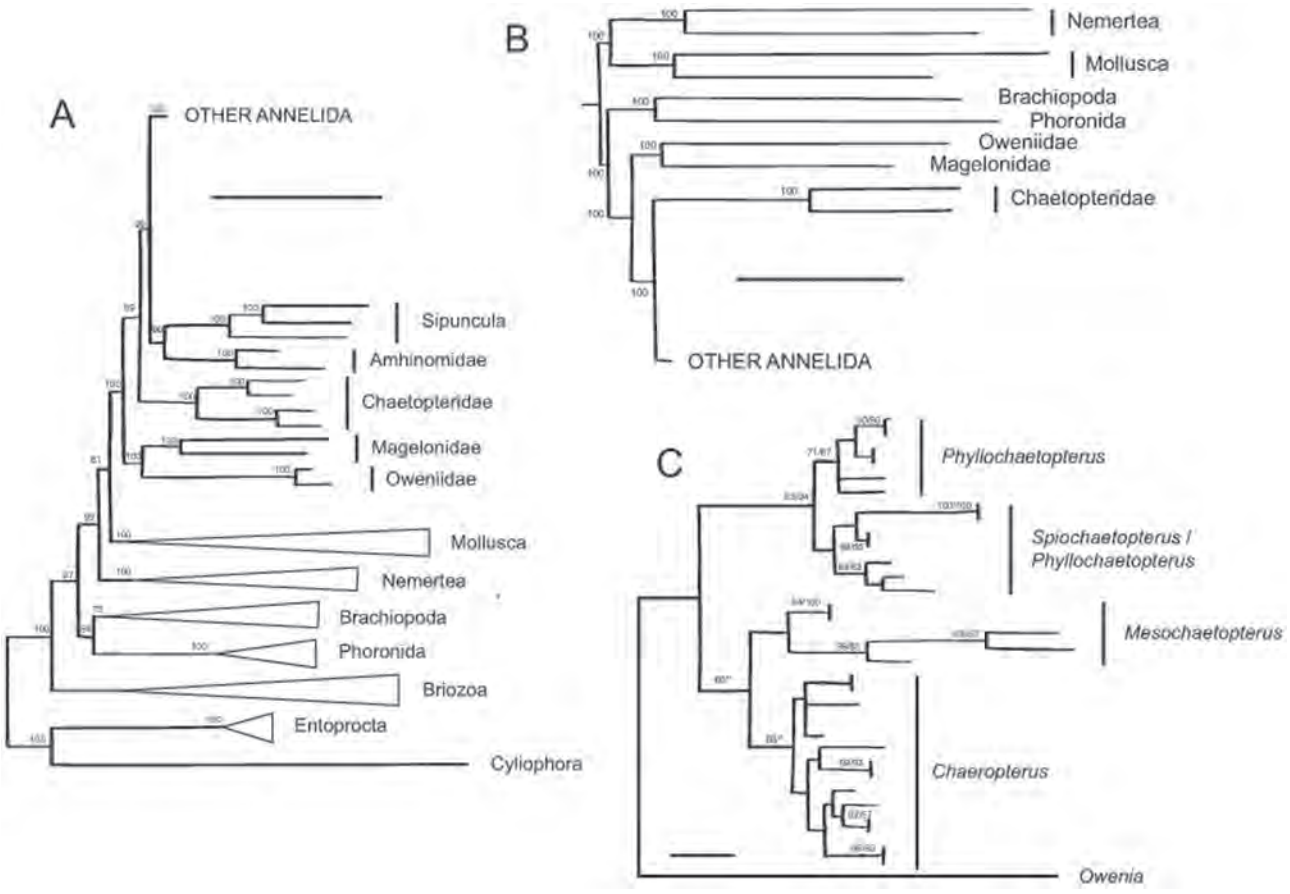


**Fig. 5.3.7:** Phylogenetic position of Chaetopteridae. A, Based on transcriptomics (Weigert *et al*. 2014). B, Based on phylogenomics (Andrade *et al*. 2015). C, Phylogenetic relationships between the four chaetopterid genera according to Zhang *et al*. (2015).

a sister group. Overall, this agrees with results reported by Brown *et al*. (1999) based on molecular analyses.

Struck (2011) considered the origin of the iterative organization of the parapodia as locomotive devices to be most likely the driving force in the evolution of segmentation, from which the direction of evolution in Annelida and Pleistoannelida (a taxon that includes both Sedentaria and Errantia) took several evolutionary trajectories. One of them led toward the tube-dwelling, filter-feeding chaetopterids. Accordingly, he refused its placement within Sedentaria suggested by Vinther *et al*. (2011). Later, Kvist and Siddall (2013) critically suggested that the different hypotheses proposed to date were neither consistent nor reasonably supported across optimality criteria, most likely due to the lack of data for some taxa. However, the most recent molecular approaches, based on a panoply of different methods, strongly support that chaetopterids are at the basis of the Annelida tree (Fig. 5.3.7 A, B) and form a branch separated from Pleistoannelida (Struck 2011, Struck *et al*. 2011, 2015, Kvist and Siddall 2013, Weigert *et al*. 2014, Andrade *et al*. 2015, Weigert and Bleidorn 2016).

Molecular phylogenetic reconstructions also consistently support the monophyly of Chaetopteridae, which contains *Mesochaetopterus*/*Chaetopterus* and *Phyllochaetopterus*/*Spiochaetopterus* as two well-supported clades (Fig. 5.3.7 C) (Osborn *et al*. 2007, Rousset *et al*. 2007, Martin *et al*. 2008, Morineaux *et al*. 2010, Zhang *et al*. 2015). The first two genera are certainly sister groups. The *Mesochaetopterus* clade often has low support, and depending on the analysis, some species may even fall into the *Chaetopterus* clade (Fig. 5.3.7 C). *Chaetopterus* and *Phyllochaetopterus* appear to be monophyletic, while the position of some species within *Spiochaetopterus* also suggests that this genus may be paraphyletic. It is also unclear whether *Mesochaetopterus* is monophyletic and whether the phylogenetic reconstructions would agree with the three groups defined on the basis of region B notopodia by Nishi (1999). As for the general position of chaetopterids in Annelida, the main problem preventing solving these questions is the lack of sequences for the different species within the family.

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**Taxonomy**

The family Chaetopteridae was defined by Audouin and Milne Edwards (1833), and *Chaetopterus* was the only known member of the family until Sars (1856) described *Spiochaetopterus*, based on a species from Norvegian waters. Grube (1863) instituted a third genus, *Phyllochaetopterus*, based on materials from the Adriatic Sea and it was not until 1914 that Potts described *Mesochaetopterus* from specimens collected in Puget Sound and the Gulf of Georgia (NE Pacific). According to him, *Mesochaetopterus* "partly bridges the gap between the remarkable form *Chaetopterus* and the other members of the family." The other genera hitherto included within the Chaetopteridae (e.g., *Ranzania*, *Ranzanides, Thelepsavus, Leptochaetopterus*, and *Sasekumaria*) are currently synonymized to one or another of the genera currently accepted as a valid (see further in the chapter). Therefore, as proposed by Bhaud (1970), the family currently includes four valid genera: *Chaetopterus, Mesochaetopterus*, *Pyllochaetopterus*, and *Spiochaetopterus*.

There are no fossil records known for the family and no specific reviews have been recently addressed to its taxonomy. However, the contributions to the local monographies by Blake (1996) for California (USA) and Wilson (2000) for Australia include extensive information on the family, while the study on Mexican sedentary polychaetes by Kudenov (1975) includes detailed diagnoses for the genera included within the family. Accordingly, most contemporary papers have been just addressed to describe new species.

The taxonomical history of *Chaetopterus* is among the most complex within the family, since Fauvel (1927, 1953) and later Hartman (1959) synonymized all nominal species with *Chaetopterus variopedatus* (Renier, 1804) based on the apparent absence of suggesting robust morphological distinctions. From an ecological point of view, the long-living planktonic, highly dispersive character of their larvae initially was considered to support the cosmopolitism of the species (Scheltema 1974). Later, Bhaud (1998b) stated that larval dispersal does not predict adult distribution. In agreement, based on morphological observations and considering only the North Atlantic and adjacent waters, Petersen (1984a,b, 1997) stated that *C. variopedatus* represents a species complex containing at least 10 species. Recent molecular studies also refute the cosmopolitan character of *C. variopedatus* (see Osborn *et al*. 2007, Martin *et al*. 2008), thus confirming the large number of morphologically defined new species with geographically limited distribution that have been recently described or redescribed. Among them are *Chaetopterus izuensis* Nishi, 2001, *Chaetopterus japonica* Nishi, 2001, *Chaetopterus pacificus* Nishi, 2001, *Chaetopterus cautus*, *Chaetopterus takahashii* Izuka, 1911, and *Chaetopterus longipes* Crossland, 1904 from Japan (Nishi 2001); *Chaetopterus pugaporcinus* from the Pacific coasts of USA; *Chaetopterus aduncus* Nishi, Hickman & Bailey-Brock, 2009, *Chaetopterus charlesdarwinii* Nishi, Hickman & Bailey-Brock, 2009, *Chaetopterus galapagensis* Nishi, Hickman & Bailey-Brock, 2009, *Chaetopterus longipes*, and *Chaetopterus macropus* Schmarda, 1861 from Galapagos (Nishi *et al*. 2009); and *Chaetopterus qiani* Sun and Qiu, 2014 from Hong Kong (Sun and Qiu 2014). All recent descriptions, as well as the rebuttal of *C. variopedatus* as cosmopolitan species, were based on species-specific morphological traits, including, among others, the tube shape, the A4 cutting chaetae (i.e., shape, color, and number), and the cirri from the lateral lobe of region C notopodia. Additionally, the habitat was found to be species specific, even at local scale. Some of these species were also confirmed by molecular analyses. Currently, there are 16 valid species within this genus.

The genus *Mesochaetopterus,* considered to be paraphyletic from a molecular point of view (Osborn *et al*. 2007, Martin *et al*. 2008, Morineaux *et al*. 2010), can also be clearly grouped according to the morphology of the notopodia of region B (i.e., slightly modified and triangular, conical, or extended and pointed) (Nishi 1999). However, the coincidence of this grouping with the phylogenetic reconstruction has not yet been proved. The genus is less controversial than *Chaetopterus*, and the morphologically robust characters allowing to describe new species precisely (particularly concerning the cutting chaetae of the fourth chaetiger and the notopodial uncini) have been well defined (Bhaud *et al*. 2006). Moreover, the discrepancies between larval dispersal and biogeographic distribution are clear for the species of this genus (Bhaud *et al*. 2002b, Bhaud 2005). Therefore, the number of newly described or redescribed species in the recent years is not so high. Among them, there are *M. rogeri* from the NW Mediterranean (Martin *et al*. 2008), *Mesochaetopterus ecuadorica* Nishi, Hickman & Bailey-Brock, 2009 from Galapagos (Nishi *et al*. 2009), *Mesochaetopterus formosana* Nishi and Hsieh, 2009 from Taiwan (Nishi and Hsieh 2009), and *Mesochaetopterus tingkokensis* Zang, Rouse & Qui, 2015 from Hong Kong (Zhang *et al*. 2015). Currently, *Mesochaetopterus* includes 16 valid species.

The species of the genus *Phyllochaetopterus* are easily distinguishable, thanks to characters such as the number and color of the cutting chaetae from chaetiger 4, the number of chaetigers of the B-region, and the morphology

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of the tube (see Nishi and Rouse 2014 for a detailed list of species and species-specific morphological characters). Despite this, the number of new species described recently is also reduced and includes *Phyllochaetopterus bhaudi* Jirkov, 2001 from the Arctic Ocean (Jirkov 2001), *Phyllochaetopterus awasensis* Nishi and Hsieh, 2009 from Okinawa (Nishi and Hsieh 2009), and three deep-sea species, *Phyllochaetopterus launensis* Nishi and Rouse, 2007, from around 1800 m deep nearby the Lau Basin hydrothermal vents at the Western Pacific (Nishi and Rouse 2007); *Phyllochaetopterus polus* Morineaux, Nishi, Ormos and Mouchel, 2010, from more than 4000 m deep at a vent field of the Mid Atlantic Ridge (Morineaux *et al*. 2010); and *Phyllochaetopterus gigas* Nishi and Rouse, 2014 from ca. 3000 m deep nearby a whale fall off California, USA (Nishi and Rouse 2014). This genus is the most diverse within the family, currently including 24 valid species.

The genus *Spiochaetopterus* has also been controversial in terms of agreement between larval dispersal and cosmopolitan adult distribution (Scheltema 1974), but the modern concept falls in favor of geographically restricted distributions (Bhaud 1998a,b, Bhaud and Fernandez-Alamo 2000). Adult specimens are easy to identify based on the number of segments in region B, tube ornamentation, relative size of prostomium and peristomium, morphology of A4 chaetae, location of the secretory part of the ventral plastron, and structure of the secretory pores. Some of these characters can also be used to distinguish among larvae (Bhaud 2003). More than half of the currently accepted species have been described recently based on these accurate definitions of the morphological characters. Among them are *Spiochaetopterus iheyaensis* Nishi, 2008, *Spiochaetopterus izuensis* Nishi, Bhaud & Koh, 2004, *Spiochaetopterus manazuruensis* Nishi, 2003, *Spiochaetopterus okinawaenis* Nishi & Bhaud, 2000, *Spiochaetopterus sagamiensis* Nishi, Miura & Bhaud, 1999, *Spiochaetopterus sanbanzensis* Nishi, Bhaud & Koh, 2004, and *Spiochaetopterus sesokoensis* Nishi & Bhaud, 2000 from Japan (Nishi *et al*. 1999, Nishi and Bhaud 2000, Nishi 2003, 2008, Nishi *et al*. 2004); *Spiochaetopterus creoceanae* Bhaud, Martin and Gil, 2003 from the Persian Gulf (Bhaud *et al*. 2003); *Spiochaetopterus koreana* Bhaud, Koh and Hong, 2002 from Korea (Bhaud *et al*. 2002a); and *Spiochaetopterus nonatoi* Bhaud and Petti, 2001 from Brazil (Bhaud and Petti 2001). *Spiochaetopterus* currently includes 17 valid species.

It must be pointed out that there is a clear bias in the number valid species of Chaetopteridae toward Japanese and adjacent waters (19 over 73), which gives proof to the relevancy of having Dr. Eijiroh Nishi as a local expert and suggests that similar efforts would likely contribute to increase the diversity of the family in other regions worldwide. This expert-related bias is even more marked if we consider that the proportion of species described by Dr. Nishi reaches 70% of those newly described during the last 15 years, and the percentage amounts to 100% by including the contributions of Dr. Michel Bhaud. The taxonomical efforts of both experts and their coauthors, as well as the additional contributions to the ecology and biology by Dr. Bhaud, must certainly be here recognized.

### Family Chaetopteridae Audouin & Milne Edwards, 1833

**Diagnosis:** Body elongate, fragile, divided into three distinct regions, A, B, and C (Figs. 5.3.1 A and 5.3.3 A, B). Prostomium small, rounded, or quadrangular. Peristomium limited to lips. Antennae absent (may be confused with notopodia from segment one in *Phyllochaetopterus*). One pair of long (except for *Chaetopterus*), grooved peristomial palps (Figs. 5.3.1 C and 5.3.3 A–D). Often with a pair of lateral eyes. Nuchal organs on sides of prostomium. Tentacular cirri absent. Body region A usually with fixed number of chaetigers (most often nine), parapodia with notopodia only (except last chaetiger in some species) and with whitish/brownish glandular ventral shield (plastron). Region B with fixed or variable number of chaetigers (from 2 to ca. 20), biramous parapodia with large achaetous flap-shaped notopodia and neuropodial tori. Region C with numerous chaetigers and biramous parapodia, with either both rami or notopodia only pointed, and neuropodial tori. Dorsal and ventral cirri absent. Gills absent. Epidermal papillae absent. Pygidial cirri absent. Lateral organs unknown. Gut straight, but often with distinct pouching in each segment; gut wall often dark green. Acicula often absent and, if present, nonprotruding from parapodia. Anterior chaetae lancet-shaped, oar-like, or sickle-like (Figs. 5.3.8 B, 5.3.9 B–D, 5.3.10 B, and 5.3.11 D), except for some large, cutting chaetae in chaetiger 4, knob or knife shaped (Figs. 5.3.8 C, 5.3.9 E, F, 5.3.10 C, and 5.3.11 B). Neuropodia with pectinate uncini.

### Genus *Chaetoperus* Cuvier, 1830

**Type species:** *Chaetopterus pergamentaceus* Cuvier, 1830.
**Synonymies:** *Tricoelia* Renier, 1804 (rejected name).
16 species
**Diagnosis:** Chaetopteridae with short peristomial palps, without "antennae" (Figs. 5.3.1 C and 5.3.8 A). Region A with 9–15 chaetigers, last one with neuropodia and pectinate uncini in some species; chaetae

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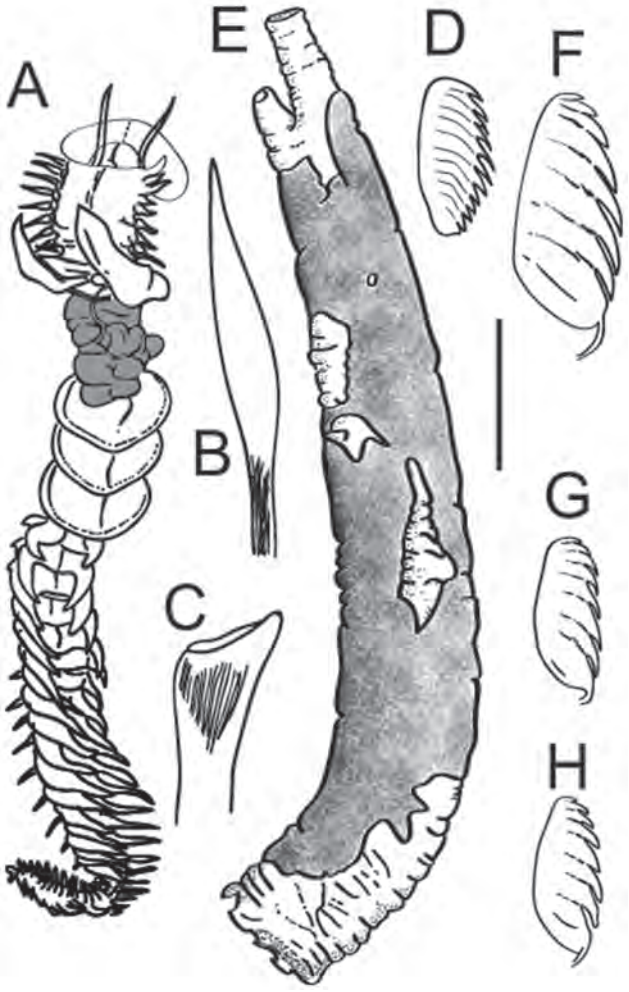


**Fig. 5.3.8:** A–E, *Chaetopterus cautus*, redrawn from Uschakov (1955). A, Whole body. B, Lanceolate simple chaetae from region A. C, Cutting chaetae. D, Uncini from region C. E, Tube fragment. F–H, *Chaetopterus galapagensis*, redrawn from Nishi *et al*. (2009). F, Uncini from last chaetiger of region A. G, Uncini from region B. H, Uncini from region C. Scale bars are 25 mm (A), 40 µm (B), 80 µm (C), 12 mm (E), and 30 µm (D, F–H).

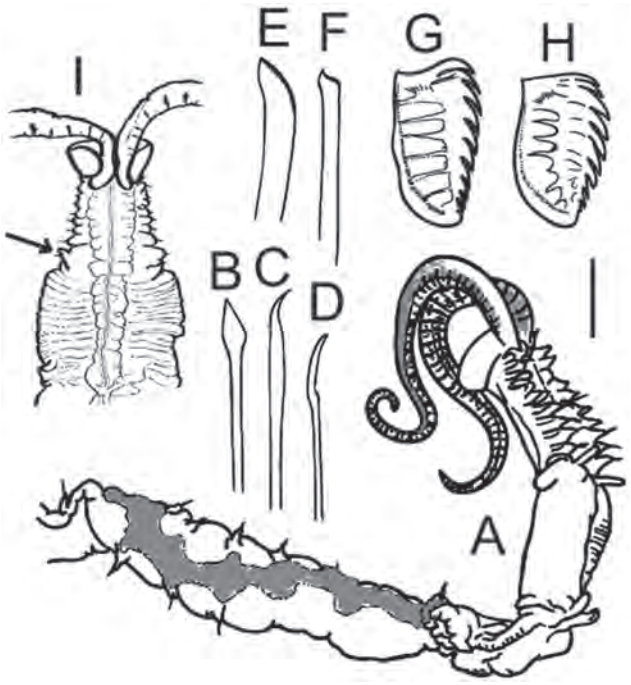


**Fig. 5.3.9:** *Mesochaetopterus rogeri*, redrawn from Martin *et al*. (2008). A, Anterior end of a preserved worm, showing regions A, B, and a few segments of region C. B, Oar-like simple chaeta from region A. C, Lanceolate simple chaeta from region A. D, Sickle-like simple chaeta from region A. E, Dorsal-most cutting chaeta. F, Ventral-most cutting chaeta. G, Uncinus from region B. H, Uncinus from region C. I, Anterior end of a preserved worm, showing a regenerated region A (starting of regenerating area marked with an arrow) and the first segment of region B in dorsal view. Scale bar is 20 mm (A), 375 µm (B, D-F), 250 µm (C), 50 µm (G, H), 2.5 cm (J).

lancet-shaped (Fig. 5.3.8 B) except at chaetiger 4, which has several long, straight-shafted cutting chaetae, distally truncate (Fig. 5.3.8 C). Region B with five chaetigers, some posterior ones fused to form dorsal fans; all notopodia achaetigerous, not bilobed; neuropodia with pectinate uncini, with less than 10 denticles in the serrated margin (Fig. 5.3.8 G). Region C with long, pointed achaetigerous notopodia, some with aciculae; neuropodia bilobed with pectinate uncini (Fig. 5.3.8 D, H). Tube parchment or paper like, nonannulated, irregularly U shaped or J shaped, with two or more tube openings, embedded inside sediment (Figs. 5.3.1 B, 5.3.4, and 5.3.8 E) or attached to hard substrates. Often bioluminescent.

### Genus *Mesochaetopterus* Potts, 1914

**Type species:** *Mesochaetopterus taylori* Potts, 1914.

**Synonyms:** *Ranzania* Claparède 1870 (junior homonym); *Ranzanides* Chamberlin, 1919 (subjective synonym); *Sasekumaria* (Rullier 1976).

16 species

**Diagnosis:** Chaetopteridae with long peristomial palps, without "antennae" (Figs. 5.3.2 and 5.3.9 A). Region A with 9 (8–12) chaetigers; chaetae of different kinds (lancet, oar, or sickle like) (Fig. 5.3.9 B–D), cutting chaetae at chaetiger 4 numerous, curved, distally inflated and truncate (Fig. 5.3.9 E, F). Region B with two to three segments, with achaetigerous, nonbilobed, nonfused notopodia; neuropodia with pectinate uncini, with less than 10 denticles in the serrated margin (Fig. 5.3.9 H). Region C with pointed notopodia with internal aciculae; neuropodia with pectinate uncini. Tube parchment-like inside, externally often coated with sand (Fig. 5.3.2 C), L shaped, J shaped, or straight, often ending blindly, sometimes with

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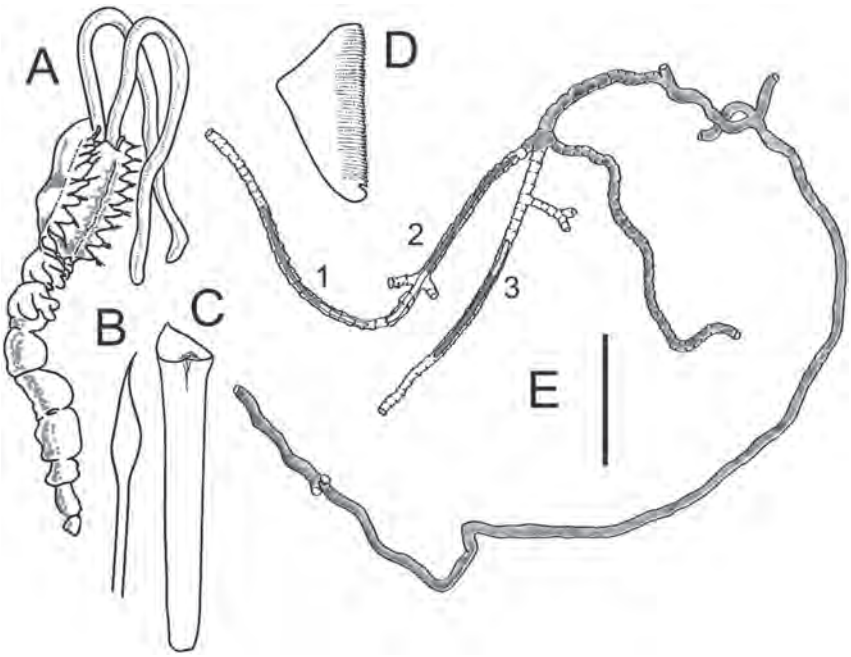


**Fig. 5.3.10:** *Phyllochaetopterus limicolus*, redrawn from Hartman and Barnard (1960). A, Whole body, showing regions A and B and some segments of region C. B, Lanceolate chaeta from anterior segments. C, Cutting chaeta. D, Uncinus from region B. E, Branched tube of *Phyllochaetopterus prolifica* with three worms (1–3) sharing the same tube, redrawn from Potts (1914). Scale bar is 20 mm (A), 13 µm (B), 1.4 µm (C), 3 cm (D).

perforations at the lower end, deeply embedded inside sediment. May be bioluminescent.

**Genus *Phyllochaetopterus* Grube, 1863**
**Type species:** *Phyllochaetopterus gracilis* Grube, 1863.
**Synonym:** *Phyllochaetoprerus* [auctt. misspelling].
24 species
**Diagnosis:** Chaetopteridae with elongated notopodia from segment 1, often referred to as "antennae" or "tentacular cirri"; palps long (Figs. 5.3.3 C and 5.3.10 A). Region A with 9–10 chaetigers and different kinds of chaetae (lancet, oar, sickle, or spoon like) (Fig. 5.3.10 B), cutting chaetae at chaetiger 4 not numerous (1–3 or 4–9), stout, cylindrical, with smooth or serrated cutting edge (Fig. 5.3.10 C). Region B with 2–24 chaetigers, foliaceous achaetigerous notopodia, bilobed, or trilobed (Fig. 5.3.3 E); neuropodia with pectinate uncini, often with more than 10 denticles in the serrated margin (Fig. 5.3.10 C). Region C with pointed notopodia supported by internal aciculae; neuropodia with pectinate uncini. Tube horny, translucent, annulated, sometimes branched (Fig. 5.3.10 D), with internal perforated partitions (i.e., septa), often partly embedded into sediment.

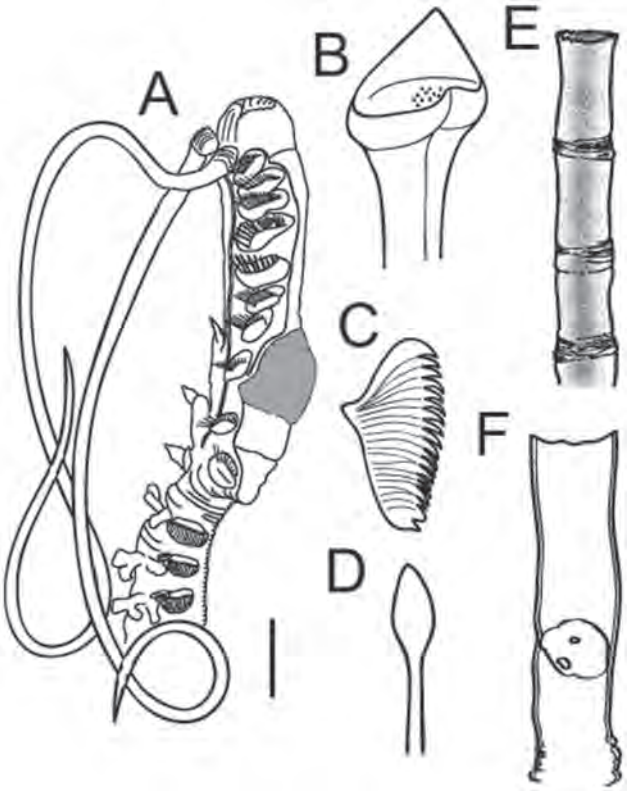


**Fig. 5.3.11:** *Spiochaetopterus creoceanae*, redrawn from Bhaud *et al*. (2003). A, Anterior end of a preserved worm, showing regions A, B, and a few segments of region C. B, Cutting chaetae. C, Uncini from region B. D, Lancet-like chaetae from region C. *Spiochaetopterus solitarius*, redrawn from Bhaud *et al*. (1994). E, Anterior end of a tube. F, Scheme of the internal part of the tube, showing the perforated septa. Scale bar is 1 mm (A), 75 µm (B), 8.5 µm (C), 15 µm (D), 574 µm (E, F).

**Genus *Spiochaetopterus* Sars, 1853**
**Type species:** *Spiochaetopterus typicus* M. Sars, 1856.
**Synonymies:** *Leptochaetopterus* Berkeley, 1927 (subjective synonym); *Telepsavus* Costa, 1861 (subjective synonym).
17 species
**Diagnosis:** Chaetopteridae with very long palps, without "antennae" (Fig. 5.3.11 A). Region A with 9–11 chaetigers, lanceolate chaetae (Fig. 5.3.11 D), except for a single stout

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club-shaped cutting chaetae at chaetiger 4, often roughly heart shaped in distal view; cutting edge finely serrated (Fig. 5.3.11 B). Region B with 2 to more than 20 segments; notopodia bi- or trilobed, foliaceous; neuropodia with pectinate uncini (Fig. 5.3.11 C). Region C with entire, pointed notopodia, supported by internal aciculae; neuropodia with pectinate uncini, with numerous (ca. 30) denticles in the serrated margin. Tube horny, translucent, annulated, or smooth, with distinct articulations, usually not branched, with internal perforated partitions (i.e., septa) (Fig. 5.3.11 E, F), sometimes with serrated upper margin.

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## References

Anctil, M. (1979): The epithelial luminescent system of *Chaetopterus variopedatus*. *Canadian Journal of Zoology* 57: 1290–1310.

Anderson, W.A. & Eckberg, W.R. (1983): A cytological analysis of fertilization in *Chaetopterus pergamentaceus*. *Biological Bulletin* 165: 110–118.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Audouin, J.V. & Milne Edwards, H. (1833): Classification des Annélides, et description de celles qui habitent les côtes de la France. *Annales des sciences naturelles* 30: 411–425.

Bailey-Brock, J.H. (1976) Habitats of tubicolous polychaetes from the Hawaiian Islands and Johnston Atoll. *Pacific Science*. *University of Hawai'i Press*, 30, 69–81.

Barnes, R.D. (1964): Tube-building and feeding in the chaetopterid polychaete, *Spiochaetopterus oculatus*. *Biological Bulletin* 127: 397–412.

Barnes, R.D. (1965): Tube-building and feeding in chaetopterid polychaetes. *Biological Bulletin* 129: 217–233.

Bergsma, G.S. (2009): Tube-dwelling coral symbionts induce significant morphological change in *Montipora*. *Symbiosis* 49: 143–150.

Berkeley, E. (1927): A new genus of Chaetopteridae from the northeast Pacific with some remarks on allied genera. *Proceedings of the Zoological Society of London* 1927: 441–445.

Bhaud, M. (1966): Etude du développement et de l'écologie de quelques larves de Chaetopteridae (Annélides Polychètes). *Vie et Milieu* 17: 531–571.

Bhaud, M. (1970): Note sur la systématique de la famille des Chaetopteridae (annélides polychètes). *Vie et Milieu* 21: 255–256.

Bhaud, M. (1975): Rapports entre époque de reproduction, biogéographie et répartition verticale. Un exemple particulier: *Spiochaetopterus costarum* (Annélide polychète). *Vie et Milieu* 25: 123–140.

Bhaud, M. (1978): Morphological variations of the modified setae of chaetopterids during ontogenesis. *Ophelia* 17: 199–206.

Bhaud, M. (1998a): The species of the genus *Spiochaetopterus* (Polychaeta, Chaetopteridae) in the Atlantic-Mediterranean biogeographic area. *Sarsia* 83: 243–263.

Bhaud, M. (1998b): The spreading potential of polychaete larvae does not predict adult distributions, consequences for conditions of recruitment. *Hydrobiologia* 375/376: 35–47.

Bhaud, M. (1998c): Variability in segment number and regeneration in *Spiochaetopterus solitarius*. Comparison with *S. costarum* (Polychaeta: Chaetopteridae). *Journal of the Marine Biological Association of the United Kingdom* 78: 1127–1141.

Bhaud, M. (2003): Identification of adults and larvae in *Spiochaetopterus* (Polychaeta, Chaetopteridae): consequences for larval transport and recruitment. *Hydrobiologia* 496: 279–287.

Bhaud, M. (2005): Evidence of a geographical variation in *Mesochaetopterus* (Polychaeta: Chaetopteridae) from the Pacific Ocean. *Journal of the Marine Biological Association of the United Kingdom* 85: 1409–1423.

Bhaud, M. & Cazaux, C. (1987): Description and identification of polychaete larvae; their implications in current biological problems. *Oceanis* 13: 596–753.

Bhaud, M. & Fernandez-Alamo, M.A. (2000): Planktonic larvae of *Spiochaetopterus* (Polychaeta, Chaetopteridae) in the Gulf of California: new evidence that the geographic distribution of species with a long planktonic larval life is relatively restricted. *Ophelia* 52: 65–76.

Bhaud, M., Koh, B.S. & Hong, J.S. (2002a): Contribution to the present status of *Spiochaetopterus costarum*: description of *Spiochaetopterus koreani*, a new species of Chaetopteridae (Polychaeta) from the West Coast of Korea. *Proceedings of the Biological Society of Washington* 115: 350–358.

Bhaud, M., Koh, B.S. & Martin, D. (2006): New systematic results based on chaetal hard structures in *Mesochaetopterus* (Polychaeta). In: Sardá, R., San Martín, G., López, E., Martin, D. & George, J. D. (eds.) *Recent Advances in Polychaete Research*. *Scientia Marina* 70: 35–44.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Bhaud, M., Lastra, M.C. & Petersen, M.E. (1994): Redescription of *Spiochaetopterus solitarius* (Rioja, 1917), with notes on tube structure and comments on the generic status (Polychaeta: Chaetopteridae). *Ophelia* 40: 115–133.

Bhaud, M., Martin, D. & Gil, J. (2003): *Spiochaetopterus creoceanae*, a new species of Chaetopteridae (Polychaeta) from the Persian Gulf belonging to the costarum-complex. *Scientia Marina* 67: 99–105.

Bhaud, M. & Petti, M. (2001): *Spiochaetopterus nonatoi*, a new species of Chaetopteridae (Polychaeta) from Brazil: biogeographical consequences. *Journal of the Marine Biological Association of the United Kingdom* 81: 225–234.

Bhaud, M., Ravara, A.A., Marcano, G. & Moreira, M.H. (2002b): *Mesochaetopterus sagittarius:* an example of a biogeography discrepancy between larval and adult boundaries: implication for recruitment studies. *Journal of the Marine Biological Association of the United Kingdom* 82: 565–572.

Blake, J.A. (1996): Family Chaetopteridae Malmgren, 1867. In: Blake, J.A., Hilbig, B. & Scott, P.H. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel.* Santa Barbara Museum of Natural History, Santa Barbara, CA: 233–251.

Britayev, T.A. (1993): *Pilargis berkeleyae* (Polychaeta, Pilargidae) as a commensal of a sedentary polychaete *Chaetopterus cautus* (Chaetopteridae). *Zoologicheski Zhurnal* 72: 147–151 [In Russian].

Britayev, T.A. & Martin, D. (2005): Scale-worms (Polychaeta, Polynoidae) associated with chaetopterid worms (Polychaeta, Chaetopteridae), with description of a new genus and species. *Journal of Natural History* 39: 4081–4099.

Britayev, T.A, Mekhova, E.S., Deart, Y.V. & Martin, D. (2017): Do syntopic host species harbour similar symbiotic communities? The case of *Chaetopterus* spp. (Annelida: Chaetopteridae). *PeerJ* 5: e2930; DOI: 10.7717/peerj.2930.

Britayev, T.A., Udalov, A.A. & Rzhavsky, A.V. (2010): Structure and long-term dynamic of the soft-bottom communities of the Barents Sea bays. *Uspehi Sovremennoj Biologii* 130: 60–52 [In Russian].

Brown, S.C. (1975): Biomechanics of water-pumping by *Chaetopterus variopedatus* Renier: skeletomusculature and kinematics. *Biological Bulletin* 148: 136–150.

Brown, S.C. (1977): Biomechanics of water-pumping by *Chaetopterus variopedatus* Renier: kinetics and hydrodynamics. *Biological Bulletin* 153: 121–132.

Brown, S.C. & McGee-Russell, S. (1971): *Chaetopterus* tubes: ultrastructural architecture. *Tissue and Cell* 3: 65–70.

Brown, S.C. & Rosen, J.S. (1978): Tube-cleaning behaviour in the polychaete annelid *Chaetopterus variopedatus* (Renier). *Animal Behaviour* 26: 160–166.

Brown, S., Rouse, G.W., Hutchings, P.A. & Colgan, D.J. (1999): Assessing the usefulness of histone H3, U2 snRNA and 28S rDNA in analyses of polychaete relationships. *Australian Journal of Zoology* 47: 499–516.

Busby, T.O. & Plante, C.J. (2007): Deposit feeding during tidal emersion by the suspension-feeding polychaete, *Mesochaetopterus taylori*. *Southeastern Naturalist* 6: 351–358.

Cazaux, C. (1965): Développement larvaire de *Chaetopterus variopedatus* (Renier). *Actes de la Société Linnéenne de Bordeaux* 102: 1–16.

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

Claparède, É. (1870): Les Annélides Chétopodes du Golfe de Naples. Seconde partie. Annélides sédentaires. *Mémoires de la Société de physique et d'histoire naturelle de Genève* 20: 1–225.

Costa, O.G. (1861): Di un nuovo genere di Anellidi dell'ordine dei tubicolarii e della fauni glia dei Chetopterini, scoperto nel mare di Napoli. *Ommagio al Re d'Italia Vittorio Emmanuele dell' Accademia Pontaniana* 1: 53–62.

Costello, D.P. & Henley, C. (1971): Annelida. pp. 59–99, *Methods for Obtaining and Handling Marine Eggs and Embryos*. Marine Biological Laboratory, Woods Hole, MA.

Cuvier, G. (1830): *Le règne animal distribué d'après son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée.* 2nd ed. 504 pp. Déterville et Crochard, Paris.

Deheyn, D, Enzor, LA, Dubowitz, A, Urbach, JS & Blair, D. (2013). Optical and physicochemical characterization of the luminous mucous secreted by the marine worm Chaetopterus sp. *Physiological and Biochemical Zoology* 86: 702–715.

Eckberg, W.R. (1981a): The effects of cytoskeleton inhibitors on cytoplasmic localization in *Chaetopterus pergamentaceus*. *Differentiation* 19: 55–58.

Eckberg, W.R. (1981b): An ultrastructural analysis of cytoplasmic localization in *Chaetopterus pergamentaceus*. *Biological Bulletin* 160: 228–239.

Eckberg, W.R. & Anderson, W.A. (1997): The initiation of development in *Chaetopterus*. pp. 109–123. In: Collier, J.R. (ed.) *Progress in Developmental Biology*. Wiley Interscience Publication, John Wiley & Sons, Chichester.

Eckberg, W.R. & Hill, S.D. (1996): *Chaetopterus* – oocyte maturation, early development, and regeneration. *Marine Models Electronic Records* 9: 1–8.

Eckberg, W.R., Johnson, M.R. & Palazzo, R.E. (1996): Regulation of maturation-promoting factor by protein kinase C in *Chaetopterus* oocytes. *Invertebrate Reproduction and Development* 30: 71–79.

Eckberg, W.R. & Kang, Y.-H. (1981): A cytological analysis of differentiation without cleavage in cytochalasin B- and colchicine-treated embryos of *Chaetopterus pergamentaceus*. *Differentiation* 19: 154–160.

Enders, H.E. (1908): Observations on the formation and enlargement of the tubes of the marine annelid, *Chaetopterus variopedatus*. *Proceedings of the Indian Academy of Science* 1907: 128–135.

Enders, H.E. (1909): A study of the life-history and habits of *Chaetopterus variopedatus*. *Journal of Morphology* 20: 479–531.

Fabri, M.C., Bargain, A., Briand, P., Gebruk, A., Fouquet, Y., Morineaux, M. & Desbruyeres, D. (2010): The hydrothermal vent community of a new deep-sea field, Ashadze-1, 12a field, Ashadze-1, 12ne annelid. *Journal of the Marine Biological Association of the United Kingdom* 91: 1–13.

Fauvel, P. (1927): Faune de France. Polychètes Sédentaires. *Faune de France* 16: 1–475.

Fauvel, P. (1953): *The Fauna of India, Including Pakistan, Ceylon, Burma and Malaya. Annelida, Polychaeta*. 507 pp. The Indian Press, Ltd., Allahabad.

Flood, P.R. & Médioni, A.F. (1982). Structure of the mucous feeding filter of *Chaetopterus variopedatus* (Polychaeta). *Marine Biology* 72: 27–33.

Fujiwara, T. (1935): On the light production and the luminous organs in a Japanese chaetopterid, *Mesochaetopterus japonicus*

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Fujiwara. *Journal of Science of the Hiroshima University* 3: 185–192.

Gaikwad, U.D. (1988): The planktonic larval stages of *Mesochaetopterus japonicus* (Polychaeta-Annelida). In: Palanichamy, S. (ed.) *Recent Advances in Invertebrate Reproduction and Aquaculture.* S. Palanichamy, Arulmigu Palaniandavar College of Arts & Culture. Palani, India: 274–279.

Gravier, C. (1904): Sur l'organe nuchal des Chétoptériens. *Compte Rendu de l'Association française pour l'avancement des Sciences* 33: 784–785.

Gravier, C. (1909a): Sur la régénération de la partie antérieure du corps chez le Chétoptère. *Comptes Rendus de l'Académie des Science* 148: 365–367.

Gravier, C. (1909b): Sur la régénération des extrémités du corps chez Chétoptère et chez le Marphyse sanquine. *Bulletin du Muséum d'Histoire Naturelle* 15: 14–17.

Grube, A.E. (1863): Beschreibung neuer order wening bekannter Anneliden. Sechster Beitrag. *Archiv für Naturgeschichte* 29: 37–69.

Harriott, V. J., &. Smith S.D.A (2000). Coral population dynamics in a subtropical coral community, Solitary Island, Marine Park, Australia. *Proceedings of the 9th International Coral Reef Symposium,* Bali, Indonesia: 23–27.

Hartman, O. (1959): Catalogue of the polychaetous Annelids of the World, Parts 1–2. *Allan Hancock Foundation Publications, Occasional Papers* 23: 1–628.

Hartman, O. & Barnard, J.L. (1960): The benthic fauna of the deep basins off southern California. Part II. *Allan Hancock Pacific Expeditions* 22: 69–284.

Irvine, S.Q., Chaga, O. & Martindale, M.Q. (1999): Larval ontogenetic stages of *Chaetopterus:* developmental heterochrony in the evolution of chaetopterid polychaetes. *Biological Bulletin* 197: 319–331.

Jirkov, I.A. (2001): *Polikhety severnogo Ledovitogo Okeana [Polychaeta of the Arctic Ocean]*. Yanus-K, Moskva.

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

Kennedy, G.Y. & Nicol, J.A.C. (1959): Pigments of *Chaetopterus variopedatus* (Polychaeta). *Proceedings of the Royal Society of London B: Biological Sciences* 150: 509–538.

Kudenov, J.D. (1975): Sedentary polychaetes from the Gulf of California, Mexico. *Journal of Natural History* 9: 205–231.

Kvist, S. & Siddall, M.E. (2013): Phylogenomics of Annelida revisited: a cladistic approach using genome-wide expressed sequence tag data mining and examining the effects of missing data. *Cladistics* 29(4): 435–448.

Loeb, J. (1901): Experiments on artificial parthenogenesis in annelids (*Chaetopterus*) and the nature of the process of fertilization. *American Journal of Physiology* 4: 423–459.

MacGinitie, G.E. (1939): The method of feeding of *Chaetopterus*. *Biological Bulletin* 77: 115–118.

Martin, D. & Britayev, T.A. (1998): Symbiotic polychaetes: review of known species. *Oceanography and Marine Biology: An Annual Review* 36: 217–340.

Martin, D., Gil, J., Carreras-Carbonell, J. & Bhaud, M. (2008): Description of a new species of *Mesochaetopterus* (Annelida, Polychaeta, Chaetopteridae), with re-description of Mesochaetopterus xerecus and an approach to the phylogeny of the family. *Zoological Journal of the Linnean Society* 152: 201–225.

Martin, N. & Anctil, M. (1984): Luminiscence control in the tube-worm *Chaetopterus variopedatus*: role of nerve cord and photogenic gland. *Biological Bulletin* 166: 583–593.

Mileikovsky, S.A. (1967): Larval development of *Spiochaetopterus typicus* M. Sars (Polychaeta, Chaetopteridae) from the Barents Sea and taxonomy of the family Chaetopteridae and the order Spiomorpha. *Doklady Akademii Nauk SSSR* 174: 403–405.

Morin, J.G. (1983): Coastal bioluminescence: patterns and functions. *Bulletin of Marine Science* 33: 787–817.

Morineaux, M., Nishi, E., Ormos, A. & Mouchel, O. (2010): A new species of *Phyllochaetopterus* (Annelida: Chaetopteridae) from deep-sea hydrothermal Ashadze-1 vent field, Mid-Atlantic Ridge: taxonomical description and partial COI DNA sequence. *Cahiers de Biologie Marine* 51: 239–248.

Nalesso, R.C., Duarte, L.F.L., Pierozzi, I., Jr. & Enumo, E.F. (1995): Tube epifauna of the polychaete *Phyllochaetopterus socialis* Claparède. *Estuarine, Coastal and Shelf Science* 41: 91–100.

Nicol, J.A.C. (1952a): Studies on *Chaetopterus variopedatus* (Renier) I. The light-producing glands. *Journal of the Marine Biological Association of the United Kingdom* 30: 417–430.

Nicol, J.A.C. (1952b): Studies on *Chaetopterus variopedatus* II. Nervous control of light production. *Journal of the Marine Biological Association of the United Kingdom* 30: 433–452.

Nicol, J.A.C. (1952c): Studies on *Chaetopterus variopedatus* (Renier) III. Factors affecting light response. *Journal of the Marine Biological Association of the United Kingdom* 31: 113–144.

Nicol, J.A.C. (1957): Spectral composition of the light of *Chaetopterus*. *Journal of the Marine Biological Association of the United Kingdom* 36: 629–642.

Nishi, E. (1996a): Asexual reproduction in the colonial polychaete *Spiochaetopterus costarum* (Claparède, 1868) (Annelida: Chaetopteridae) in Okinawa, Japan. *Natural History Research* 4: 37–40.

Nishi, E. (1996b): Dense aggregation of *Chaetopterus longipes* Crossland, 1904 (Chaetopteridae, Polychaeta) in coral reefs at Okinawa, Japan. *Natural History Research* 4: 41–47.

Nishi, E. (1999): Redescription of *Mesochaetopterus seanglosus* (Polychaeta: Chaetopteridae), based on type specimens and recently collected material from Morib Beach, Malaysia. *Pacific Science* 53: 24–36.

Nishi, E. (2001): Partial revision of Japanese *Chaetopterus* (Chaetopteridae, Polychaeta), including description of three new species from southern Pacific side of central Japan. *Actinia*. *Bulletin of Manazuru Marine Laboratory for Science Education* 14: 1–26.

Nishi, E. (2003): A new shallow-water species of *Spiochaetopterus* (Polychaeta: Chaetopteridae) from Sagami Bay, Japan. *Actinia*. *Bulletin of Manazuru Marine Laboratory for Science Education* 15: 1–6.

Nishi, E. (2008): A new species of *Spiochaetopterus* (Chaetopteridae: Polychaeta) from the Iheya Seamount off Okinawa in East China Sea, Japan. *Proceedings of the Biological Society of Washington* 121: 289–294.

Nishi, E. & Arai, Y. (1996): Chaetopterid polychaetehs from Okinawa Island, with notes on the feeding behaviour of *Spiochaetopterus costarum costarum*. *Publications of the Seto Marine Biological Laboratory* 37: 51–61.

Nishi, E., Arai, H. & Sasanuma, S.-i. (2000): A new species of *Chaetopterus* (Polychaeta: Chaetopteridae) from off Tokyo Bay, Central Japan, with comments on its Bioluminescence. *Actinia*.

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*Bulletin of Manazuru Marine Laboratory for Science Education* 13: 1–12.

Nishi, E. & Bhaud, M. (2000): Two new species of *Spiochaetopterus* (Polychaeta: Chaetopteridae) from Okinawa, Japan, with notes on Pacific Spiochaetopterus. *Pacific Science* 54: 15–26.

Nishi, E., Bhaud, M. & Koh, B.S. (2004): Two new species of *Spiochaetopterus* (Annelida: Polychaeta) from Sagami Bay and Tokyo Bay, Central Japan with a comparative table of species from Japanese and adjacent waters. *Zoological Science* 21: 457–464.

Nishi, E., Hickman Jr., C.P. & Bailey-Brock, J. (2009): *Chaetopterus* and *Mesochaetopterus* (Polychaeta: Chaetopteridae) from the Galapagos Islands, with descriptions of four new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 158: 239–259.

Nishi, E. & Hsieh, H.-L. (2009): Chaetopterid polychaetes from Taiwan and Okinawa Island (Japan), with descriptions of two new species. *Zoological Studies* 48: 370–379.

Nishi, E. & Kikuchi, T. (2008): A new species of *Phyllochaetopterus* (Chaetopteridae: Polychaeta) from the Iheya Seamount off Okinawa in East China Sea, Japan. *Proceedings of the Biological Society of Washington* 121: 289–294.

Nishi, E., Miura, T. & Bhaud, M. (1999): A new species of *Spiochaetopterus* (Chaetopteridae: Polychaeta) from a cold-seep site off Hatsushima in Sagami Bay, central Japan. *Proceedings of the Biological Society of Washington* 112: 210–215.

Nishi, E. & Rouse, G.W. (2007): A new species of *Phyllochaetopterus* (Chaetopteridae: Annelida) from near hydrothermal vents in the Lau Basin, western Pacific Ocean. *Zootaxa* 1621: 55–64.

Nishi, E. & Rouse, G.W. (2014): First whale fall chaetopterid; a gigantic new species of *Phyllochaetopterus* (Chaetopteridae: Annelida) from the deep sea off California. *Proceedings of the Biological Society of Washington* 126: 287–298.

Osborn, K.J., Rouse, G.W., Goffredi, S.K. & Robison, B.H. (2007): Description and relationships of *Chaetopterus pugaporcinus*, an unusual pelagic polychaete (Annelida, Chaetopteridae). *Biological Bulletin* 212: 40–54.

Pearse, A.S. (1913): On the habits of the crustaceans found in *Chaetopterus* tubes at Woods Hole, Massachusetts. *Biological Bulletin* 24: 102–114.

Petersen, J.A. & Fanta, E.S. (1969): On two new species of *Mesochaetopterus* (Polychaeta) from the Brazilian coast. *Beiträge zur Neotropischen Fauna* 6: 120–136.

Petersen, M.E. (1984a): *Chaetopterus variopedatus* (Annelida, Polychaeta): another victim of the "characteristic species" disease. *American Zoologist* 24: 62A.

Petersen, M.E. (1984b): *Chaetopterus variopedatus* (Renier) (Annelida: Polychaeta: Chaetopteridae): a species complex. What species are being used at MBL? *Biological Bulletin* 167: 513.

Petersen, M.E. (1997): Contribution to a revision of *Chaetopterus* Cuvier (Polychaeta: Chaetopteridae): redescription of C. appendiculatus Grube and *C. cautus* Marenzeller, with comments on some other species. *Bulletin of Marine Science* 60: 619–619.

Petersen, M.E. & Britayev, T.A. (1997): A new genus and species of polynoid scaleworm commensal with *Chaetopterus appendiculatus* Grube from the Banda Sea (Annelida: Polychaeta), with a review of commensals of Chaetopteridae. *Bulletin of Marine Science* 60: 261–276.

Pettibone, M.H. (1982): Annelida. Polychaeta. In: Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill Book Company, New York: 1–43.

Polk, P.M., Anderson, W.A. & Eckberg, W.R. (1987): The *Chaetopterus* vitelline envelope is not necessary for the gamete interactions that lead to fertilization. *Journal of Experimental Zoology* 243: 323–330.

Potts, F.A. (1914): Polychaetes from the NE Pacific: Chaetopteridae. With an account of the phenomenon of asexual reproduction in *Phyllochaetopterus* and the description of two new species of Chaetopteridae from the Atlantic. *Proceedings of the Zoological Society of London* 67: 955–994.

Probst, G. (1929): Das Blutgefaesssystem von *Chaetopterus variopedatus* Renier. *Pubblicazioni della Stazione Zoologica di Napoli* 9: 317–387.

Rouse, G.W. (1999): Trochophore concepts: ciliary bands and the evolution of larvae in spiralian Metazoa. *Biological Journal of the Linnean Society* 66: 411–464.

Rouse, G.W. (2000): Bias? What bias? The evolution of downstream larval-feeding in animals. *Zoologica Scripta* 29: 213–236.

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

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

Rullier, F. (1976): Description d'un nouveau genre et d'une nouvelle espèce de Chaetopteridae *Sasekumaria selangora* (Annélides Polychètes) de Malaisie. *Bulletin de la Société Zoologique de France* 101: 199–202.

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

Scheltema, A.H. (1974): Relationship of dispersal to geographical distribution and morphological variation in the polychete family Chaetopteridae. *Thalassia Jugoslavica* 10: 297–312.

Sendall, K.A., Fontaine, A.R. & O'Foighil, D. (1995): Tube morphology and activity patterns related to feeding and tube-building in the polychaete *Mesochaetopterus taylori* Potts. *Canadian Journal of Zoology* 73: 509–517.

Shah, D.U., Vollrath, F., Porter, D., Stires, J. & Deheyn, D.D. (2014): Housing tubes from the marine worm *Chaetopterus* sp.: biomaterials with exceptionally broad thermomechanical properties. *Journal of the Royal Society Interface* 11: 20140525.

Shimomura, O. & Johnson, F.C. (1968): *Chaetopterus* photoprotein: crystallization and cofactor requirements for bioluminescence. *Science* 159: 1239–1240.

Smith, S.D.A. & Harriott, V.J. (1998) Tube-building polychaete worms smother corals in the Solitary Islands Marine Park, northern NSW. *Coral Reefs* 17: 342.

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

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hosel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C., Halanych, K.M. (2015). The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

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Sumida, B.H. & Case, J.F. (1983): Food recognition by *Chaetopterus variopedatus* (Renier): synergy of mechanical and chemical stimulation. *Marine Behaviour and Physiology* 9: 249–274.

Sun, Y. & Qiu, J.W. (2014): A new species of *Chaetopterus* (Annelida, Chaetopteridae) from Hong Kong. *Memoirs of Museum Victoria* 71: 303–309.

Sveshnikov, V.A. (1978): The morphology of larval polychaetes. *Akademiya Nauk SSSR 1978*, 1–151.

Thompson, M.L. & Schaffner, L.C. (2001): Population biology and secondary production of the suspension feeding polychaete *Chaetopterus* cf. *variopedatus:* implications for benthic-pelagic coupling in lower Chesapeake Bay. *Limnology and Oceanography* 46: 1899–1907.

Turner, E.J. & Miller, D.C. (1991): Behavior of a passive suspension-feeder (*Spiochaetopterus oculatus* (Webster)) under oscillatory flow. *Journal of Experimental Marine Biology and Ecology* 149: 123–137.

Uschakov, P.V. (1955): Polychaetous annelids of the Far Eastern seas of the USSR [In Russian]. *Akademiya Nauk SSSR* 56: 1–433.

Vinther, J., Eibye-Jacobsen, D. & Harper, D.A.T. (2011): An Early Cambrian stem polychaete with pygidial cirri. *Biology Letters* 7: 929–932.

Weigert, A., Bleidorn, C. (2016) Current status of annelid phylogeny. *Organisms Diversity & Evolution*, Online First 1–18.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Wells, G.P. & Dales, R.P. (1951): Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller. *Journal of the Marine Biological Association of the United Kingdom* 29: 661–680.

Werner, B. (1953): Beobachtungen über den Nahrungserwerb und die Metamorphose der Metatrochophora von *Chaetopterus variopedatus* Renier und Claparède (Polychaeta Sedentaria). *Helgoländer wissenschaftliche Meeresuntersuchungen* 4: 225–238.

Wilson, E.B. (1883): Observations on the early developmental stages of some polychaetous annelides. *Studies from the biological Laboratory, John Hopkins University* 2: 271–299.

Wilson, R.S. (2000): Family Chaetopteridae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 191–193.

Zhang, Y., Rouse, G.W. & Qiu, J.-W. (2015): A new species of *Mesochaetopterus* (Annelida, Chaetopteridae) from Hong Kong, with comments on the phylogeny of the family. *Zootaxa* 3974: 495–506.

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# 6 Amphinomida/Sipuncula*

Anja Schulze, Michael J. Boyle and Gisele Y. Kawauchi

## 6.1 Sipuncula

### Introduction

Sipuncula display a unique combination of morphological, anatomical, and developmental traits. They are nonsegmented coelomates with a simple, sac-like trunk and a retractable introvert typically carrying an array of tentacles at its distal end (Fig. 6.1.1). While the monophyly of the Sipuncula is well established, their taxonomic rank is still debatable (see "Phylogeny and Taxonomy" section). Long considered a distinct phylum, the phylum status has recently been called into question by phylogenomic analyses which recognize Sipuncula as an early branch within the annelid radiation (e.g., Weigert *et al.* 2014, 2016). Two major monographs on Sipuncula have been published to date by Cutler (1994) and Stephen and Edmonds (1972). Whereas Stephen and Edmonds (1972) recognized 320 sipunculan species, Cutler (1994) synonymized many and reduced the number to roughly 150.

Several different Anglicized versions of the name Sipuncula have been in usage, including "sipunculoid" and "sipunculid," but we are following Stephen and Edmonds' (1972) compelling arguments for using the term *sipunculan*. Common names for sipunculans are "peanut worms" and, perhaps more appropriately, "star worms." Whereas the name peanut worms refers to the shape of some of these worms when the introvert is withdrawn into the trunk and the occasionally rough texture of the body wall, the name star worms is a literal translation from Japanese *hoshimushi* and refers to the tentacles radiating from the mouth in a star-like pattern (Ruppert *et al.* 2004, Nishikawa 2017).

Sipunculans have recently attracted increased attention in the scientific community as a key taxon to understanding the evolution of segmentation (or loss thereof) (Wanninger *et al.* 2005, Dordel *et al.* 2010) and a model taxon in the field of evolutionary developmental biology, or "evo-devo" (Schulze and Rice 2009, Boyle and Seaver 2010, Boyle and Rice 2014). They are also used as ecological indicator species (Bedini *et al.* 2004, Fonseca *et al.* 2006), as bait (Carvalho *et al.* 2013, Saito *et al.* 2014), as sources of food (Liu and Qiu 2016), and in pharmaceuticals (Fu *et al.* 2016).

### Morphology

#### External morphology

**Body regions.** The two-partite body of a sipunculan worm consists of a nonsegmented trunk and a retractable introvert. The tip of the introvert carries the mouth, a presumed chemosensory nuchal organ, and an array of tentacles. Recurving, proteinaceous hooks are often present along the introvert, particularly in the distal section (Fig. 6.1.2). These can either be scattered or arranged in rings. In many sipunculan taxa, the structural details and arrangement of the introvert hooks are used as taxonomic characters. Hooks may be simple or ornamented with secondary tips as is often the case in species of *Phascolosoma* Leuckart, 1828 and *Aspidosiphon* Diesing, 1851. The posterior transition between the hook and the epidermis often carries distinctive basal processes. When viewed under light microscopy, the internal structure of the hooks can also be diagnostic for identification purposes (Fig. 6.1.2). The sipunculan body is covered by an epithelium overlain by a cuticle. The body surface may be smooth or form papillae of various types and sizes, which tend to be most prominent at the anterior and posterior ends of the trunk. The anus is typically located near the anterior end of the trunk on the dorsal side. Two nephridiopores are usually present at a similar height as the anus, but on the ventral side, although not always easily detectable externally.

**Cuticle.** The cuticle covers the outer body surfaces and can form specialized structures such as hooks, spines, scales, and platelets. The cuticle is collagenous and chitin-free (Voss-Foucart *et al.* 1977). Cuticular platelets can reach high densities and merge together. This is particularly noticeable in the Aspidosiphonidae Baird, 1868, which are characterized by hardened shields anterior to the anus (anal shields) and often at the posterior end of the body (caudal shields). In most Aspidosiphonidae, the anal shield is located dorsally and causes the introvert to emerge from the trunk at angle toward the ventral side or forms a calcareous cone covered by a layer of horny material (Rice 1969, Hughes 1974). *Cloeosiphon* Grube, 1868 has a unique and conspicuous anal shield surrounding the base of the introvert and composed of polygonal calcareous plates (Rice 1969).

* **Note:** The authors of this chapter disagree with this classification based on recent phylogenomic analyses and regard it as very premature.

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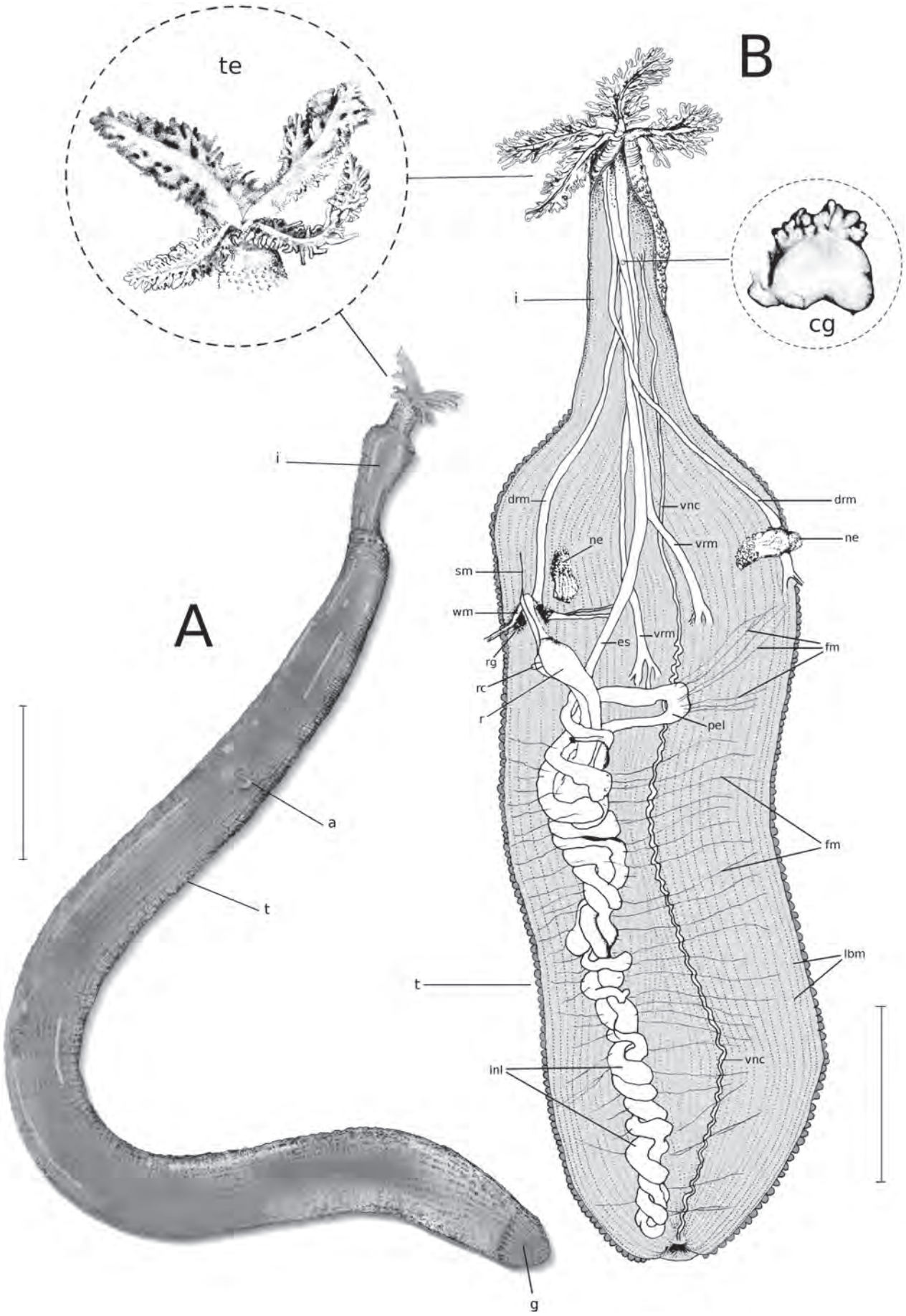


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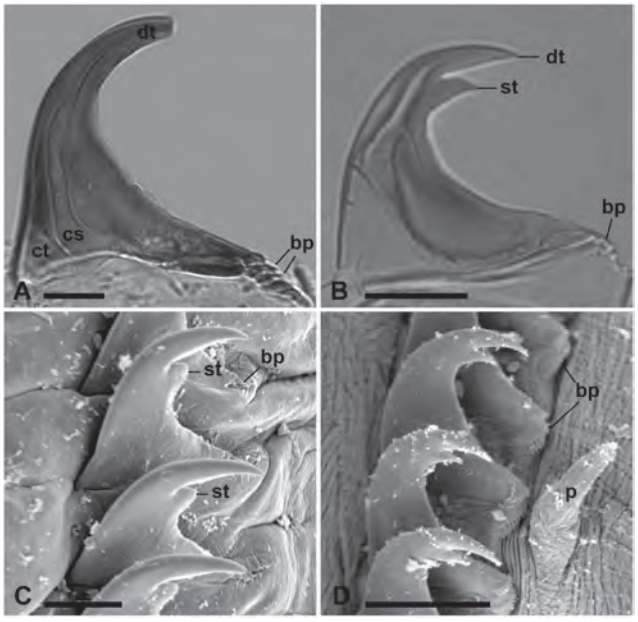


**Fig. 6.1.2:** Light (LM) and scanning electron (SEM) micrographs of sipunculan introvert hooks. LMs show diagnostic internal structures. A, *Phascolosoma agassizii*, LM (©A. Schulze). B, Compressed, bidentate hook of *Aspidosiphon steenstrupii*, LM (©A. Schulze). C, *Phascolosoma perlucens*, SEM (©A. Schulze). D, *Aspidosiphon fischeri*, SEM (©A. Schulze). bp, basal process; cs, clear streak; ct, clear triangle; dt, distal tip; st, secondary tooth; p, papilla. Scale bars: 20 µm.

### Anatomy

Anatomically, the most distinctive characteristics are the coiled intestine, the introvert retractor muscles, and the nephridia (Fig. 6.1.1).

**Epidermis and cuticle.** The epidermis consists of a single layer of cuboidal cells connected to each other by different types of intercellular junctions (Rice 1993). In postmetamorphic juveniles and adults, the only ciliated epidermal cells are present in the mouth region and on the tentacles. The cilia function to transport food particles into the digestive tract. Many different types of epidermal glands exist in sipunculans, ranging from unicellular to multicellular (Cutler 1994). Epidermal glands are often closely associated with sensory cells forming complex epidermal organs (Andreae 1882, Åkesson 1958, Müller *et al.* 2015). The cuticle is secreted by epidermal supportive cells and covers the outer body surfaces. It is made up of layers of parallel collagen fibers and is free of chitin (Voss-Foucart *et al.* 1977). Its structure corresponds to that of other large polychaetes.

The epidermis is separated from the underlying dermis by a basal lamina. The dermis is formed by connective tissue consisting of collagenous fibers embedding various cell types such as fibrous cells, pigment cells, and amoebocytes (Cutler 1994).

**Digestive system.** The simple digestive system consists of the mouth, the esophagus, the intestine, a short rectum, and the anus. The mouth region is heavily ciliated (Rice 1993), receiving food particles from the ciliated grooves of the tentacles. The esophagus runs posteriorly from the mouth to the junction between the introvert and trunk. Usually, no discernable stomach is present, although stomach regions have been reported in a few species (Andrews 1890, Cutler 1994). In the trunk, the descending branch of the intestine runs toward the posterior end, then transitions into an ascending branch leading toward the anus. The descending and ascending branches of the intestine wind around each other in a double helix. The degree of coiling can vary from species to species. Whereas the coil is tightly wound in most species, in some cases, the coiling is irregular or loose (Cutler 1994). The rectum is surrounded by a set of wing muscles. A small rectal caecum is present in many species. In *Siphonosoma vastum* (Selenka and Bülow, 1883) and sometimes in *Aspidosiphon laevis* Quatrefages, 1865, multiple rectal caeca are present near the anus. The intestinal coil is fastened to the posterior end of the trunk by a spindle muscle, which also holds the coil together. In the genus *Onchnesoma* Koren and Danielssen, 1875, as well as several *Phascolion* Théel, 1875 species, the anus has shifted anteriorly onto the introvert. This is particularly pronounced in *Onchnesoma steenstrupii* Koren and Danielssen, 1875, where the anus actually lies in close proximity to the mouth, near the tip of the long introvert. The esophagus, the descending branch of the intestine, and the rectum are usually characterized by longitudinal grooves (Rice 1983). The ascending branch of the intestine has a single, ciliated groove that opens into the rectal diverticulum or caecum (Rice 1993).

◂ **Fig. 6.1.1**: Sipunculan morphology, exemplified by *Sipunculus phalloides*. A, External morphology (©M. Anacleto). B, Internal anatomy (©G.Y. Kawauchi and M. Anacleto). a, anus; cg, cerebral ganglion; drm, dorsal retractor muscle; es, esophagus; fm, fixing muscle; g, glans; i, introvert; inl, intestinal loop; lbm, longitudinal muscle band; ne, nephridia; pel, post-esophageal loop; r, rectum; rc, rectum caecum; rg, racemose gland; sm, spindle muscle; t, trunk; te, tentacle; vnc, ventral nerve cord; vrm, ventral retractor muscle; wm, wing muscle (according to Ditadi 1982). Scale bars: 1 cm.

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**Musculature.** The introvert retractor muscles connect the tip of the introvert to the interior wall of the trunk. The number of introvert retractor muscles varies from one to four, with four being the most common and most likely ancestral condition (Schulze and Rice 2009). If four introvert retractors are present, they group into a dorsal and a ventral pair, with the ventral pair usually inserting onto the trunk wall posterior to the dorsal pair. The left and right muscle of each pair may be fused together to some degree, but separate insertion points are usually still present.

The body wall musculature consists of an outer layer of circular and an inner layer of longitudinal musculature, sometimes with oblique fibers between them. Both the longitudinal and circular muscles may form a smooth sheath or may be split into distinct, often anastomosing, bands. Other muscles, as mentioned earlier, include the wing muscles surrounding the rectum and anus and the spindle muscle fastening the intestinal coil to the posterior end of the trunk.

**Nervous system and sensory organs.** The main components of the central nervous system of Sipuncula are the dorsal brain (=cerebral ganglion), a pair of circumesophageal connectives, and a single, ventral nerve cord (Fig. 6.1.1 B). The brain is bilobed and is surrounded by a capsule of connective tissue (Gerould 1938, Åkesson 1958). It is located at the tip of the introvert, directly posterior to the tentacles, but is often withdrawn into a "cerebral pit" (Åkesson 1958). The circumesophageal connectives originate from the lateral margins of the cerebral ganglion. Another pair of nerves branches off from the anterior-lateral margin toward the nuchal organ (Åkesson 1958). At least two pairs of tentacular nerves originate from the circumesophageal connectives near their origin on the cerebral ganglion (Åkesson 1958). Several sensory structures are closely associated with the cerebral ganglion: the cerebral organ, the nuchal organ, and the ocular tubes. The cerebral organ lies at the anterior margin of the cerebral ganglion (Åkesson 1958, Purschke *et al.* 1997). It is nonciliated and contains sensory cells, but its function is unknown (Purschke *et al.* 1997). The nuchal organ is a ciliated patch dorsal to the cerebral organ, which often appears bilobed. Externally, the nuchal organ is surrounded by an incomplete circle of tentacles or it lies outside of the tentacular apparatus. It is richly innervated and consists of sensory cells, as well as ciliary and nonciliary supporting cells (Purschke *et al.* 1997). Sometimes, secretory cells have been reported as well (Åkesson 1958). The function of the nuchal organ is not fully understood but is presumed to be chemosensory (Rice 1993, Cutler 1994, Purschke *et al.* 1997) and may form a functional unit with the cerebral organ (Åkesson 1958, Purschke *et al.* 1997). The ocular tubes are epidermal invaginations, which extend into the brain. Pigment cells and photoreceptor cells are usually present in the deeper parts of the ocular tube (Åkesson 1958, Rice 1993). Åkesson (1958) describes different levels of complexity in sipunculan eyespots, ranging from simple invaginations to a more complex organization with a refractive body.

The single ventral nerve cord shows no evidence of segmental ganglia in juveniles and adults. It is more or less circular in cross-section and its length and shape can change slightly in different body regions (Åkesson 1958). In *Sipunculus nudus* Linnaeus, 1766, the terminal end of the nerve cord is thickened, and this region has been referred to as a "terminal ganglion" (Åkesson 1958). Generally, the nerve cord is not connected to the ventral body wall, although Åkesson (1958) reports that in the anterior introvert of *Phascolosoma* Leuckart, *Aspidosiphon* Diesing, 1828, and *Siphonosoma* Spengel, 1912, it is connected to the ventral body wall by a mesentery. In other species, only the lateral nerves emerging from the ventral nerve cord connect it to the body wall. The lateral nerves branch off without any regular or opposing pattern. The ventral nerve cord and the sections of the lateral nerves are covered by the epithelial lining of the coelomic cavity (Åkesson 1958).

**Body cavity and nephridia.** The coelomic spaces in sipunculans fulfill a variety of functions, including hydrostatic support, storage of gametes, excretion, gas exchange, and circulation. Separate circulatory and gas exchange organs are lacking. The large primary coelom fills most of the sipunculan body (Fig. 6.1.1). The smaller tentacular system supplies the tentacles and extends into one or two elongate, blind-ending tubes known as compensation sacs or contractile vessels, which extend along the esophagus. In some cases, the surface of the contractile vessel forms finger or hair-like extensions known as contractile vessel villi. In addition to the primary and tentacular coelom, members of the genera *Sipunculus* Linnaeus, 1766, *Xenosiphon* Fischer, 1947, and *Siphonomecus* Fisher, 1947 have coelomic canals running longitudinally through the dermis layer, apparently facilitating gas exchange over the body surface.

The primary body coelom contains several different types of coelomocytes (Rice 1993). Hemocytes, which carry the respiratory pigment hemerythrin, are the most abundant. Multicellular complexes known as "urns" are unique and distinctive in the coelom of sipunculans. They are ciliated structures that are either attached to

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the peritoneum or float freely in the coelomic fluid. Free urns are only known in *Sipunculus* Linnaeus, 1766 and *Phascolosoma* Leuckart, 1828. Urns appear to play a role in waste removal and immune response, as debris and bacteria have been observed to collect in their cilia and mucus (Matozzo *et al.* 2001). Apart from hemocytes and urns, various types of granular and agranular amoeboid cells of uncertain function may be present in the coelom (Rice 1993).

The nephridial system usually includes two elongate sacs located on the anterior ventral side of the trunk, each with its own nephridiopore and a ciliated nephrostome anterior to the nephridiopore. Members of the genera *Phascolion* Théel, 1875 and *Onchnesoma* Koren & Danielssen, 1876 only have a single nephridium. The anterior part of the nephridial sacs can be enlarged to form a bladder-like structure. The nephridial system accomplishes osmoregulation and excretion, and the sacs also temporarily store mature gametes before release. The peritoneal lining of the nephridial sacs includes podocytes, suggesting that ultrafiltration occurs from the primary coelomic cavity into the nephridial sac. The primary urine would then be modified by the epithelial cells that form the inner lining of the nephridial sac before release of the final urine through the nephridiopore.

## Reproduction and development

### Historical Perspective

Early development in Sipuncula exemplifies the quartet spiral cleavage program observed within several clades of the Spiralia (Lophotrochozoa). Multiple features of the spiralian developmental program are considered highly conserved (Freeman and Lundelius 1992, Henry and Martindale 1999), including a relatively stereotypic pattern of early cleavage symmetries seen in mollusks, nemerteans, polyclad turbellarian flatworms, and annelids, including polychaetes and oligochaetes and, more recently, siboglinids, echiurans, and sipunculans (Struck *et al.* 2011, Weigert *et al.* 2014). Early studies by Selenka (1875) and Hatschek (1883) revealed morphological characteristics of sipunculan development that were distinct from other spiralians, such as the metatroch, used exclusively for locomotion, a terminal organ, and formation of a pelagosphera larva, which is unique among all metazoan larval types. Gerould (1906) produced the most comprehensive study of development with embryos from two sipunculan species including maturation of the egg, external fertilization, cleavage and gastrulation, and larval morphogenesis. Subsequent workers began to characterize the details of gamete formation and morphology, spawning and fertilization, embryogenesis, life history patterns, and metamorphic transitions across a diversity of sipunculan species.

### Gametogenesis

**Reproductive organs and gametes.** Within Sipuncula, there is no evidence of sexual dimorphism and reproduction typically involves dioecious individuals, but there are four known exceptions. One species, *Nephasoma minutum* (Keferstein, 1862), is a protandrous hermaphrodite (Paul 1910, Gibbs 1975); *Themiste lageniformis* (Baird, 1868) can reproduce through facultative parthenogenesis (Pilger 1987); *Aspidosiphon elegans* (Chamisso and Eysenhardt, 1821) can reproduce asexually through budding (Rice 1970); and *Sipunculus robustus* Keferstein, 1865 can reproduce by transverse fission and lateral budding (Rajulu and Krishnan 1969). Male and female gonads are observed as small transient strips or transverse fringes of tissue within a peritoneum on the coelomic wall located posterior to the individual bases of ventral introvert retractor muscles (Paul 1910, Åkesson 1958, Rice 1974, Cutler 1994). Oogonia within ovaries vary in size, exhibiting a sequence of larger cells and more advanced stages of the first meiotic prophase when observed from proximal to distal along the length of the ovary (Gonse 1956a, Rice 1974). As new oogonia divide by mitosis within proximal regions of the gonad, oocytes may extend into the coelom (Gonse 1956b, Rice 1974). When oocytes are shed from the ovary into the coelom, they undergo maturation, growth, and morphological changes in shape that are characteristic for their particular species (Rice 1993). Across species, the extent and sizes of ovaries vary throughout the year relative to spawning season, as do the sizes and numbers of free-floating oocytes within the coelom, although there are typically some eggs within the coelom during the entire year with higher numbers of mature eggs present just prior to spawning (Gonse 1956b, Åkesson 1958, Rice 1966, 1974, 1989, Sawada *et al.* 1968, Gibbs 1975, Pilger 1987). Within Sipuncula, coelomic oocytes also vary in shape, from irregular to spherical or ovoid, and may or may not have follicle cells associated with the egg envelope during growth and maturation within the coelom.

As with oogenesis, spermatogonia differentiate into spermatocytes within the male gonad before release into the coelom. Rice (1974) noted that in at least three species, clumps of spermatocytes exit or "break off from the testis" into the coelom, followed by growth and maturation into spermatids with tails. Based on observations in *Phascolion cryptum* Hendrix, 1975, spermatocytes develop synchronously within the clumps or

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"clusters," with their anterior ends connected by intercellular bridges and their tails extending outward to form a morula (Rice 1974, Reunov and Rice 1993). When differentiated, this "primitive" type of spermatozoan of sipunculans consists of the head with a large spherical nucleus surmounted with a rounded or cap-like acrosome, a midpiece with four to five mitochondria, and the standard (9 + 2) arrangement of microtubules comprising the axoneme of an elongate flagellum, or tail (Franzén 1956, 1977, Gibbs 1975). In *Thysanocardia nigra* (Ikeda, 1904), *Themiste pyroides* (Chamberlain, 1920), and *Themiste alutacea* (Grube & Oersted, 1858), free sperm are released from the morula into the coelom when the spermatids have undergone differentiation and may be found within the coelom throughout the year. In *Phascolosoma agassizii* Keferstein, 1866, it is not known how or when differentiated sperm are released within the coelom (Rice 1974). However, sperm flagella are not always active in the coelom prior to entering the nephridia from which individual sperm are spawned into seawater and subsequently become motile (Baltzer 1931, Åkesson 1958, Rice 1974, 1983, Gibbs 1975).

**Fertilization mechanisms**

Sperm and eggs are released into seawater through broadcast spawning, which is facilitated by extension of the body and elevation of nephridiopores above sediments, crevices or burrows in rubble, the apertures of gastropod shells, and other substrates in which adult worms are found. Although the process of oocyte maturation begins within the coelom, breakdown of the germinal vesicle may not occur until egg cells have entered a nephridium, or until after they exit nephridiopores during spawning events (Gibbs 1975, Rice 1988, 1993). Nephridial uptake of mature oocytes is thought to be a selective process, with the ciliated nephrostome actively sorting large oocytes from immature oocytes and coelomocytes prior to storage and spawning. Mechanisms for the regulatory sorting of mature gametes have been proposed (Gerould 1906, Åkesson 1958, Rice 1975b), and the overall process, including unanswered questions of prespawning mechanisms, has been addressed (Rice 1974, 1989). When released, oocytes are typically in their first meiotic metaphase and maturation is completed in seawater following sperm penetration and the release of two polar bodies, with notable exceptions of hermaphroditism (Gibbs 1975) and parthenogenesis (Pilger 1987). Knowledge of species-specific spawning periods is critical when planning for studies of sipunculan development, as there is notable variation in both the period and the number of periods when mature eggs are available for spawning in the laboratory.

The mature multilayered egg envelope typical of most sipunculan species consists of three discernible layers (outer, middle, and inner) when imaged with a transmission electron microscope (Sawada *et al.* 1968, Rice 1993). Microvilli extend from cortical cytoplasm to the surface of the egg within pore canals, passing through all three layers of the envelope (Sawada *et al.* 1968, Rice 1975b). Cytochemical analyses of the egg envelope indicate that the inner layer contains mucoprotein, the middle layer is primarily protein, and the outer layer is an acid mucopolysacharide (Gonse 1956b, Rice 1974, 1975b). Sipunculan egg envelopes vary in thickness from 2 μm in *Golfingia margaritacea* (Sars, 1851) to 10 μm in *Phascolosoma agassizii* (see Sawada *et al.* 1968, Rice 1974). The variation in thickness of these envelopes reflects both the composition and geometry of egg shapes that range from spherical to lens shaped or ovoid across the clade (Fig. 6.1.3). For review and appreciation of the diversity of egg size, shape, and dimension, see Rice (1989, Table 1). During fertilization, species-specific sperm initially attach to the outer egg envelope by an acrosomal filament and then digest a canal through the envelope, leaving an entry hole that is visible for several days following a fertilization event. For eggs that have a jelly coat surrounding the envelope, the acrosomal filaments of sperm can be extensive, with some measuring up to 50 μm in length in order to reach the envelope surface (Rice 1966, 1975b). Chemical analyses of gamete recognition proteins or envelope digestion by acrosomal proteins and associated enzymes have not been performed for any sipunculan species. Once inside, the male pronucleus increases in size and migrates toward the center of the egg. The female pronucleus is located toward the animal pole in spawned eggs. Meiotic divisions reduce the diploid number of chromosomes in the egg from 20 to 10 and generate two or three haploid polar bodies (Fig. 6.1.3 B, C, F) that are extruded outside the egg envelope at the animal pole to complete the process of egg maturation (Gerould 1906, Rice 1975b, 1988, 1989). Following meiosis and polar body release, male and female pronuclei fuse in the region between the center of the egg and the animal pole to form the zygotic nucleus, followed by the formation of the cleavage asters, mitosis, and cytokinesis of the zygote.

**Development.** In all sipunculan species observed, division of the zygote exhibits an unequal, holoblastic, spiral cleavage program of early development (Selenka 1875, Gerould 1906, Åkesson 1958, 1961, Rice 1967, 1975a, Boyle and Seaver 2010). The alternating orientation of cleavage divisions and resulting topology of embryonic blastomeres around the egg axis during embryogenesis

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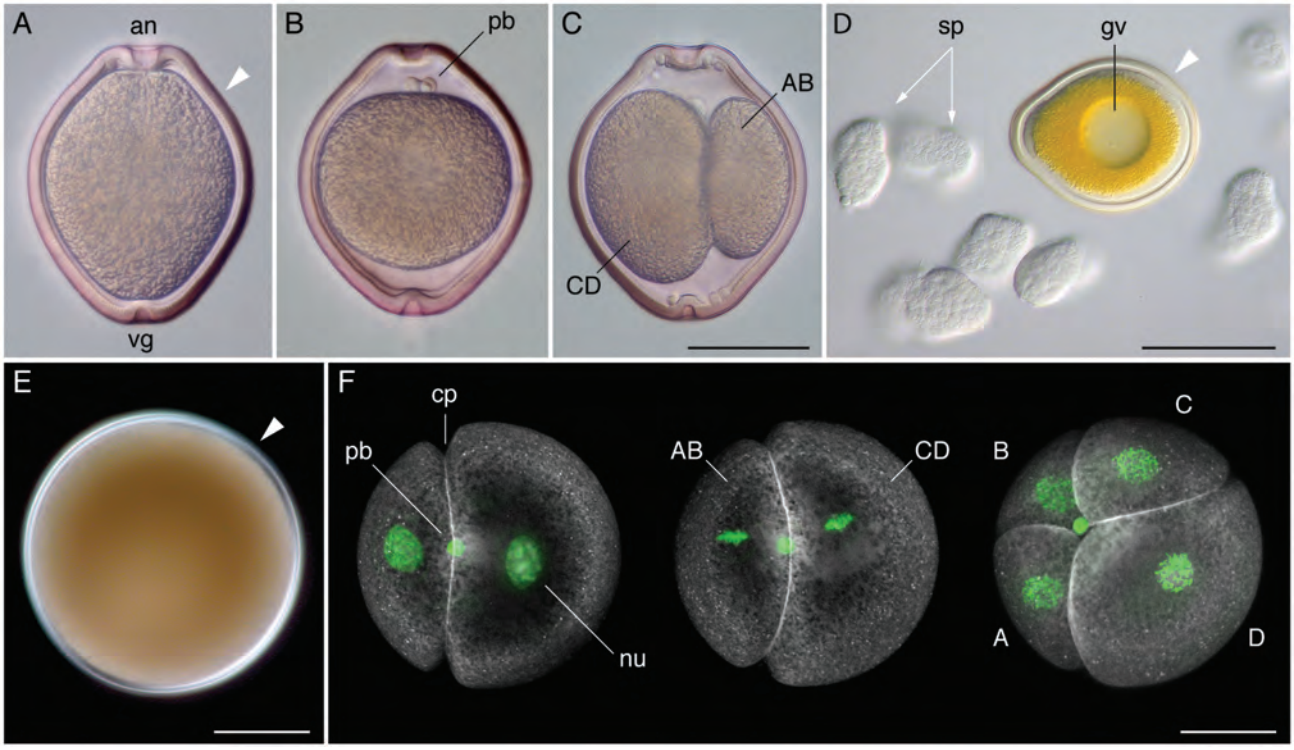


**Fig. 6.1.3:** Egg morphology and cleavage symmetry in early stages of sipunculan development. A–C, *Phascolosoma perlucens*. A, Ovoid oocyte with a thick egg envelope (arrowhead) and distinct animal and vegetal pole morphologies (©M.J. Boyle). B, Fertilized egg internally rounded up with three polar bodies extruded at the animal pole (©M.J. Boyle). C, First mitotic division showing unequal spiral cleavage into CD and AB blastomeres. Note the asymmetry and relative size differences of the blastomeres (©M.J. Boyle). D, *Phascolosoma* sp. Ovoid coelomic oocyte with large germinal vesicle. Clusters of coelomic spermatocytes were added to oocytes on a microscope slide (©M.J. Boyle). E, F, *Themiste lageniformis*. E, Spherical oocyte with egg envelope (arrowhead) (©M.J. Boyle). F, Confocal laser scanning micrographs of first and second mitotic divisions. Green, DNA; grayscale, cytoskeleton; egg envelope is not visible in these micrographs. From left to right: first mitotic division with unequal cleavage; nuclear position shift of metaphase chromosomes prior to second cleavage of AB and CD blastomeres; animal pole view of second mitotic division with unequal cleavage most notable between the C and D blastomeres (©M.J. Boyle). Abbreviations: an, animal pole; cp, cleavage plane; gv, germinal vesicle; nu, nucleus; pb, polar body; sp, spermatocytes; vg, vegetal pole. All scale bars = 50 µm.

resemble the quartet pattern observed in polyclad turbellarians, most mollusks, and the annelids (including echiurans) (Costello and Henley 1976). As with these other taxa, quartet spiral cleavage in sipunculans is most obvious during the third round of cleavage divisions, when each of four macromeres divides to produce one of four animal blastomeres, collectively referred to as the first quartet of micromeres. However, unlike annelids and mollusks, each of which exhibits both equal and unequal blastomere divisions within their clades, and the nemerteans and echiurans with predominantly equal cleavage, embryogenesis in Sipuncula (Fig. 6.1.3 C, F) proceeds exclusively through a series of unequal cleavage divisions (Boyle and Rice 2014). Another distinct feature of early sipunculan development includes the production of a first quartet of micromeres that are equal to or larger in size than their respective parent macromeres in the A, B, and C quadrants of the eight-cell embryo, which is not seen in the D-quadrant (Rice 1985b). This condition is found in nemerteans, although only in a few polychaete species, and is not observed in mollusks or polyclads (Boyer *et al*. 1998, Henry and Martindale 1999, Boyle and Rice 2014). In Sipuncula, these larger first quartet micromeres contain relatively large volumes of yolk granules that will subsequently provide nutritional resources to developing larvae or juvenile worms (Gerould 1906). Daughters of the first quartet (1a–1d) will give rise to the large "girdle" of prototroch cells (Fig. 6.1.4 C–E) in sipunculan trochophore larvae (Åkesson 1958, Rice 1975a, 1988). In indirect developers, the blastula is ciliated and motile within the water column and may include an apical tuft of cilia (Fig. 6.1.2 C). Gastrulation is typically achieved by epiboly of animal micromeres and, in some species, also by the invagination of vegetal macromeres and micromeres that generate endodermal and mesodermal precursor cells, respectively. In

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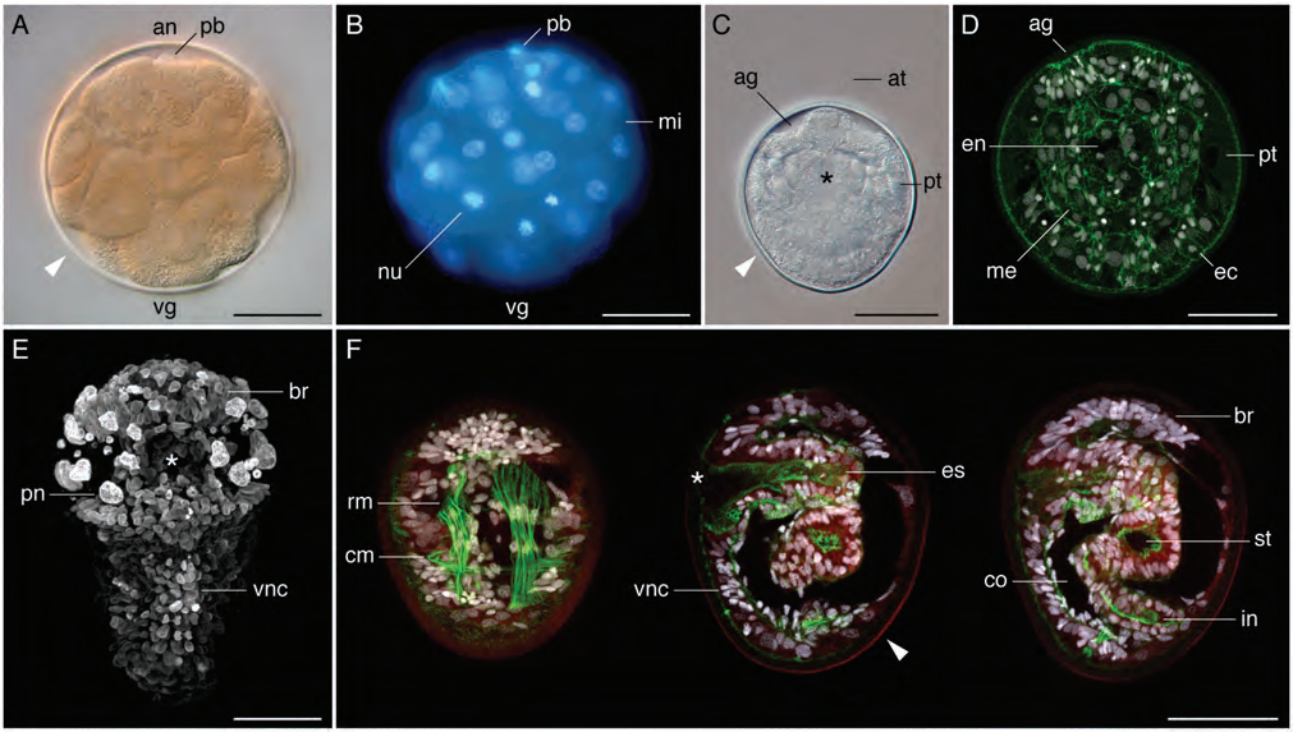


**Fig. 6.1.4:** Common characters of development in lecithotrophic and planktotrophic sipunculans. A, B, *Themiste lageniformis*. A, Gastrula stage embryo with an egg envelope (arrowhead) surrounding blastomeres with high yolk content, a polar body, and macromeres extended at the vegetal pole (©M.J. Boyle). B, Same embryo as in A showing DNA in cell nuclei (nu), including large pre-trochal micromeres in the episphere (©M.J. Boyle). C, *Nephasoma pellucidum*. Trochophore larva with apical tuft passing through the egg envelope (arrowhead) and apical grooves at the anterior end, with large prototrochal micromeres and stomodeum (asterisk). D, *Phascolion cryptum* (©M.J. Boyle); confocal laser scanning micrograph (CLSM); grayscale, DNA; green, cytoskeleton. The view is through a central z-stack region of the embryo showing germ layers, apical grooves, and large prototrochal micromeres (nonciliated) in direct development (©M.J. Boyle). E, *Themiste lageniformis*. CLSM of hatching cone-shaped stage with conspicuously large prototrochal nuclei (pn) surrounding the stomodeum. Posterior end shows a developing ventral nerve cord (©M.J. Boyle). F, *Nephasoma pellucidum*. CLSM; grayscale, DNA; green, F-actin; red, acetylated tubulin-like immunoreactivity. All views are lateral with anterior to the top and ventral to the left. Series of three z-stacks moving deeper through the embryo from left to right, showing circular and retractor muscles, ventral nerve cord, brain, coelom, stomach, and intestine, all within the egg envelope (arrowhead), which stretches during metamorphosis of the trochophore larva (see trochophore in C) (©M.J. Boyle). ag, apical groove; an, animal; at, apical tuft; br, brain; cm, circular muscle; co, coelom; ec, ectoderm; en, endoderm; es, esophagus; in, intestine; me, mesoderm; mi, micromere; nu, nucleus; pb, polar body; pn, prototrochal nucleus; pt, prototroch cell; rm, retractor muscle; st, stomach; vg, vegetal; vnc, ventral nerve cord. An asterisk marks the position of the stomodeum. All scale bars = 50 µm

*Phascolosoma* species that have been studied, invagination produces a narrow archenteron within their embryos, as also found in *Sipunculus nudus* (Hatschek 1883, Rice 1988). On the anterior end of all sipunculan embryos, there is an apical plate of ectoderm from which marginal cells ingress internally to form an apical groove around the anterior-most plate of cells (Fig. 6.1.4 C, D). The ingressing cells are a source of ectomesoderm that gives rise to the two sets of ventral and dorsal introvert retractor muscles characteristic of all sipunculan juvenile worms (Gerould 1906). These cells are thought to also derive from first quartet micromeres and likely represent a source of ectomesoderm unique to sipunculans and that has not been designated as ectomesoderm in cell-lineage or cell-fate map studies of mollusks, polychaete annelids, nemerteans, or polyclads (Boyer *et al.* 1998, Maslakova *et al.* 2004, Hejnol *et al.* 2007, Meyer and Seaver 2010). Mesodermal bands appear to derive from endomesoderm precursor cells of the D-quadrant, and the macromere lineages of the A–D quadrants contribute to the intestine, both of which are typical developmental patterns observed throughout most spiralian groups (Gerould 1906). Notably, a second source of ectomesoderm contributes to circular muscles (Gerould 1906). This second ectomesoderm is posterior to the level of oral ectoderm and is on midlateral sides of developing trochophores. Considerable cell proliferation is observed in this region, and it is thought to act as a main center for longitudinal growth, and thus, there is no prominent region of terminal growth in Sipuncula

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that is analogous to the posterior growth zone (PGZ) facilitating prepygidial segment formation among polychaete annelids (Åkesson 1958, Wanninger *et al.* 2005, Boyle and Rice 2014). For a more comprehensive treatment of early sipunculan development, the following resources should be reviewed: Åkesson (1958, 1961), Boyle and Rice (2014), Boyle and Seaver (2010), Rice (1967, 1973, 1975a,b, 1989).

**Larval forms and metamorphosis.** Within Sipuncula, development proceeds through four recognized life history pattern categories: (I) direct development from a fertilized egg to a crawling juvenile worm; (II) indirect development with a trochophore larva; (III) indirect development with a trochophore larva, followed by a lecithotrophic pelagosphera larva; and (IV) indirect development with a trochophore larva followed by a planktotrophic pelagosphera larva (Table 1 life histories). All sipunculan trochophores are lecithotrophic (nonfeeding). These life history patterns are distinct from one another in their species-specific developmental and ecological characteristics (Table 2). With the exception of category II, trochophore larvae undergo a metamorphosis to the pelagosphera, which then undergoes a second metamorphosis

**Tab. 6.1:** Developmental life history patterns in the Sipuncula

DIRECT DEVELOPMENT *lecithotrophic*
(I) Egg ⟶ Worm

INDIRECT DEVELOPMENT *lecithotrophic*
(II) Egg ⟶ Trochophore ⟶ Worm
(III) Egg ⟶ Trochophore ⟶ Pelagosphera ⟶ Worm

INDIRECT DEVELOPMENT *lecithotrophic/planktotrophic*
(IV) Egg ⟶ Trochophore *lecitho.* ⟶ Pelagosphera *plankto.* ⟶ Worm

Table 1 is from Boyle and Rice (in press), Courtesy Smithsonian Institution.

**Tab. 6.2:** Developmental characteristics of species-specific life history patterns in the Sipuncula

| | **Direct development (I)** *Phascolion cryptum* | **Indirect lecithotrophy (III)** *Themiste alutacea* | **Indirect planktotrophy (IV)** *Nephasoma pellucidum* |
|---|---|---|---|
| **Egg size (dia)** | 136 μm[1] | 138 μm[1] | 105 μm[2] |
| **8-cell blastomeres (A,B,C quadrants)** | micromeres > macromeres[1] | micromeres > macromeres | micromeres = macromeres[3] |
| **Yolk reserves** | high, cellular and coelomic | high, cellular and coelomic | moderate, primarily cellular |
| **Prototroch cells** | large, non-ciliated | large, ciliated | small, ciliated |
| **Trochophore larva** | no trochophore | present, ~20 hpf | present, ~48 hpf[3] |
| **Apical tuft** | absent | present | present |
| **Circular muscles ~30 hpf** | distinct circular muscle bands | non-distinct circular muscle bands | circular muscle bands not detected |
| **Retractor muscles ~30 hpf** | distinct ventral and dorsal fibers | diffuse ventral and dorsal fibers | retractor muscles not detected |
| **Pelagosphera larva with metatroch** | no pelagosphera, crawling worm | lecithotrophic, ~30 hpf[1] crawling-swimming larva | planktotrophic, ~72 hpf[1] swimming larva |
| **Terminal organ** | absent | absent[1] | present[3] |
| **Circular muscles ~3.0 dpf** | thick bands of A-P | thick bands of A-P | thin bands at anterior |
| **Retractor muscles ~3.0 dpf** | extend length of A-P | extend length of A-P | extend 2/3 of A-P additonal musculature |
| **Functional gut** | one week[1] | two weeks[1] | 3 days[3] |
| **Juvenile worm** | one week[1] | four weeks[1] | ~ six weeks[3] |

1. Rice 1975a; 2. Rice 1975b; 3. Schulze and Rice 2009. Referenced and non-referenced characteristics are from laboratory observations. Abbreviations: dia, diameter; hpf, hours post fertilization; dpf, days post fertilization; A-P, anterior-posterior axis.

Table 2 is from Boyle and Rice (in press), Courtesy Smithsonian Intstitution.

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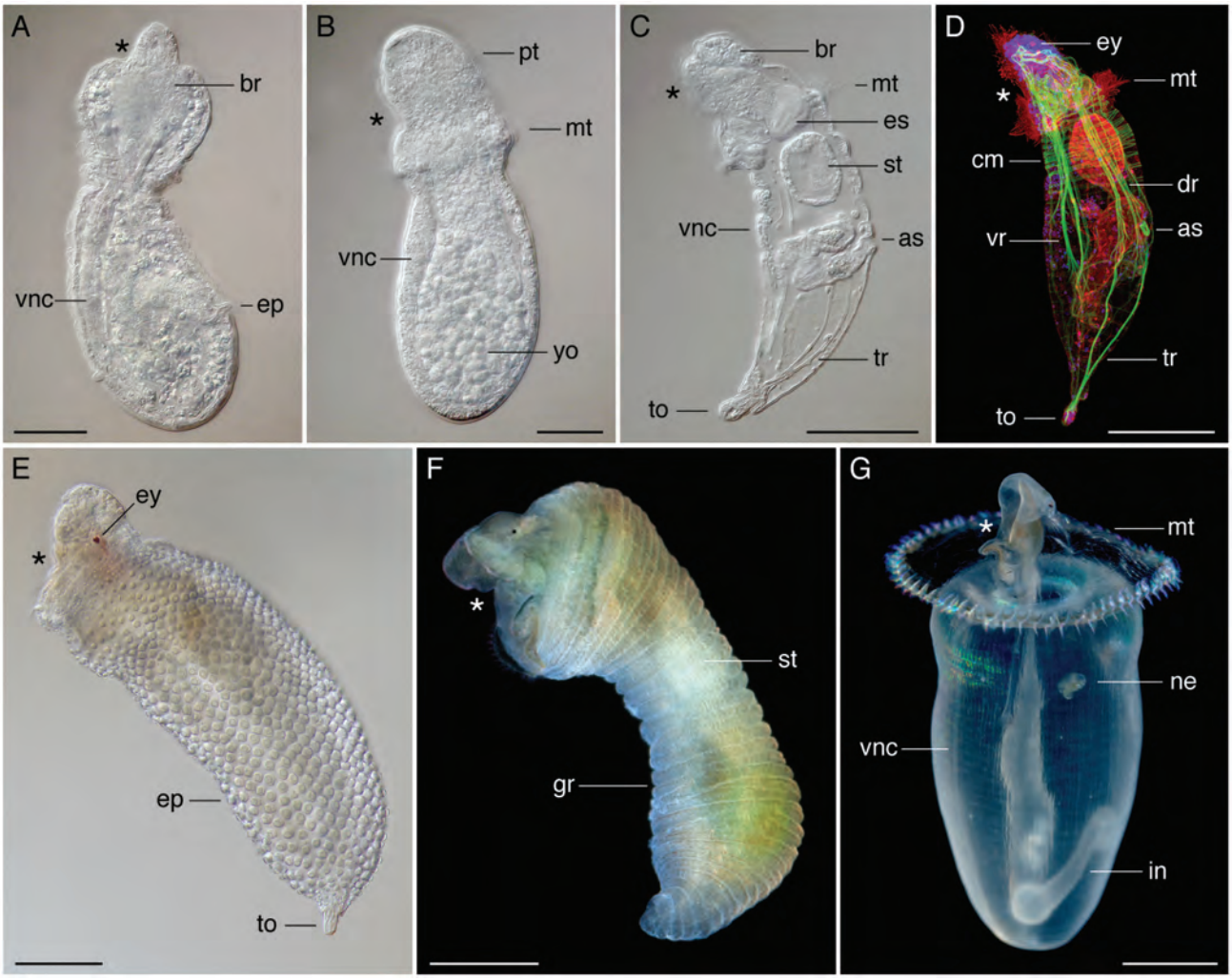


**Fig. 6.1.5:** Morphological characters among the predominant dispersal stages of sipunculans. A–C, Differential interference contrast (DIC) micrographs of each specimen after 3 days of development. A, *Phascolion cryptum*. Direct development showing a crawling vermiform stage (©M.J. Boyle). B, *Themiste alutacea*. Indirect development showing a lecithotrophic pelagosphera larva (©M.J. Boyle). C, *Nephasoma pellucidum*. Indirect development showing a planktotrophic pelagosphera larva (©M.J. Boyle). D, *Nephasoma pellucidum*. CLSM of a 4-day pelagosphera larva; green, F-actin; red, acetylated tubulin-like immunoreactivity; blue, DNA. Labeling reveals circular and retractor muscle pairs, eyes, metatrochal cilia, functional digestive system, and the terminal organ system with a pair of retractor muscles and adhesive organ (©M.J. Boyle). E, *Phascolosoma* sp. white papillated pelagosphera larva from the Caribbean of Panama, scale bar = 100 µm (©M.J. Boyle). F, *Siphonosoma* sp. transverse groove pelagosphera larva from the Florida Current of the Gulf Stream, scale bar = 200 µm (©M.J. Boyle). G, *Sipunculus* sp. large, smooth transparent pelagosphera larva from Florida Current of the Gulf Stream, scale bar = 400 µm (©M.J. Boyle). The larger pelagosphera larvae in F and G are considered teleplanic larvae that may spend weeks to months in the open ocean. All specimens (A–G) are oriented anterior to the top and ventral to the left side. as, anus; br, brain; cm, circular muscle; dr, dorsal retractor; ep, epidermal papilla; ey, eye; es, esophagus; gr, grooves; in, intestine; mt, metatroch; ne, nephridia; pt, prototroch; st, stomach; to, terminal organ; tr, terminal retractor; vnc, ventral nerve cord; vr, ventral retractor; yo, yolk. An asterisk marks the position of the stomodeum or mouth. Scale bars in A–D = 50 µm. A–C, From Boyle and Rice (in press), courtesy of the Smithsonian Institution.

to a juvenile sipunculan. Both larval forms are distinct from one another, and the pelagosphera is unique within Metazoa. Specific characteristics of the sipunculan pelagosphera (Fig. 6.1.5) include two pairs of internal retractor muscles, a postoral metatrochal band of cilia used exclusively for locomotion, a terminal organ with distinct retractors and adhesive properties, and a U-shaped digestive system with descending and ascending regions of the intestine (Rice 1976, 1985b, Ruppert and Rice 1983, Boyle and Rice 2014). There have been a number of studies on sipunculan metamorphosis, including histological and behavioral descriptions, as well as attempts to describe culture and follow the development of the long-lived, teleplanic pelagosphera larvae (Fig. 6.1.5 F, G) from the

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open ocean (Hall and Scheltema 1975, Rice 1981, Scheltema and Rice 1990). Additionally, several studies have focused specifically on the development of the sipunculan musculature (Wanninger *et al.* 2005, Schulze and Rice 2009, Kristof *et al.* 2011), digestive system (Boyle and Seaver 2010), nervous system (Åkesson 1958, Wanninger *et al.* 2005, Kristof *et al.* 2008), and life history evolution (Rice 1985b, Boyle and Rice in press, Schulze *et al.* in press). Regarding myogenesis, it was suggested that circular ring-like muscle bands develop synchronously along the anterior-posterior axis, and there is no evidence of a PGZ during elongation of the larvae of *Phascolion strombus* (Montagu, 1804) (see Wanninger *et al.* 2005). Furthermore, Schulze and Rice (2009) suggest that although the final number of retractor muscles may vary in adult worms, four retractors are present during the development of species with contrasting life histories and therefore likely represent the ancestral condition. The first gene expression studies for a member of Sipuncula showed that gut-specific transcription factors, known to be conserved in patterning and specification of the digestive system across metazoans (Boyle *et al.* 2014), are expressed subregionally along the gut during development in *T. lageniformis* and *P. cryptum* (Boyle and Seaver 2010, Boyle and Rice 2014). This work should be followed up with experiments characterizing the expression patterns of additional "gut-specific" genes to evaluate similarities and differences between sipunculans and other spiralian models during gut formation. Regarding the development of the central nervous system, one confocal imaging study of serotonin-like immunoreactivity indicated that there may be transient segmental organization along the developing ventral nerve cord in *P. agassizii* (see Kristof *et al.* 2008). However, this interpretation is questionable and should be reinvestigated since developmental chronology, as presented in that study, is not replicable. Other than one interpretation by Kristof *et al.* (2008), the conclusion from more than a century of studies on sipunculan development is that there is no evidence of segmentation during the formation of any tissues or organ systems derived from the primary germ layers (ectoderm, endoderm, mesoderm) within any stages (embryos, larvae, juvenile worms) of the four recognized life history patterns (Hatschek 1883, Gerould 1906, Åkesson 1958, 1961, Hyman 1959, Clark 1969, Rice 1973, 1985b, 1993, Wanninger *et al.* 2005, Schulze and Rice 2009, Boyle and Rice 2014). Relatively recently, the molecular phylogenetic hypotheses of sipunculan genera (Kawauchi *et al.* 2012) and families (Lemer *et al.* 2015) have provided additional support for the relationship of Sipunculidae as the sister clade to all remaining families (Fig. 6.1.6), further supporting an inference of planktotrophic pelagosphera larvae within the ancestral sipunculan life history pattern, as previously suggested from morphological, systematic, and developmental studies (Rice 1985b, Boyle and Rice in press).

In the two recognized larval types in Sipuncula, the trochophore and pelagosphera, there are morphological, functional, and behavioral transitions to a subsequent species-specific life history stage (Gerould 1906, Åkesson 1958, Rice 1978). Those transitions have been described as a first and second metamorphosis (Jägersten 1963, 1972, Rice 1985b). Whether the first or second metamorphic transition occurs depends upon the category of indirect development (II–IV) exhibited by a particular life history pattern, as well as the degree of morphogenesis required to reach the juvenile sipunculan stage. Although embryos are often ciliated and motile, in many species, there appears to be a definitive trochophore stage that undergoes a series of changes to the lecithotrophic or planktotrophic pelagosphera larval stage. Prior to metamorphosis, the top-shaped trochophore has an apical tuft of cilia on the anterior end; a dorsolateral pair of reddish colored eyes; a broad double band of multiciliated, yolk-rich prototroch cells; and a uniformly thick egg envelope surrounding the entire larva (Fig. 6.1.4 C, F).

During the first metamorphosis, multiple larval-specific changes take place. The development of circular, longitudinal, and introvert retractor muscles and their contraction and extension within the body, in addition to somatic cell proliferation, cause a stretching and thinning of the egg envelope and elongation of the larva in the post-trochal region along the antero-posterior axis (Åkesson 1958). Concurrently, the coelomic cavity expands, the prototroch is reduced to a narrow semicircular band of cilia on the dorso-posterior of the pretrochal head region, a distinct metatrochal band of cilia develops around the thorax between the head and future trunk (Fig. 6.1.5 B, C, D), and a terminal organ with adhesive properties and a designated pair of retractor muscles develop at the posterior end of the larva (Rice 1976, Ruppert and Rice 1983). This emerging pelagosphera larva also develops a broad field of cilia lining the ventral-anterior head and surrounding a stomodeum anterior to the metatroch, both open to the exterior and functional in planktotrophic life history stages (Fig. 6.1.5 C, D). The metatroch is now the primary organ of locomotion in the pelagosphera, and the high yolk content previously stored within the band of large prototroch cells has been transferred into the coelom to nourish growth of this second larval stage (Gerould 1906, Åkesson 1958, Rice 1976, 1985b, 1988). Internally, there is one pair of metanephridia, an elaborate centralized

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nervous system, and a U-shaped gut with the rectum and anus typically positioned on the dorsal-anterior of the larval trunk (Fig. 6.1.5 C, D, G). Furthermore, the egg envelope of the trochophore is liberated from the epispheric or head region in many species, and posteriorly, it is transformed into an "extensible and flexible cuticle" of the trunk in pelagospherae (Rice 1976). The variability and extent of these and other metamorphic changes between trochophore and pelagosphera stages are species specific and particular to lecithotrophic or planktotrophic forms. For species without a pelagosphera stage, metamorphosis of the trochophore generates a crawling juvenile worm. Development to a planktotrophic larva also entails the formation of a complex feeding morphology for growth and survival within a pelagic environment, especially among species with the comparatively larger forms of inferred long-duration teleplanic pelagosphera larvae found within major surface currents circulating around and across much of the world's open ocean (Hall and Scheltema 1975, Rice 1981, Boyle and Rice in press, Rice *et al.* in press). For example, planktotrophic pelagospherae possess a protrusible buccal organ supported and operated by extensive pharyngeal musculature, and the combined apparatus of a grooved ciliated lip with a lip pore and two to four lobate secretory glands, which, collectively, are most likely involved in handling food particles and the conspicuous behavior of "tasting" or sampling substrates in connection with settlement. These anterior feeding-associated structures are closely aligned along the esophagus, which in planktotrophic larvae leads to a well-defined stomach region that connects posteriorly to an intestinal section of the digestive system (Fig. 6.1.5 C, G). Planktotrophic larvae may also vary in the number and pattern of their dorsal eyespots, pigmentation of the body and head, arrangement of body-wall muscles, and both the morphology and presence or absence of papillae extending from larval cuticle (Fig. 6.1.5 A, E), with this last feature correlating with a range of papillated structures that have been characterized on the juvenile and adult worms that they will develop into (Rice 1975a, 1981, 1988).

The second metamorphic transition is from the pelagosphera larva to a juvenile sipunculan (Jägersten 1972, Rice 1985b). Lecithotrophic pelagospherae have a considerable resource of yolk to facilitate growth and metamorphosis, which in all pelagosphera larvae includes the loss of prototrochal and metatrochal ciliary bands, morphogenetic rotation of the mouth and esophagus from ventral-anterior to an apical position, and the formation of tentacle buds surrounding the mouth, or surrounding a nuchal sensory organ with the mouth positioned outside the developing crown of ciliated tentacles. The second metamorphosis of planktotrophic species is more complex and involves the reduction and disappearance of associated feeding structures (buccal organ, lip gland), including loss of a defined stomach region with elongation of the body, formation and growth of descending and ascending loops of the intestine, transformation of the larval cuticle with sensory papillae, secretory papillae, and, in many but not all species, the formation of hooks in different arrangements on the anterior introvert. Additionally, it is not known whether the larval eyes are retained or if juvenile eyes develop independently; however, the eyes are now located internally on the dorsal side of the brain, which is positioned dorsally along the esophagus and internal to the tentacular crown. Another mystery involves the final morphology and/or transformation and function of the larval terminal organ within the adult. In species where such changes have been observed in the laboratory, the second metamorphic transition occurs over a period of 1 to 5 days, although specific, generic, and familial characters become distinguishable over periods of weeks to months (Åkesson 1958, Rice 1976, 1988). Furthermore, some characters such as hooks or particular retractor muscles may be absent in adult stages, while some epidermal structures become distinct or fully functional only in adult stages (Rice 1976, Schulze and Rice 2009, Boyle and Rice 2014, Rice *et al.* in press).

Overall, when following sipunculan development in each of the four life history patterns (I–IV), and by comparison with closely related taxa in Annelida or among other members of the spiralian superclade, there are a number of sipunculan-specific characters that distinguish this group of coelomate marine worms. The sipunculan character complex includes unequal spiral cleavage in all species studied, conspicuously large first quartet micromeres, introvert retractor muscles derived from 1q ectomesoderm, mid-body growth zone, all trochophore larvae being lecithotrophic, a unique pelagosphera larva, metatroch with exclusive locomotor function, U-shaped gut with middorsal anus, a terminal organ with apparent adhesive properties, and no segmental rudiments in embryonic, larval, or juvenile life history stages (Rice 1985b, Boyle and Rice 2014).

Although there are extensive comparative observations and a broad range of descriptive studies on sipunculan reproduction and development, there is very little information about the blastomeric or even germ-layer origins of multiple sipunculan-specific characteristics. To date, no cell-lineage or intracellular fate map has been constructed for a member of Sipuncula. These resources will be required for any critical understanding of the origins of a sipunculan character complex or

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any of the many other features characteristic of their ontogeny. Therefore, any inferences of homology appropriately based upon cellular and germ-layer-specific studies tracing the cellular origins of particular tissues and organ systems are currently unavailable to allow direct comparison of developmental or functional morphology between sipunculan worms and other members of Spiralia (e.g., metatroch, buccal organ, tentacles). When such studies are eventually published, there already is in place an impressive breadth of comparative literature across multiple species-specific life history patterns, from first cleavage through second metamorphosis of sipunculan development. Attempts to permeabilize and inject sipunculan embryos are underway but remain a considerable challenge due to their complex multilayered egg envelope and its mostly unknown biochemical composition. Once such technical challenges are overcome, a delivery system will be available to pursue functional genomics through multiple molecular tools. Previously, gene expression studies have been performed (Boyle and Seaver 2010, Boyle and Rice 2014) and have been now verified to work in four species with distinctly contrasting life history patterns. Comparative developmental transcriptome sequencing and genome sequencing and assembly have been completed. With genomic sequence resources, in combination with working protocols for gene expression by in situ hybridization, a number of studies, focused on when and where developmental genes pattern and build the sipunculan body plan, should be pursued. Interesting targets include the sipunculan hox code, nervous and digestive system architecture, the elaborate musculature of feeding and introvert retraction, and the locomotory-related ciliation and neural regulation of the metatroch. Moreover, when and where are the so-called segmentation genes expressed during the development of nonsegmented sipunculans currently considered to be among the basal branches of the overtly segmented and extremely diverse radiation of worms within the annelid tree of life? There are insightful experiments to be performed on sipunculan developmental models and a rich history of in-depth morphological and taxonomic studies to guide future interpretations of new research efforts on these underrepresented marine worms.

## Biology and ecology

Sipuncula generally lead a cryptic life but can reach high local abundances (e.g., Rice *et al.* 1983). They have been reported from the intertidal zone to the abyss and all latitudes (Cutler 1994). Most species appear to have wide environmental tolerances (Cutler 1994). The Indo-Pacific *Phascolosoma arcuatum* (Gray, 1828), which inhabits mangrove swamps, is particularly tolerant to air exposure and salinity fluctuations and has been referred to as semiterrestrial (Green 1975).

Some species, such as *Sipunculus* spp., burrow into sand or mud, sometimes 50 cm or more below the sediment surface (Voss-Foucart *et al.* 1977, Romero-Wetzel 1987, Cutler 1994, Shields and Kedra 2009, Maiorova and Adrianov 2010) and can be major contributors to bioturbation of the sediment (Graf 1989, Li *et al.* 2015). Other species are common in roots or holdfasts of submerged vegetation, sponges, algal mats, or bivalve aggregations. *Phascolosoma turnerae* Rice, 1985 was first reported from submerged wood (Rice 1985a) and is also abundant in areas of hydrocarbon or methane seepage, where it inhabits sediment at the base of tubeworm (siboglinid) aggregations (MacAvoy *et al.* 2005). *Phascolosoma saprophagicum* Gibbs, 1987 was discovered in the crevices of a whale bone recovered from 800-m depth off the coast of New Zealand (Gibbs 1987). Several species, in particular *Phascolion* spp., inhabit abandoned gastropod shells, polychaete tubes, or foraminiferan tests. Sipunculans also commonly bore into hard substrates, including coral rubble, mollusc shells, calcareous rock, or sandstone, and contribute to the bioerosion of these materials (Stearley and Ekdale 1989, Glynn and Manzello 2015), sometimes with detrimental effects (Antonelli *et al.* 2015).

Most sipunculans are presumed to be semisessile in the juvenile and adult stage, and their locomotion is largely limited to the introvert. Introvert extension and retraction are achieved by antagonistic interaction between the body wall musculature and the introvert retractor muscles. Contraction of the body wall musculature increases the hydrostatic pressure in the main body coelom, causing the eversion of the introvert (Zuckerkandl 1950). Retraction is achieved by contraction of the introvert retractor muscles.

Little is known about the normal activity patterns of sediment burrowing species. The small *Nephasoma lilljeborgi* (Danielssen & Koren, 1880) forms complex networks of burrows up to at least 30 cm deep and rapidly moves organic matter to the subsurface (Shields and Kedra 2009). Large species, such as *Sipunculus* spp., make almost straight vertical burrows up to 1 m deep (Maiorova and Adrianov 2010). When removed from the sediment, the worms can very quickly rebury themselves by using a combination of peristaltic movement and digging with the introvert.

The paucity of morphologically diagnostic features in sipunculans makes species delineation a difficult task.

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A number of species have only been reported from their type localities. Some of these have been synonymized with other, more widespread, species or are now regarded *Incertae Sedis* or *Species Inquirenda* (Cutler 1994). The majority of sipunculan species, however, have large reported distribution ranges and some are referred to as "cosmopolitan." This view of generally wide geographic distributions is supported by the existence of pelagic larval stages (pelagosphera), which can potentially cross large swaths of ocean to disperse to remote areas (Hall and Scheltema 1975). On the other hand, over the past two decades, molecular data have challenged the notion of cosmopolitan sipunculan species by revealing significant genetic differences among geographically separated populations, leading to the detection of "cryptic" (i.e., morphologically unrecognizable but genetically distinct) or "pseudo-cryptic" (i.e., morphologically and genetically distinct but lumped together in the taxonomic literature) species. These include *Apionsoma misakianum* Ikeda, 1904 (Staton and Rice 1999), *Sipunculus nudus* Linnaeus, 1766 (Kawauchi and Giribet 2014), *Phascolosoma perlucens* Baird, 1868 (Kawauchi and Giribet 2010), *Phascolosoma agassizii* Keferstein, 1866 (Schulze *et al.* 2012, Johnson *et al.* 2016, Johnson and Schulze 2016), *Themiste pyroides* (Chamberlin, 1919) (Schulze *et al.* 2012), and *Thysanocarida nigra* (Ikeda, 1904) (Schulze *et al.* 2012). These newly detected species have not, as yet, been formally described.

Three feeding modes are dominant among sipunculans: nonselective deposit feeding, surface grazing, and suspension feeding. In sediment-dwelling species, the intestine is usually filled with particles that seem to resemble the surrounding sediment in composition and grain size (Edmonds 1962), suggesting nonselective ingestion of sediment and subsequent digestion of organic particles, including detritus and meiofaunal organisms. Species that burrow into or inhabit the crevices of hard substrates, such as coral rubble or mollusc aggregations, generally have a long introvert, often with numerous hooks and a relatively small tentacular apparatus. These species tend to extend their introverts from the opening of the burrow and scrape bacteria and microalgae off the surface using their introvert hooks (Cutler 1994). Members of the genus *Themiste* Gray, 1828 are suspension feeders and possess elaborate branched tentacles for food capture (Pilger 1982, Adrianov *et al.* 2006). A few additional species, such as *Antillesoma antillarum* Grube, 1858, members of the genus *Thysanocardia* (Fisher, 1950), and possibly *Sipunculus* spp., also have large tentacles and may use them for suspension as well as surface deposit feeding (Jumars *et al.* 2015).

Sipunculans are commonly recovered in the stomach contents of bottom-feeding fish (reviewed in Cutler 1994), some crustaceans (Woods and McLay 1996, Cristo 1998), octopods (Villegas *et al.* 2014), and gastropods. Remarkably, among gastropods, the diet of members of the gastropod family Mitridae consists exclusively of sipunculans (Taylor 1984, 1989). Sipunculans have also occasionally been recovered in the stomach contents of olive ridley sea turtles (Bjorndal 1996) and gray whales (Ferguson *et al.* 2015).

## Phylogeny and taxonomy

### Phylogeny

The evolutionary origin and phylogenetic relationships of sipunculans have long been mysterious and contentious (for a review, see Saiz-Salinas 2018). Linnaeus (1766) placed *S. nudus,* still one of the most referenced sipunculan species today, into the "Vermes Intestina," a group that included a number of worm-like taxa without appendages, such as *Fasciola*, *Lumbricus, Hirudo,* and others. Apparently, due to a superficial resemblance to sea cucumbers, Lamarck (1816) regarded them as echinoderms without appendages. Quatrefages (1847) proposed the concept of "Gephyrea" (literally meaning bridge) to include a number of superficially similar groups that he considered a bridge between segmented worms and echinoderms. Apart from sipunculans, this group also included holothurians, echiurans, and priapulids. Although Sedgwick (1898) recognized "Sipunculoidea" as a separate phylum, the Gephyrea concept lingered in the scientific literature for over a century. Hyman (1959: 611) finally put the concept to rest by recognizing that "...adopting the concept of Gephyrea offers an easy way of disposing of three groups of very uncertain affinities. But as all modern students of these groups are agreed that there is no close relationship between them *the name and the concept of the Gephyrea must be obliterated from zoology*" (emphasis by original author). Although she assumed a close relationship between annelids and sipunculans, Hyman treated sipunculans as a distinct phylum, which she named "Sipunculida." The name was later changed to "Sipuncula" by Stephen (1964).

Embryonic development, in particular the occurrence of spiral cleavage (Gerould 1906), clearly places the Sipuncula in the Spiralia/Lophotrochozoa clade, and their monophyly is uncontested (Maxmen *et al.* 2003, Schulze *et al.* 2005, 2007, Kawauchi *et al.* 2012, Lemer *et al.* 2015). However, it still remained unclear what the sister taxon to the Sipuncula is. Embryological data such as the

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presence of a "molluscan cross" in the 64-cell stage initially seemed to point to a sister group relationship with molluscs (Scheltema 1993), but in light of more recent cell lineage studies (Maslakova *et al.* 2004), the concept of the molluscan vs. the annelid cross is no longer supported. Several phylogenetic and phylogenomic studies have placed sipunculans in the annelid radiation (Boore and Staton 2002, Telford *et al.* 2005, Dunn *et al.* 2008, Hejnol *et al.* 2009, Mwinyi *et al.* 2009, Struck *et al.* 2011), most notably near the base of the annelid tree as the sister taxon to Amphinomidae (e.g., Weigert *et al.* 2014, 2016). However, this placement is not supported by cladistic and probabilistic analyses based on combined data from fossil and extant taxa (Parry *et al.* 2014, 2016). The fossil record, although sparse, shows a remarkable conservation of the basic sipunculan morphology since the Cambrian (Huang *et al.* 2004, Muir and Botting 2007).

### Taxonomy

Higher classification was recently revised based on multigene phylogenetic (Kawauchi *et al.* 2012) and phylogenomic analyses (Lemer *et al.* 2015). The new classification scheme differs in several respects from older ones (Stephen and Edmonds 1972, Cutler 1994), although some of the family names were retained. The new classification recognizes six families, but no higher taxonomic ranks (Fig. 6.1.6).

### Sipuncula Stephen, 1964

### Family Sipunculidae Rafinesque, 1814

**Type genus:** *Sipunculus* Linnaeus, 1766

**Synonyms:** Sipunculidae Baird, 1868:77 [partim]; Stephen and Edmonds 1972:19 [partim]; Cutler and Gibbs 1985:166 [partim]; Gibbs and Cutler 1987:47 [partim]; Cutler, 1994:24 [partim]

**Diagnosis:** Large sipunculans, commonly 100–200 mm long, with introvert shorter than the trunk. Oral disk with tentacles surrounding a central mouth. Hooks absent; prominent triangular papillae arranged irregularly, covering most of the length of the introvert. Trunk cylindrical and covered externally by swollen rectangular "mini pillows." Longitudinal and circular muscle layers of the inner trunk divided into distinct bands (Longitudinal muscle bands, LMBs and Circular muscle bands, CMBs, respectively). Functional pore present between each pair of overlapping longitudinal and circular bands, allowing direct contact between coelomic fluid and the skin to facilitate gas exchange. Pore opens in a closed space (sac) or into parallel longitudinal canals limited in length to the width of one circular muscle band (coelomic extensions), extending through most of the trunk length. Thread-like muscle (spindle muscle) extends through the center of gut coil from anterior to posterior; not attached to the wall of the posterior trunk. Two pairs (two dorsal and two ventral) of introvert retractors muscles extend from the head to the anterior trunk wall. Intestinal coil attached to body wall along most of its length by many connective tissue strands (fixing muscle). A pair of nephridia opening anterior or posterior to the anus.

#### Genus *Sipunculus* Linnaeus, 1766 (Fig. 6.1.7 A)

**Type species:** *Sipunculus nudus* Linnaeus, 1766

**Synonyms:** *Syrinx* Bohadsch, 1761:63–97, *Sipunculus* Linnaeus, 1766:1078; Quatrefages, 1865b:613; Selenka *et al.*, 1883:88; Stephen and Edmonds, 1972:21; E. Cutler and Cutler, 1985b:232

**Diagnosis:** Large species with trunk longer than 50 mm in adults. Introvert shorter than trunk (5–30%). Two pairs of stemlike tentacles with ventral pair shorter than dorsal pair. Well-defined longitudinal muscles bands between 20 and 50 in number. Coelomic extensions in body wall in the form of canals between longitudinal muscle bands extending along most of the trunk. Two smooth contractile vessels without villi. Esophagus with long and loose loop before entering intestine coil (postesophageal loop). Rectal caecum present. Nephridiopores opening anterior to the anus.

#### Genus *Xenosiphon* Fisher, 1947 (Fig. 6.1.7 B)

**Type species:** *Sipunculus mundanus* var. *branchiatus* Fischer, 1865

**Synonyms:** *Xenosiphon* Fisher, 1947:360; 1954a:311; Stephen and Edmonds, 1972:38; E. Cutler and Cutler, 1985b:228

**Diagnosis:** Large species. Introvert shorter than trunk. Tentacular crown consisting of many stemlike tentacles of the same size around mouth. Between 29 and 37 well-defined longitudinal muscles bands. Coelomic extension in the body wall consist of short, diagonal canals limited in length by the limit of one CMB. An extra pair of thin muscles (protractor muscles) attaches near the brain. Gut without a postesophageal loop. Spindle muscle arises on the ventral wall of the rectum; not attached to the trunk wall posteriorly. Nephridiopores opening posterior to anus.

### Family Golfingiidae Stephen & Edmonds, 1972

**Type species:** *Golfingia* Lankester, 1885

**Synonyms:** Sipunculidae Baird, 1868:77[partim]; Stephen and Edmonds, 1972:19 [partim]; Cutler and Gibbs 1985:166 [partim]; Gibbs and Cutler, 1987:47, Cutler:24 [partim]

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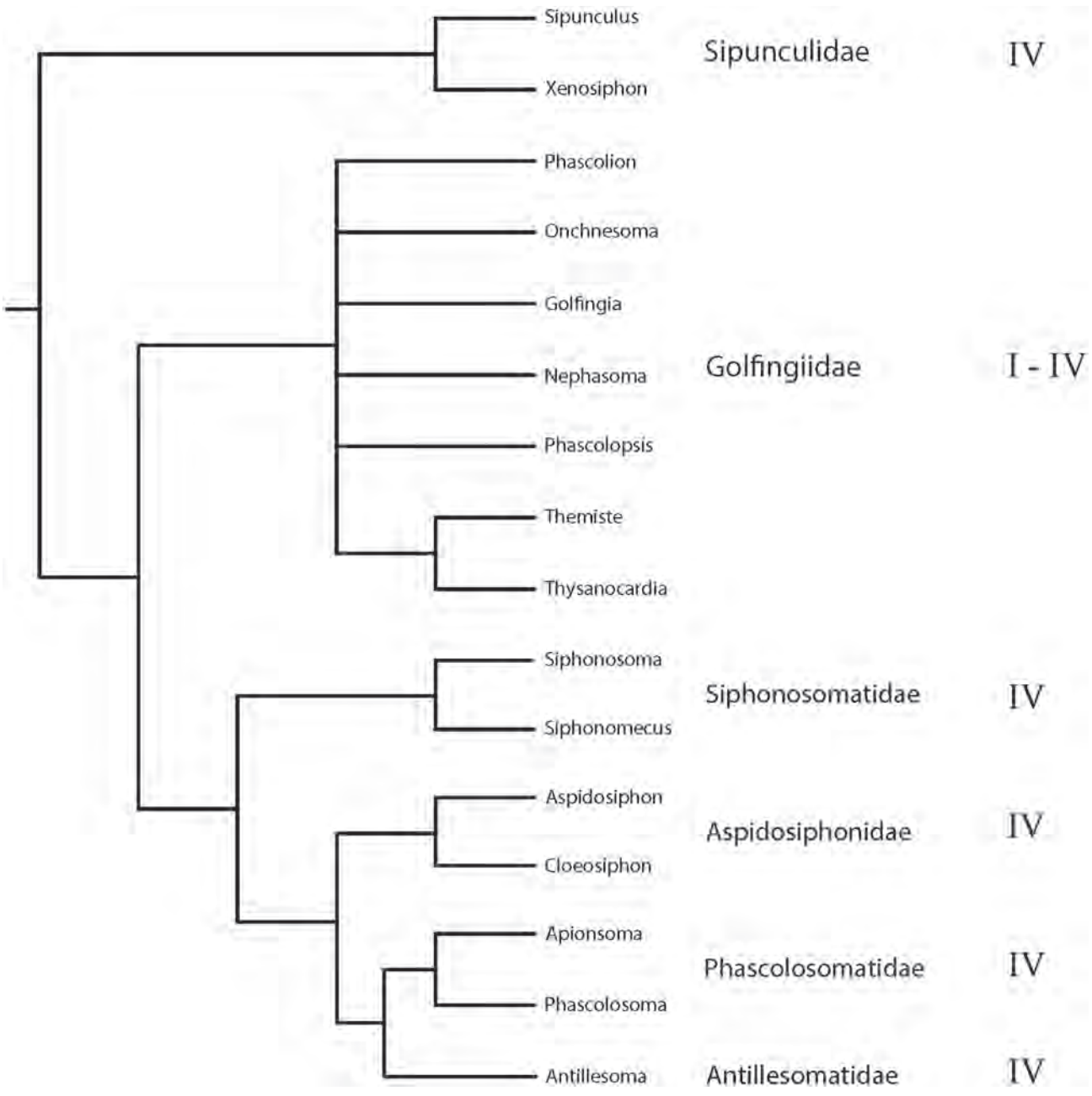


**Fig. 6.1.6:** Phylogeny and distribution of developmental life history patterns within Sipuncula. Sipunculan genera are located at the terminal branch tips. Six recognized sipunculan families (Sipunculidae, Golfingiidae, Siphonosomatidae, Aspidosiphonidae, Phascolosomatidae, and Antillesomatidae) are placed to the right of the clades of related sipunculan genera that are found within each of the six families. Roman numerals are placed to the right of the six families to designate the developmental life history patterns found within each family. In all but one family, a life history including planktotrophic larval development (IV) is the exclusive pattern observed for species in that family, with few exceptions (see text). Within Golfingiidae, all four developmental patterns (I, II, III, and IV) have been characterized. The cladogram topology combines two phylogenetic hypotheses (Kawauchi *et al.* 2012, Lemer *et al.* 2015). Modified from Boyle and Rice (in press), courtesy of the Smithsonian Institution.

Golfingiidae Stephen and Edmonds, 1972:77 [partim]; Cutler and Gibbs 1985:167 [partim]; Gibbs and Cutler, 1987:50, Cutler:60 [partim]

Themistidae Cutler and Gibbs, 1985:167 [partim]; Gibbs and Cutler, 1987:53, Cutler:140 [partim]

Phascolionidae Cutler and Gibbs, 1985:166 [partim]; Gibbs and Cutler, 1987:51, Cutler:107

**Diagnosis:** Small to medium sipunculans (trunk no longer than 200 mm). Introvert equal to or shorter than the trunk. Tentacles surround the central mouth. Hooks

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**Fig. 6.1.7**: Sipunculidae. A; *Sipunculus nudus* (©G.Y. Kawauchi). B, *Xenosiphon branchiatus* (©G.Y. Kawauchi). All scale bars = 10 mm.

may be deciduous, absent, or simple when present, not sharply curved and generally scattered, but sometimes arranged in rings. Tentacles organized in a close-set array of digitiform, filiform, leaflike, or stemlike extensions of the oral disk or reduced to lobes. External trunk wall generally smooth or with papillae, the latter usually small in diameter and height. In small worms (few millimeters), trunk wall sometimes transparent or translucent, but specimens larger than 20 mm with opaque trunk wall (often yellow or whitish). Longitudinal musculature of inner trunk continuous, except in *Phascolopsis*. One to four retractor muscles. Contractile vessel simple or with numerous villi. One or two nephridia. Nephridiopore opening anterior or posterior to the anus.

**Genus *Golfingia* Lankester, 1885**

**Type species:** *Golfingia macintoshii* Lankester, 1885 (= *Sipunculus vulgaris* sensu Blainville, 1827)

**Synonyms:** *Golfingia* Lankester, 1885a:469

*Golfingia* (*Golfingia*) Fisher, 1950a:549

*Golfingia* (*Dushana*) Murina, 1975c:1085

*Themiste* (*Stephensonum*) Edmonds, 1980:19

*Centrosiphon* Shipley, 1903:173; Edmonds, 1980:19

**Diagnosis:** Small- to medium-sized worms (very few exceed 30 mm in length). Introvert equal to or shorter than trunk (65–100% of trunk length, only one species up to 200%). Tentacles a series of digital circumoral tentacles, whose number and complexity increase with age within species of this genus. Hooks when present commonly small (20–40 μm) and scattered. Body wall with continuous muscle layer. Four retractor muscles. Contractile vessel without villi. Spindle muscle attached terminates posteriorly within gut coil. Two nephridia open anterior to the anus.

**Genus *Nephasoma* Pergament, 1940**

**Type species:** *Nephasoma marinki* Pergament, 1940 (= *Onchnesoma glaciale* Danielssen and Koren: E. Cutler and Murina, 1977; = *Phascolosoma lilljeborgii* Danielssen and Koren: Gibbs, 1982).

**Synonyms:** *Nephasoma* Pergament, 1940:1; N. Cutler and Cutler, 1986:548

*Golfingia* (*Phascoloides*) Fisher, 1950:550; Stephen and Edmonds, 1972:131

**Diagnosis:** Small- to medium-sized worms, with trunk less than 50 mm in length. Introvert commonly shorter than trunk. Tentacular crown around mouth commonly with flattened, digitate tentacles, shorter and lobate tentacles or reduced in size and numbers. Hooks, when present, generally scattered. Longitudinal musculature of inner trunk continuous. Two retractor muscles, often partially fused. Contractile vessel without villi. Spindle muscle not attached to the posterior end of the trunk. Two nephridia usually open at the level of the anus but can vary opening anterior and posterior to the anus.

**Genus *Onchnesoma* Koren and Danielssen, 1875**

**Type species:** *Onchnesoma steenstrupii* Koren and Danielssen, 1875

**Synonyms:** *Onchnesoma* Koren and Danielssen, 1875:133; 1877:142; Selenka *et al.*, 1883; Théel, 1905:13; Stephen and Edmonds, 1972:161; E. Cutler and Cutler, 1985a:840

**Diagnosis:** Small specimens with trunk less than 10 mm long. Introvert always longer than trunk. Anus on distal half of the introvert. Tentacle crown with few tentacles (less than 10) and sometimes reduced in size or completely absent. Trunk with papillae and/or radiating folds of skin (keels) on posterior end. Hooks absent. Longitudinal musculature of inner trunk continuous. Retractor muscles almost completed fused forming a single retractor

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column. Contractile vessel, when visible, without villi. Spindle muscles apparently absent. Anus always opening on the distal half of the introvert. Only one nephridium opening posterior to the anus.

**Genus *Phascolion* E. Cutler and Gibbs, 1985**
**Type species:** *Sipunculus strombus* Montagu, 1804
**Synonyms:** *Phascolion* Théel, 1875b; Selenka *et al.*, 1883:41; Stephen and Edmonds, 1972:164
**Diagnosis:** Small- to medium-sized worms (less than 50 mm in length). Common inhabitants of empty gastropod shells. Introvert one-half to four times the trunk length. Tentacular crown around mouth with tentacles varying from only few lobes, broad digitiform, slender digitiform, or reduced in number and with dendritic pattern. Hooks present or absent. Longitudinal musculature of inner trunk continuous. In most species, trunk with unique holdfast papillae forming dark, horny protein structures, shaped like a U, V, or broken O. Holdfast papillae distributed around the trunk, usually in midregion, and probably functioning as anchors in the protective shelter. Retractor muscles fused into dorsal and ventral pair, giving the appearance of only one or two muscles. Degree of fusion and relative size define subgenera. Intestinal coil loose and without axial spindle muscle. Anus positioned 20–95% of the distance toward distal tip of introvert or at anterior end of trunk. One nephridium (generally the right one) usually opening posterior to the anus.

**Genus *Phascolopsis* (Fisher, 1950)**
**Type species:** *Sipunculus gouldii* (Portalés, 1851)
*Golfingia* (*Phascolopsis*) Fisher, 1950:550
*Phascolopsis* Stephen, 1964:459; Stephen and Edmonds, 1972:74; E. Cutler, 1986:460
**Diagnosis:** Medium to large worms. Introvert about one-third of trunk length. Tentacular crown consisting of many filiform peripheral tentacles. Trunk up to 150 mm long (commonly 50–100 mm in length). Hooks deciduous and only present in very young worms up to 3 or 4 cm long. Longitudinal musculature of the inner trunk gathered into anastomosing bands; circular muscle layer continuous. Four introvert retractor muscles. Contractile vessel without villi. Spindle muscle not attached to the posterior end of trunk. Two nephridia open slightly anterior to the anus.

**Genus *Themiste* Gray, 1828** (Fig. 6.1.8 A)
**Type species:** *Themiste hennahi* Gray, 1828
**Synonyms:** *Themiste* Gray, 1828:8; Baird, 1868:98; Stephen, 1965:58; Stephen and Edmonds, 1972:193

**Fig. 6.1.8**: Golfingiidae and Siphonosomatidae. A, *Themiste alutacea* (©A. Schulze), scale bar = 5 mm. B, *Thysanocardia catharinae* (©G.Y. Kawauchi), scale bar = 20 mm. C, *Siphonosoma cumanense* (©G.Y. Kawauchi), scale bar = 20 mm.

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*Dendrostomum* Grube and Oersted, 1858:118; Quatrefages, 1865b:629
*Dendrostoma* Keferstein, 1865b:438; Selenka *et al.*, 1883:83
**Diagnosis:** Small to large sized worms (4 to 400 mm). Introvert shorter than trunk. Tentacles surrounding mouth with unique dendritic branching patterns emerging from a few individual stems. Hooks are present or absent in adults. Inner trunk wall with continuous muscle layer. Four introvert retractor muscles. Contractile vessel with short villi or long tubules. Spindle muscle not attached posteriorly to trunk. Two nephridia open posterior to the anus.

**Genus *Thysanocardia* (Fisher, 1950)** (Fig. 6.1.8 B)
**Type species:** *Phascolosoma procerum* Möbius, 1875
**Synonyms:** *Golfingia* (*Thysanocardia*) Fisher, 1950a:551; Stephen and Edmonds, 1972:120;
*Thysanocardia* Gibbs *et al.*, 1983:295
**Diagnosis:** Small to medium size worms (adult specimens with trunk less than 70 mm). Introvert longer than trunk. Tentacular crown consisting of up to 26 festoons with many tentacles around the mouth and up to 30 tentacles enclosing the nuchal organ. Hooks present in very young worms but absent in adults. Longitudinal musculature of inner trunk continuous. Two introvert retractor muscles. Contractile vessel with many distinct short villi. Spindle muscle not attached to posterior end of trunk. Two nephridia.

**Family Aspidosiphonidae Baird, 1868**
**Type genus:** *Aspidosiphon* Diesing, 1851
**Synonyms:** Aspidosiphonidae Baird, 1868: 100 [partim]; Stephen and Edmonds, 1972:215; Cutler and Gibbs:166; Gibbs and Cutler, 1987:55; Cutler, 1994: 199
Loxosiphonidae Baird, 1868: 103
**Diagnosis:** Generally small worms (5–30 mm). Introvert usually longer than trunk protruding at an angle of 45–90° ventral to the main axis of the trunk. Tentacles encircling nuchal organ. Three types of hooks may be present (compressed uni- and bidentate, pyramidal, and conical) in a combination of two or three of them. Outer trunk wall with some kind of cuticular structure at one or both ends (anal and caudal shield). Inner trunk wall usually as a continuous muscle layer (some species with anastomosing bands). Two introvert retractor muscles. Contractile vessel, when visible, without villi. Spindle muscle attached to posterior end of trunk. Two nephridia usually open posterior to the anus.

**Genus *Aspidosiphon* Diesing, 1851** (Fig. 6.1.9 A–C)
**Type species:** *Aspidosiphon muelleri* Diesing, 1851
**Synonyms:** *Aspidosiphon* Diesing, 1851:67–68
*Pseudaspidosiphon* Baird, 1868: 102 [partim]
**Diagnosis:** Small- to medium-sized worms (most species are less than 40 mm). Introvert usually longer than or as long as trunk and protruding from ventral margin of anal shield. Hooks recurved and present in numerous rings but can be scattered or absent in some species. Tentacular crown generally with very short finger tentacles enclosing the dorsal nuchal organ. Trunk with hardened structure composed of a horny protein (anal shield) or by a subcuticular calcareous conical structure. Inner-body wall either with continuous muscle layer or in anastomosing bands, sometimes ill-defined. Two introvert retractor muscles, often almost completed fused. Contractile vessel smooth or with villi. Spindle muscle attached to posterior end of trunk. Two nephridia.

**Genus *Cloeosiphon* Grube, 1868**
**Type species:** *Loxosiphon aspergillus* Quatrefages, 1865
**Synonyms:** *Loxosiphon* Quatrefages, 1865 [partim]
*Cloeosiphon* Grube, 1868a:48–49.–Selenka *et al.*, 1883:126.–Stephen and Edmonds, 1972:297
**Diagnosis:** Medium-sized worms. Introvert longer than trunk, protruding from the center of anal shield. Unique anal shield composed of calcareous plates with a pineapple skin appearance. Hooks recurved and present in numerous rings. Tentacular crown enclosing dorsal nuchal organ. Inner trunk wall with continuous muscle layer. Two introvert retractor muscles, often almost completed fused. Contractile vessel with no villi. Spindle muscle attached posteriorly. Two nephridia.

**Family Phascolosomatidae Stephen & Edmonds, 1972**
**Type genus:** *Phascolosoma* Leuckart, 1828
**Synonyms:** Sipunculidae Baird, 1868:77 [partim]
Phascolosomatidae Stephen and Edmonds, 1972:269 [partim]; Gibbs and Cutler 1987:54 [partim]; Cutler, 1994:156 [partim]
**Diagnosis:** Small to medium sized worms (trunk up to 12 cm in length). Introvert usually of equal size or much longer than trunk. Hooks recurved, usually with internal structures or series of basal spinelets. Hooks typically closely packed in regularly spaced rings. Short tentacles surrounding the nuchal organ in an arc. Outer trunk wall with obvious papillae covering the whole body, concentrated at anterior and/or posterior end of trunk. Internally longitudinal muscle subdivided into anastomosing bands or a thinner continuous layer. Four introvert retractor muscles. Contractile vessel smooth but may be large with

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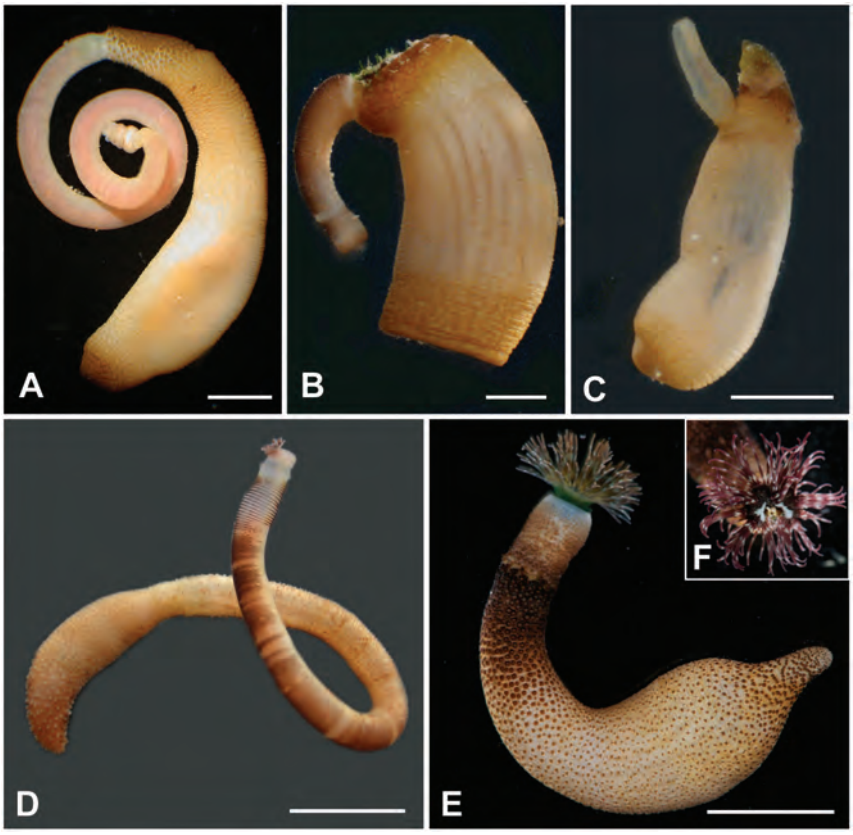


**Fig. 6.1.9:** Aspidosiphonidae, Phascolosomatidae and Antillesomatidae. A, *Aspidosiphon parvulus* (©G.Y. Kawauchi), scale bar = 2 mm. B, *Aspidosiphon steenstrupii* (©A. Schulze), scale bar = 5 mm. C, *Aspidosiphon cristatus* (©A. Schulze), scale bar = 2 mm. D, *Phascolosoma nigrescens* (©A. Schulze), scale bar = 10 mm. E, *Antillesoma antillarum* (©G. Y. Kawauchi), scale bar = 10 mm. F, *Antillesoma antillarum* tentacular crown (©G.Y. Kawauchi).

bulbous pouches or swelling in some species. Spindle muscle attached or not posteriorly. Two nephridia, uni or bilobed.

**Genus *Phascolosoma* Leuckart, 1828** (Fig. 6.1.9 D)
**Type species:** *Phascolosoma granulatum* Leuckart, 1828
**Synonyms:** *Phascolosoma* Leuckart, 1828:22; Fisher, 1950a:551; Stephen and Edmonds, 1972:270; Gibbs and Cutler, 1987:54; N. Cutler and Cutler, 1990:691
*Phascolosomum* Diesing, 1851:63 [partim]
*Phymosomum* Quatrefages, 1865b:621
*Phymosoma* Selenka *et al.* 1883:54
*Physcosoma* Selenka, 1897:460
**Diagnosis:** Introvert length commonly equal to trunk. Hooks recurved with internal structures organized in rings at distal tip of introvert. Tentacular crown consisting of fewer than 30 tentacles surrounding the nuchal organ. Inner trunk wall in continuous or occasionally anastomosing bands. Contractile vessel without bulbous pouches or swelling, not true villi. Spindle muscle attached posteriorly. A pair of unilobed nephridia.

**Genus *Apionsoma* Sluiter, 1902**
**Synonyms:** *Apionsoma* Sluiter, 1902:42; E. Cutler *et al.*, 1984:299; Gibbs and Cutler, 1987:55
*Golfingia* (*Apionsoma*) Murina, 1975d: 1748; E. Cutler, 1979:382
*Golfingia* (*Mitosiphon*) Fisher, 1950a:550; Stephen and Edmonds, 1972:113; E. Cutler, 1973:139
*Golfingia* (*Phascolana*) Wesenberg-Lund, 1959a:183; Stephen and Edmonds, 1972:116
**Diagnosis:** Small specimens commonly less than 20 mm in trunk length. Introvert much longer than trunk. Hooks recurved, organized in rings with series of accessory spinelets at the bases. Longitudinal musculature of inner trunk in bands or continuous. Contractile vessel without bulbous pouches or swelling, not true villi. Spindle muscle unattached or attached posteriorly. A pair of bilobed nephridia.

**Family Siphonosomatidae Kawauchi *et al.*, 2012**
**Type genus:** *Siphonosoma* Spengel, 1012
Sipunculidae Baird, 1868:77 [partim], Stephen and Edmonds 1972:19 [partim], Cutler and Gibbs 1985:166 [partim, Gibbs and Cutler, 1987:47 [partim], Cutler, 1994:24 [partim]
**Diagnosis:** Medium to large worms (trunk >50 mm). Introvert much shorter than trunk. Hooks, if present, in rings; likewise, prominent conical papillae. Oral disc bearing tentacles arranged around the mouth. Inner trunk wall

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with small irregular sac-like coelomic extensions. Circular and longitudinal muscle layers in anastomosing, sometimes indistinct, bands. Two to four introvert retractor muscles. Contractile vessel with or without villi. Spindle muscle attached posteriorly. Two nephridia.

**Genus *Siphonosoma* Spengel, 1912** (Fig. 6.1.8 C)
*Siphonosoma* Spengel, 1912:264.–Stephen and Edmonds, 1972:43.–E. Cutler and Cutler, 1982:748
*Siphonosoma* (*Dasmosiphon*) Fisher, 1950b:805.–Stephen and Edmonds, 1972:44
*Siphonosoma* (*Siphonosoma*) Fisher, 1950b:805.–Stephen and Edmonds, 1972:58
*Siphonosoma* (*Hesperosiphon*) Fisher, 1950b:805.–Stephen and Edmonds, 1972:43
**Diagnosis:** Usually large specimens with trunk longer than 50 mm in adults. Introvert shorter than trunk, with conical papillae, and sometimes hooks, arranged in rings. Coelomic extensions in body wall, irregular and saclike. Anastomosing longitudinal muscles, sometimes divided into distinct bands. Two pairs of retractor muscles. Contractile vessels, with or without villi. A pair of nephridia.

**Genus *Siphonomecus* Fisher, 1947**
**Type species:** *Siphonosoma australe* (Keferstein, 1865)
*Siphonomecus* Fisher, 1947:363.–Stephen and Edmonds, 1972:73.–E. Cutler, 1986:490
**Diagnosis:** Introvert shorter than trunk, with hooks and conical papillae in rings. Tentacular crown around mouth. Coelomic extensions in body wall. Circular and longitudinal muscle layers assemble into anastomosing bands. A pair of retractor muscles. The contractile vessel with villi. Spindle muscle attached posteriorly. A pair of nephridia.

**Family Antillesomatidae Kawauchi *et al.*, 2012**
**Type genus:** *Antillesoma* Stephen and Edmonds, 1972
Phascolosomatidae Stephen and Edmonds, 1972:269 [partim]; Cutler and Gibbs 1985:166; Gibbs and Cutler, 1987:51 [partim]; Cutler 1994:156 [partim]
**Diagnosis:** Medium-sized worms with trunk up to 80 mm in length. Introvert shorter than trunk. Few hooks present only in small individuals (less than 10 mm in length). Oral disc bearing numerous tentacles (30–200) in adults, enclosing nuchal organ. Body wall with longitudinal muscle layer gathered into anastomosing bands. Contractile vessel with many villi. Two pairs of introvert retractor muscles, the lateral pair often extensively fused. Spindle muscle attached posteriorly. Two nephridia.

**Genus *Antillesoma* (Stephen and Edmonds, 1972)**
(Fig. 6.1.9 E, F)
**Types species:** *Antillesoma antillarum* (Grube and Oersted, 1858)
**Synonyms:** *Phascolosoma* (*Antillesoma*) Stephen and Edmonds, 1972:277; E. Cutler, and Cutler, 1983:176
*Antillesoma* E. Cutler, and Cutler, 1985:163; Gibbs and Cutler, 1987:55
**Diagnosis:** Small- to medium-sized worms (up to 80 mm long). Introvert variable in length, but often about equal to trunk. Numerous slender digitiform tentacles (>30 in adults), arranged around nuchal organ. No hooks in adults. Introvert and trunk covered by dark brown papillae. Inner trunk wall with longitudinal muscle layer divided into anastomosing bands. A pair of introvert retractor muscles, but each lateral pair may be considerably fused, appearing as one muscle on each side of the nerve cord, with a small bifurcation near the origin. Contractile vessel with distinct digitiform villi. Spindle muscle attached posteriorly. Two nephridia.

## References


Adrianov, A.V., Malakhov, V.V. & Maiorova, A.S. (2006): Development of the tentacular apparatus in sipunculans (Sipuncula): I. *Thysanocardia nigra* (Ikeda, 1904) and *Themiste pyroides* (Chamberlin, 1920). *Journal of Morphology* 267(5): 569–583.

Åkesson, B. (1958): A study of the nervous system of the Sipunculoideae. With some remarks on the development of the two species *Phascolion strombi* Montagu and *Golfingia minuta* Keferstein. Undersökningar över Öresund 38: 1–249.

Åkesson, B. (1961): The development of *Golfingia elongata* Keferstein (Sipunculidea) with some remarks on the development of neurosecretory cells in sipunculids. *Arkiv for Zoologi* 13(23): 511–531.

Andreae, J. (1882): Beiträge zur Anatomie und Histologie des *Sipunculus nudus* L. *Zeitschrift für Wissenschaftliche Zoologie* 36: 201–255.

Andrews, E.A. (1890): Notes on the anatomy of *Sipunculus gouldii* Pourtalès. *Johns Hopkins University Biological Laboratory Studies* 4: 390–430.

Antonelli, F., Perasso, C.S., Ricci, S. & Petriaggi, B.D. (2015): Impact of the sipunculan *Aspidosiphon muelleri* Diesing, 1851 on calcareous underwater cultural heritage. *International Biodeterioration & Biodegradation* 100: 133–139.

Baltzer, F. (1931): Sipunculida. In: Kükenthal, W. & Krumbach, T. (eds.) *Handbuch der Zoologie*. De Gruyter, Berlin: 15–61.

Bedini, R., Pucciarelli, S., Gatta, R., Nannelli, A. & Miceli, C. (2004): HSP70 gene expression in sipunculids: a new biomarker for monitoring marine deposits. *Chemistry and Ecology* 20(sup1): 345–352.

Bjorndal, K.A. (1996): 8 Foraging ecology and nutrition of sea turtle. pp 199–232 in Lutz, P.L. & Musick, J.A. (eds.) The biology of sea turtles. CRC Press, Boca Raton, FL.


EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Boore, J.L. & Staton, J.L. (2002): The mitochondrial genome of the sipunculid *Phascolopsis gouldii* supports its association with Annelida rather than Mollusca. *Molecular Biology and Evolution* 19(2): 127–137.

Boyer, B.C., Henry, J.J. & Martindale, M.Q. (1998): The cell lineage of a polyclad turbellarian embryo reveals close similarity to coelomate spiralians. *Developmental Biology* 204(1): 111–23.

Boyle, M.J. & Rice, M.E. (2014): Sipuncula: an emerging model of spiralian development and evolution. *The International Journal of Developmental Biology* 58: 485–499.

Boyle, M.J. & Rice, M.E. (in press): Comparative development and the evolution of life history diversity in sipuncula. In: Boyle, M.J. & Kawauchi, G.Y. (eds.) Proceedings of the 2nd International Symposium on the Biology of the Sipuncula. Smithsonian Contributions to the Marine Sciences, Vol. 42 Smithsonian Institution Scholarly Press, Washington, DC: 11–34.

Boyle, M.J. & Seaver, E.C. (2010): Expression of FoxA and GATA transcription factors correlates with regionalized gut development in two lophotrochozoan marine worms: *Chaetopterus* (Annelida) and *Themiste lageniformis* (Sipuncula). *EvoDevo* 1(1): 2.

Boyle, M.J., Yamaguchi, E. & Seaver, E.C. (2014): Molecular conservation of metazoan gut formation: evidence from expression of endomesoderm genes in *Capitella teleta* (Annelida). *EvoDevo* 5: 39.

Carvalho, S., Constantino, R., Cerqueira, M., Pereira, F., Subida, M.D., Drake, P. & Gaspar, M.B. (2013): Short-term impact of bait digging on intertidal macrobenthic assemblages of two south Iberian Atlantic systems. *Estuarine, Coastal and Shelf Science* 132: 65–76.

Clark, R.B. (1969): Systematics and phylogeny: Annelida, Echiura, Sipuncula. In: Florkin, M. & Scheer, B.T. (eds.) *Chemical Zoology*. Academic Press, London: 1–62.

Costello, D.P. & Henley, C. (1976): Spiralian development: a perspective. *American Zoologist* 16(3): 277–291.

Cristo, M. (1998): Feeding ecology of *Nephrops norvegicus* (Decapoda: Nephropidae). *Journal of Natural History* 32(10–11): 1493–1498.

Cutler, E.B. (1994): *The Sipuncula. Their Systematics, Biology and Evolution*. Cornell University Press, Ithaca, NY.

Ditadi, A.S.F. (1982): Intertidal sipunculans (*Sipunculus*) from Southern Brazil. *Revista Brasileira de Biologia* 42 (4): 785–800.

Dordel, J., Fisse, F., Purschke, G. & Struck, T.H. (2010): Phylogenetic position of Sipuncula derived from multi-gene and phylogenomic data and its implication for the evolution of segmentation. *Journal of Zoological Systematics and Evolutionary Research* 48(3): 197–207.

Dunn, C.W., Hejnol, A., Matus, D.Q., *et al.* (2008): Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452(7188): 745–749.

Edmonds, S.J. (1962): Some notes on the abundance, environment, and nutrition of *Sipunculus nudus* L. (Sipunculoidea) at Morgat, Brittany. *Cahiers de Biologie Marine III:* 183–190.

Ferguson, M.C., Waite, J.M., Curtice, C., Clarke, J.T. & Harrison, J. (2015): Biologically important areas for cetaceans within U.S. waters – Aleutian Islands and Bering Sea region. *Aquatic Mammals* 41(1): 79–93.

Fonseca, A.C., Dean, H.K. & Cortés, J. (2006): Non-colonial coral macro-borers as indicators of coral reef status in the south Pacific of Costa Rica. *Revista de Biología Tropical* 54(1): 101–115.

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

Franzén, Å. (1977): Sperm structure with regard to fertilization biology and phylogenetics. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 1977: 123–138.

Freeman, G. & Lundelius, J.W. (1992): Evolutionary implications of the mode of D quadrant specification in coelomates with spiral cleavage. *Journal of Evolutionary Biology* 5(2): 205–247.

Fu, X.-M., Zhang, M.-Q., Shao, C.-L., Li, G.-Q., Bai, H., Dai, G.-L., Chen, Q.-W., Kong, W., Fu, X.-J. & Wang, C.-Y. (2016): Chinese marine materia medica resources: status and potential. *Marine Drugs* 14(46): 1–27.

Gerould, J.H. (1906): The Development of *Phascolosoma* (Studies on the embryology of the Sipunculidae II). *Zoologische Jahrbücher. Abtheilung für Anatomie und Ontogenie der Tiere* 23(1): 77–162.

Gerould, J.H. (1938): The eyes and nervous system of *Phascolosoma verrillii* and other sipunculids. *Travaux Station zoologique de Wimereux* 13: 313–325.

Gibbs, P.E. (1975): Gametogenesis and spawning in a hermaphroditic population of *Golfingia minuta* (Sipuncula). *Journal of the Marine Biological Association of the United Kingdom* 55(1): 69–82.

Gibbs, P.E. (1987): A new species of *Phascolosoma* (Sipuncula) associated with a decaying whale's skull trawled at 880 m depth in the South-west Pacific. *New Zealand Journal of Zoology* 14(1): 135–137.

Glynn, P.W. & Manzello, D.P. (2015): Bioerosion and coral reef growth: a dynamic balance. In: Birkeland, C. (ed.) *Coral Reefs in the Anthropocene*. Springer Netherlands, Dordrecht: 67–97.

Gonse, P.H. (1956a): L'ovogenèse chez *Phascolosoma vulgare*. I. Définition cytologique des stades de croissance des ovocytes. *Acta Zoologica* 37(3): 193–224.

Gonse, P.H. (1956b): L'ovogenèse chez *Phascolosoma vulgare*. II. Recherches biométriques sur les ovocytes. *Acta Zoologica* 37(3): 255–233.

Graf, G. (1989): Benthic-pelagic coupling in a deep-sea benthic community. *Nature* 341(6241): 437–439.

Green, W.A. (1975): *Phascolosoma lurco*: a semi-terrestrial sipunculan. In: Rice, M.E. & Todorovic, M. (eds.) *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura*. Naucno Delo Press, Belgrade: 267–280.

Hall, J.R. & Scheltema, R.S. (1975): Comparative morphology of open-ocean pelagosphera. Rice, M.E. & Todorovic, M. (eds.) *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura.* Naucno Delo Press, Belgrade: 183–197.

Hatschek, B. (1883): Ueber Entwicklung von *Sipunculus nudus*. In Claus, D.C. (ed.) *Arbeiten aus dem Zoologischen Institute der Universität-Wien und der Zoologischen Station in Triest*. Alfred Hölder, Wien: 61–140.

Hejnol, A., Martindale, M.Q. & Henry, J.Q. (2007): High-resolution fate map of the snail *Crepidula fornicata*: the origins of ciliary bands, nervous system, and muscular elements. *Developmental Biology* 305(1): 63–76.

Hejnol, A., Obst, M., Stamatakis, A., *et al.* (2009): Assessing the root of bilaterian animals with scalable phylogenomic methods.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

*Proceedings of the Royal Society B: Biological Sciences* 276(1677): 4261.
Henry, J.Q. & Martindale, M.Q. (1999): Conservation and innovation in spiralian development. Hydrobiologia 402(0): 255–265
Huang, D., Chen, J., Vannier, J. & Saiz-Salinas, J.I. (2004): Early Cambrian sipunculan worms from southwest China. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271(1549): 1671.
Hughes, R.N. (1974): A re-description of *Lithacrosiphon maldivensis* Shipley, 1902. *Zoological Journal of the Linnean Society* 55(3): 235–240.
Hyman, L.H. (1959): Phylum Sipunculida. In: L.H. Hyman (ed) *The Invertebrates. Smaller Coelomate groups*. McGraw-Hill, New York: 610–690.
Jägersten, G. (1963): On the morphology and behaviour of pelagosphaera larvae (Sipunculoidea). *Zoologiska Bidrag Fran Uppsala* 36(1): 27–35.
Jägersten, G. (1972): *Evolution of the Metazoan Life Cycle*. Academic Press, London.
Johnson, N.D., Sanders, C., Maiorova, A. & Schulze, A. (2016): Cryptic species in Pacific sipunculans (Sipuncula: Phascolosomatidae): east-west divergence between non-sister taxa. *Zoologica Scripta* 45(4): 455–463.
Johnson, N.D. & Schulze, A. (2016): Genetic structure in two *Phascolosoma* species in the Pacific Ocean. *Marine Biology Research* 12(7): 739–747.
Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.
Kawauchi, G. & Giribet, G. (2010): Are there true cosmopolitan sipunculan worms? A genetic variation study within *Phascolosoma perlucens* (Sipuncula, Phascolosomatidae). *Marine Biology* 157(7): 1417–1431.
Kawauchi, G.Y. & Giribet, G. (2014): *Sipunculus nudus* Linnaeus, 1766 (Sipuncula): cosmopolitan or a group of pseudo-cryptic species? An integrated molecular and morphological approach. *Marine Ecology* 35(4): 478–491.
Kawauchi, G.Y., Sharma, P.P. & Giribet, G. (2012): Sipunculan phylogeny based on six genes, with a new classification and the descriptions of two new families. *Zoologica Scripta* 41(2): 186–210.
Kristof, A., Wollesen, T., Maiorova, A.S. & Wanninger, A. (2011): Cellular and muscular growth patterns during sipunculan development. *Journal of Experimental Zoology. Part B: Molecular and Developmental Evolution* 316B(3): 227–240.
Kristof, A., Wollesen, T. & Wanninger, A. (2008): Segmental mode of neural patterning in Sipuncula. *Current Biology* 18(15): 1129–1132.
Lamarck, J.B. (1816): *Histoire naturelle des animeaux sans vertèbres*. Verdière, Paris.
Lemer, S., Kawauchi, G.Y., Andrade, S.C.S., González, V.L., J. Boyle, M. & Giribet, G. (2015): Re-evaluating the phylogeny of Sipuncula through transcriptomics. *Molecular Phylogenetics and Evolution* 83: 174–183.
Li, J., Zhu, C., Guo, Y., Xie, X., Huang, G. & Chen, S. (2015): Experimental study of bioturbation by *Sipunculus nudus* in a polyculture system. *Aquaculture* 437: 175–181.
Linnaeus, C. (1766): *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Holmiae, Stockholm.
Liu, Y. & Qiu, C. (2016): Calculated taste activity values and umami equivalences explain why dried sha-chong (*Sipunculus nudus*) Is a valuable condiment. *Journal of Aquatic Food Product Technology* 25(2): 177–184.
MacAvoy, S.E., Fisher, C.R., Carney, R.S. & Macko, S.A. (2005): Nutritional associations among fauna at hydrocarbon seep communities in the Gulf of Mexico. *Marine Ecology Progress Series* 292: 51–60.
Maiorova, A. & Adrianov, A.V. (2010): Distribution of peanut worms (Sipuncula) in the West Pacific. In: Sun, S., Liu, R., Adrianov, R. & Lutaenko, K. (eds.) Proceedings of China-Russia Bilateral Symposium on "Comparison on Marine Biodiversity in the Northwest Pacific Ocean"; Qingdao, China: 13–17.
Maslakova, S.A., Martindale, M.Q. & Norenburg, J.L. (2004): Fundamental properties of the spiralian developmental program are displayed by the basal nemertean *Carinoma tremaphoros* (Palaeonemertea, Nemertea). *Developmental Biology* 267(2): 342–360.
Matozzo, V., Cima, F., Perin, L. & Ballarin, L. (2001): Phagocytic and enzymatic activities of cells and urn cell complexes in the coelomic fluid of the marine worm *Sipunculus nudus* (Sipuncula). *Italian Journal of Zoology* 68(4): 273–280.
Maxmen, A.B., King, B.F., Cutler, E.B. & Giribet, G. (2003): Evolutionary relationships within the protostome phylum Sipuncula: a molecular analysis of ribosomal genes and histone H3 sequence data. *Molecular Phylogenetics and Evolution* 27(3): 489–503.
Meyer, N.P. & Seaver, E.C. (2010): Cell lineage and fate map of the primary somatoblast of the polychaete annelid *Capitella teleta*. *Integrative and Comparative Biology* 50(5): 756–767.
Muir, L.A. & Botting, J.P. (2007): A Lower Carboniferous sipunculan from the Granton Shrimp Bed, Edinburgh. *Scottish Journal of Geology* 43(1): 51–56.
Müller, C.H.G., Hylleberg, J. & Michalik, P. (2015): Complex epidermal organs of *Phascolion* (Sipuncula): insights into the evolution of bimodal secretory cells in annelids. *Acta Zoologica* 96(3): 343–374.
Mwinyi, A., Meyer, A., Bleidorn, C., Lieb, B., Bartolomaeus, T. & Podsiadlowski, L. (2009): Mitochondrial genome sequence and gene order of *Sipunculus nudus* give additional support for an inclusion of Sipuncula into Annelida. *BMC Genomics* 10(1): 27.
Nishikawa, T. (2017): Some comments on the taxonomy of the peanut worms (Annelida: Sipuncula) in Japanese waters toward a future revision. In: Motokawa, M. & Kajihara, H. (eds.) *Species Diversity of Animals in Japan*. Springer Japan, Tokyo: 469–476.
Parry, L., Tanner, A. & Vinther, J. (2014): The origin of annelids. *Palaeontology* 57:(6) 1091–1103.
Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D. & Vinther, J. (2016): The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society B: Biological Sciences* 283(1837): 20161378.
Paul, G. (1910): Über *Petalostoma minutum* Keferstein und verwandte Arten nebst einigen Bemerkungen zur Anatomie von *Onchnesoma steenstrupii*. *Zoologische Jahrbücher, Abtheilung fur Anatomie und Ontogenie der Tiere* 29: 1–50.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Pilger, J.F. (1982): Ultrastructure of the tentacles of *Themiste lageniformis* (Sipuncula). *Zoomorphology* 100(2): 143–156.

Pilger, J.F. (1987): Reproductive biology and development of *Themiste lageniformis*, a parthenogenic sipunculan. *Bulletin of Marine Science* 41(1): 59–67.

Purschke, G., Wolfrath, F. & Westheide, W. (1997): Ultrastructure of the nuchal organ and cerebral organ in *Onchnesoma squamatum* (Sipuncula, Phascolionidae). *Zoomorphology* 117(1): 23–31.

de Quatrefages, A. (1847): Études sure les types inférieures de l'embranchement des Annelés. *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences (Paris)* 24(18): 776–779.

Rajulu, G.S. & Krishnan, N. (1969): Occurrence of asexual reproduction by budding in Sipunculida. *Nature* 223(5202): 186–187.

Reunov, A. & Rice, M.E. (1993): Ultrastructural observations on spermatogenesis in *Phascolion cryptum* (Sipuncula). *Transactions of the American Microscopical Society* 112(3): 195–207.

Rice, M.E. (1966) Reproductive biology and development of Sipuncula [dissertation]: University of Washington.

Rice, M.E. (1967): A comparative study of the development of *Phascolosoma agassizii*, *Golfingia pugettensis*, and *Themiste pyroides* with a discussion of developmental patterns in the Sipuncula. *Ophelia* 4: 143–171.

Rice, M.E. (1969): Possible boring structures of Sipuncula. *American Zoologist* 9(3): 803–812.

Rice, M.E. (1970): Asexual reproduction in a sipunculan worm. *Science* 167(3925): 1618–1620.

Rice, M.E. (1973): *Morphology, Behavior, and Histogenesis of the Pelagosphera Larva of Phascolosoma agassizii (Sipuncula)*. Smithsonian Institution Press, Washington, DC.

Rice, M.E. (1974): Gametogenesis in three species of Sipuncula: *Phascolosoma agassizii*, *Golfingia pugettensis*, and *Themiste pyroides*. *La Cellule* 70(2–3): 295–313.

Rice, M.E. (1975a): Observations on the development of six species of Caribbean Sipuncula with a review of development in the phylum. In: Rice, M.E. & Todorovic, M. (eds.) *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura*. Naučno Delo Press, Belgrade: 35–49.

Rice, M.E. (1975b): Sipuncula. In: Giese, A.C. & Pearse, J.S. (eds.) *Reproduction of Marine Invertebrates: Entoprocts and Lesser Coelomates*. Academic Press, New York: 67–127.

Rice, M.E. (1976): Larval development and metamorphosis in Sipuncula. *American Zoologist* 16(3): 563–571.

Rice, M.E. (1978): Morphological and behavioral changes at metamorphosis in the Sipuncula. In: Rice, M.E. & Chia, F.S. (eds.) *Settlement and Metamorphosis of Marine Invertebrate Larvae*. Elsevier North-Holland Biomedical, Amsterdam: 83–102.

Rice, M.E. (1981): Larvae adrift: patterns and problems in life histories of sipunculans. *American Zoologist* 21(3): 605–619.

Rice, M.E. (1983): Sipuncula. In: Adiyodi, K.G. & Adiyodi, R.G. (eds.) *Reproductive Biology of Invertebrates, Oogenesis, Oviposition and Oosorption*. John Wiley & Sons Ltd, Chichester and New York: 283–296.

Rice, M.E. (1985a): Description of a wood dwelling sipunculan, *Phascolosoma turnerae*, new species. *Proceedings of the Biological Society of Washington* 98(1): 54–60.

Rice, M.E. (1985b): Sipuncula: developmental evidence for phylogenetic inference. In: Morris, S.C., George, J.D., Gibson, R. & Platt, H.M. (eds.) *The Origins and Relationships of Lower Invertebrates*. Oxford University Press, Oxford: 274–296.

Rice, M.E. (1988): Observations on development and metamorphosis of *Siphonosoma cumanense* with comparative remarks on *Sipunculus nudus* (Sipuncula, Sipunculidae). *Bulletin of Marine Science* 42(1): 1–15.

Rice, M.E. (1989): Comparative observations of gametes, fertilization, and maturation in sipunculans. Ryland, J.S. & Tyler, P.A. (eds.) *Proceedings of the 23rd European Biology Symposium: Reproduction, Genetics and Distributions of Marine Organisms*. Olsen and Olsen, Fredensborg, Denmark: 167–182.

Rice, M.E. (1993): Sipuncula. In: Harrison, F.W. & Rice, M.E. (eds.) *Microscopic Anatomy of Invertebrates: Onychophora, Chilopoda, and Lesser Protostomata*. Wiley-Liss, New York: 237–325.

Rice, M.E., Piraino, J. & Reichardt, H.F. (1983): Observations on the ecology and reproduction of the sipunculan *Phascolion cryptus* in the Indian River Lagoon. *Florida Scientist* 46(3/4): 382–396.

Rice, M.E., Piraino, J., Reichardt, H.F. & Boyle, M.J. (in press): Observations on oceanic pelagosphera larvae (Sipuncula): morphology, behavior, and metamorphosis. In: Boyle, M.J. & Kawauchi, G.Y. (eds.) *Proceedings of the 2nd International Symposium on the Biology of the Sipuncula*. Smithsonian Contributions to the Marine Sciences, Vol. 42, Smithsonian Institution Scholarly Press, Washington, DC: 41–81.

Romero-Wetzel, M.B. (1987): Sipunculans as inhabitants of very deep narrow burrows in deep-sea sediments. *Marine Biology (Berlin)* 96(1): 87–92.

Ruppert, E.E., Fox, R.S. & Barnes, R.D. (2004): *Invertebrate Zoology. A Functional Evolutionary Approach*. Brooks/Cole, Belmont, CA.

Ruppert, E.E. & Rice, M.E. (1983): Structure, ultrastructure, and function of the terminal organ of a pelagosphera larva (Sipuncula). *Zoomorphology* 102(2): 143–163.

Saito, H., Kawai, K., Umino, T. & Imbayashi, H. (2014): Fishing bait worm supplies in Japan in relation to their physiological traits. *Memoirs of Museum Victoria* 71: 279–287.

Saiz-Salinas, J. I. (2018): Special contribution: almost five centuries of scientific study on the enigmatic sipunculan worms. In: Boyle, M.J. & Kawauchi, G.Y. (eds.) *Proceedings of the 2nd International Symposium on the Biology of the Sipuncula*. Smithsonian Contributions to the Marine Sciences, Smithsonian Institution Scholarly Press, Washington, DC: 219–235.

Sawada, N., Noda, Y. & Ochi, O. (1968): An electron microscope study on the oogenesis of *Golfingia ikedai*. *Memoirs of the Ehime University, Science, Series B (Biology)* 6(1): 25–39.

Scheltema, A.H. (1993): Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *Biological Bulletin* 184(1): 57–78.

Scheltema, R.S. & Rice, M.E. (1990): Occurrence of teleplanic pelagosphera larvae of sipunculans in tropical regions of the Pacific and Indian Oceans. *Bulletin of Marine Science* 47(1): 159–181.

Schulze, A., Cutler, E.B. & Giribet, G. (2005): Reconstructing the phylogeny of the Sipuncula. In: Bartolomaeus, T. & Purschke, G. (eds.) *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa*. Springer Netherlands, Dordrecht: 277–296.

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Schulze, A., Cutler, E.B. & Giribet, G. (2007): Phylogeny of sipunculan worms: a combined analysis of four gene regions and morphology. *Molecular Phylogenetics and Evolution* 42(1): 171–192.

Schulze, A., Hipes, J., Borda, E. & Rice, M. E. (in press). Who is who in the Sipuncula? Matching larvae and adults using DNA. In Boyle, M.J. & Kawauchi, G.Y. (eds.) *Proceedings of the 2nd International Symposium on the Biology of the Sipuncula*. Smithsonian Contributions to the Marine Sciences, Vol. 42 Smithsonian Institution Scholarly Press, Washington DC: 83–93.

Schulze, A., Maiorova, A., Timm, L.E. & Rice, M.E. (2012): Sipunculan larvae and "cosmopolitan" species. *Integrative and Comparative Biology* 52(4): 497–510.

Schulze, A. & Rice, M.E. (2009): Musculature in sipunculan worms: ontogeny and ancestral states. *Evolution & Development* 11(1): 97–108.

Sedgwick, A. (1898): Sipunculoidea (Gephyrea, Achaeta). In: *A student's handbook of zoology*. Schwan Sonnenschein, London; Macmillan, New York: 534–539.

Selenka, E. (1875): Eifurchung und larvenbildung von *Phascolosoma elongatum* Kef. *Zeitschrift für Wissenschaftliche Zoologie* 25: 442–450.

Shields, M.A. & Kedra, M. (2009): A deep burrowing sipunculan of ecological and geochemical importance. *Deep Sea Research Part I: Oceanographic Research Papers* 56(11): 2057–2064.

Staton, J. & Rice, M.E. (1999): Genetic differentiation despite teleplanic larval dispersal: allozyme variation in sipunculans of the *Apionsoma misakianum* species complex. *Bulletin of Marine Science* 65(2): 467–480.

Stearley, R.F. & Ekdale, A.A. (1989): Modern marine bioerosion by macroinvertebrates, northern Gulf of California. *Palaios* 4(5): 453–467.

Stephen, A.C. (1964): A revision of the classification of the phylum Sipuncula. *The Annals and Magazine of Natural History*, ser. 13 VII: 457–462.

Stephen, A.C. & Edmonds, S.J. (1972): *The Phyla Sipuncula and Echiura*. Trustees British Mus. (Nat. Hist.), London.

Struck, T.H., Paul, C., Hill, N., *et al.* (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471(7336): 95–98.

Taylor, J.D. (1984): A partial food web involving predatory gastropods on a Pacific fringing reef. *Journal of Experimental Marine Biology and Ecology* 74(3): 273–290.

Taylor, J.D. (1989): The diet of coral-reef Mitridae (Gastropoda) from Guam; with a review of other species of the family. *Journal of Natural History* 23(1): 261–278.

Telford, M.J., Wise, M.J. & Gowri-Shankar, V. (2005): Consideration of RNA secondary structure significantly improves likelihood-based estimates of phylogeny: examples from the bilateria. *Molecular Biology and Evolution* 22(4): 1129–1136.

Villegas, E.J.A., Ceballos-Vázquez, B.P., Markaida, U., Abitia-Cárdenas, A., Medina-López, M.A. & Arellano-Martínez, M. (2014): Diet of *Octopus bimaculatus* Verril, 1883 (Cephalopoda: Octopodidae) in Bahía De Los Ángeles, Gulf of California. *Journal of Shellfish Research* 33(1): 305–314.

Voss-Foucart, M.F., Barzin, S., Jeuniaux, C. & Bussers, J.C. (1977): Étude comparée de la composition chimique des regions souples et durcies de la cuticule de quatre espèces de siponculiens. *Cahiers de Biologie Marine* 18: 135–145.

Wanninger, A., Koop, D., Bromham, L., Noonan, E. & Degnan, B.M. (2005): Nervous and muscle system development in *Phascolion strombus* (Sipuncula). *Development, Genes and Evolution* 215(10): 509–518.

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

Weigert, A., Helm, C., Meyer, M., *et al.* (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31(6): 1391–1401.

Woods, M.C. & McLay, C.L. (1996): Diet and cryptic colouration of the crab *Eurynolambrus australis* (Brachyura: Majidae) at Kaikoura, New Zealand. Crustacean Research 25: 34–43.

Zuckerkandl, E. (1950): Coelomic pressures in *Sipunculus nudus*. *The Biological Bulletin* 98(2): 161–173.

Alexandra Kerbl and Katrine Worsaae

# 6.2 Lobatocerebridae Rieger, 1980

### Introduction

Lobatocerebridae is an exclusively meiofaunal annelid family with sizes of 1–3 mm in length and 40–110 µm in diameter, comprising an elongated head and a cylindrical, unsegmented body (Fig. 6.2.1 A, B). It contains only two described species: *Lobatocerebrum psammicola* Rieger, 1980 and *Lobatocerebrum riegeri* Kerbl, Bekkouche, Sterrer & Worsaae, 2015 from the shallow waters of the West Atlantic and Red Sea, respectively, and one undescribed species (*L.* sp. 1) from fine silty sediment at 800 m depth off Beaufort, North Carolina (Rieger 1980).

Lobatocerebridae have elongated, cylindrical, entirely ciliated bodies, which appear slightly greenish in light microscopes (LMs) due to the glandular epidermis (Fig. 6.2.1 B, F, G). They lack the usual characteristics of annelids such as distinct segmentation, parapodia, chaetae, or nuchal organs. The body may be divided into a head and a trunk region; a distinct prostomium and a pygidium are lacking. The head carries a ventral mouth opening and a large brain and is not clearly separated posteriorly from the uniform trunk or anteriorly from the elongated rostrum, which makes up 20–30% of the total body length. The distinct lobular, large brain with two frontal and four posterior lobes embracing the central neuropil is visible in LM and has prompted the family name (Fig. 6.2.1 B) (Rieger 1980, 1981, 1988, 1991, Kerbl *et al.* 2015). They are hermaphrodites, and the single male gonopore opens mid-dorsally, whereas lateral openings of the seminal receptacles are found in the posterior region of the body, anterior to the dorsal, subterminal anus (Fig. 6.2.1 A, B, D, E) (Rieger 1980, 1981, Kerbl *et al.* 2015).

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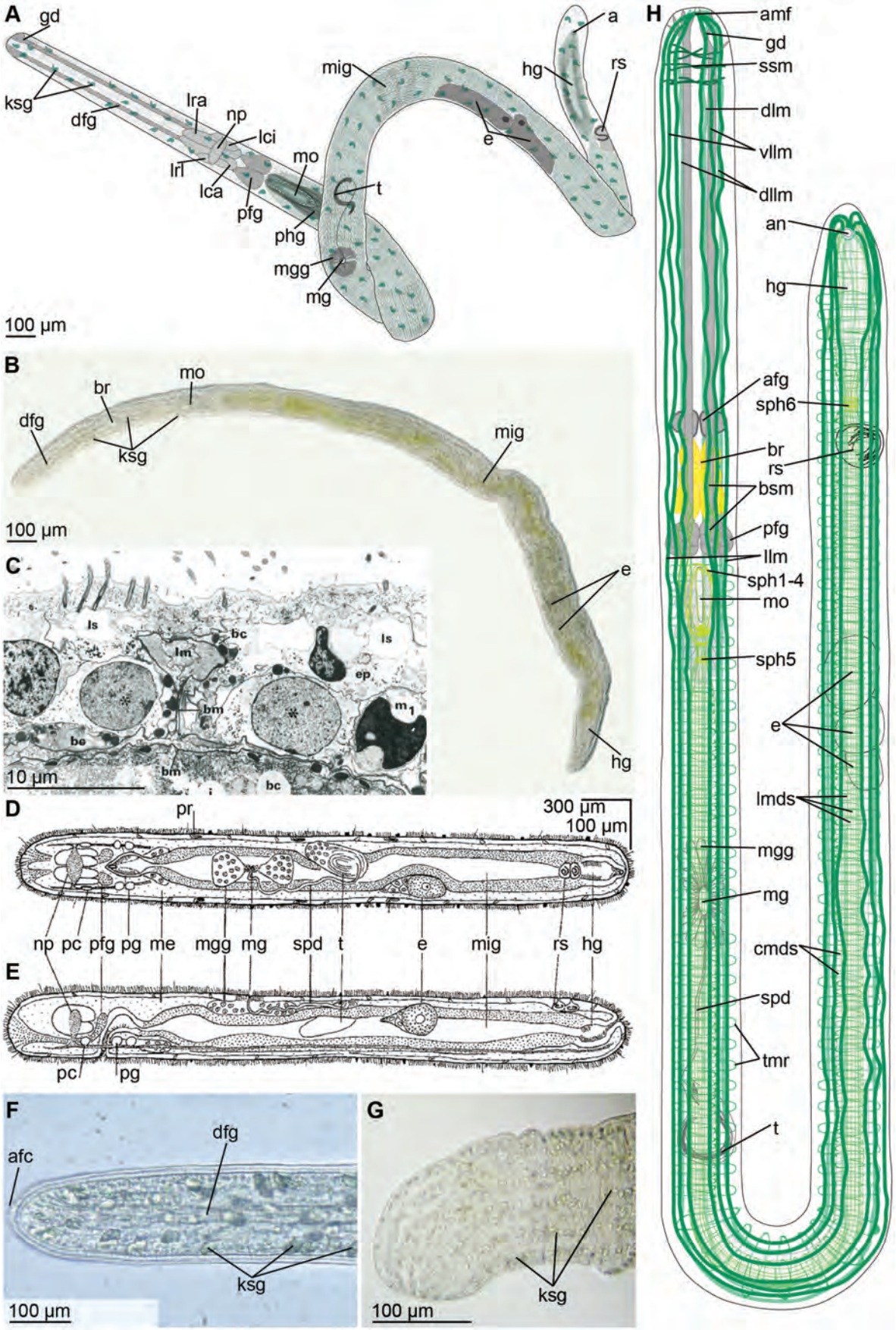


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The lack of common annelid traits and the exhibition of certain platyhelminthes-like characters, such as ciliated epidermis and musculature, originally made it difficult to address the affinity of this family in the tree of life: The initial detailed description with light and electron microscopy, as well as the following articles about selected organ systems, pointed out similarities to platyhelminthes, meiofaunal molluscs, and annelids. Whereas resemblances to flatworms and molluscs were mainly regarded as convergent adaptations to the confined interstitial habitat and the small body size, the resemblance to annelids could not be dismissed as easily (Rieger 1980, 1981, 1988, 1991). Yet, their lack of segmentation, nuchal organs, chaetae, and other annelid characteristics, as well as the presence of a unique muscular arrangement and several apomorphies (e.g., complete ciliation, unpaired middorsal gonopore, and acoelomate body cavity), made Rieger and colleagues end up placing them in a new phylum, Lobatocerebromorpha in 1991 (Haszprunar *et al.* 1991). Their ongoing status as "Problematicum" reflecting their unique morphology and rare occurrences was only recently addressed in a phylogeny based on transcriptomic data, finding Lobatocerebridae to group with Sipuncula within Annelida (Laumer *et al.* 2015). The support for this exact relationship was not strong, but they were consistently nested within and not next to Annelida, a relationship also suggested in a morphology-based phylogeny (Zrzavý 2003) and further supported by a recent neuromuscular study (Kerbl *et al.* 2015).

## Morphology

### External morphology

Lobatocerebridae are elongated, completely ciliated microscopic animals with a body length of 1–3 mm and a diameter of 40–110 µm. They do not show any external signs of segmentation, as well as lack an obvious differentiation between the anterior and posterior end of body, which are both rounded off (Fig. 6.2.1 A, B, D–H). Both *L. psammicola* and *L. riegeri* have an overall speckled appearance due to large, randomly scattered, slightly green epidermal glands (Fig. 6.2.1 A, B, F, G) (Rieger 1980, 1981, 1991, Kerbl *et al.* 2015). Rieger (1980) further assigned some of the greenish tint of *L. psammicola* to numerous small granules found with transmission electron microscopy (TEM) in a complex of highly branched cells (basal granule cells, also called gliointerstitial cell system; Fig. 6.2.2 D) (Rieger 1980, 1981); these granules could not be identified in the TEM sections of *L. riegeri* (Kerbl *et al.* 2015).

### Anatomy

**Cuticle.** A well-developed cuticle covers the entire body and consists of a thick collagenous fiber grid and a fine fibrous matrix covered by a thin epicuticle with glycocalyx lining (Fig. 6.2.1 C) (Rieger 1980, 1981). The epicuticle is electron-dense, fibrous, and covered by a 50-nm-thick layer of glycocalyx-filaments in *L. psammicola*, which are oriented perpendicular to the cuticular surface. It differs between some of the species, as the surface coat of the epicuticle is nearly three times more massive in *L.* sp. I from 800 meters depth (Rieger 1981). Although this configuration seems to be more complex than in other meiofaunal annelids such as Protodrilidae, Hesionidae, Nerillidae, and Dinophilidae (Rieger and Rieger 1976, Westheide and Rieger 1978, Hausen 2005, Worsaae 2014, Martinez *et al.* 2017), it resembles the microvillar cuticle of larger annelids more closely than the cuticle-like extracellular fibrous matrices present in certain free-living Platyhelminthes and Acoela (Rieger and Rieger 1976, Rieger 1980).

**Epidermis.** The epidermis is dominated by multiciliated cells, interspersed with different types of gland cells, and

▸ **Fig. 6.2.1:** Overall morphology, integument, and musculature of *Lobatocerebrum*. A, Schematic drawing of *Lobatocerebrum riegeri*. B, Light microscopic image of *Lobatocerebrum psammicola* from Bocas del Toro. C, Electron micrograph of *L. psammicola*. D, E, Schematic habitus drawing including most organ systems of *L. psammicola*, in dorsal (D) and lateral (E) views. F, G, The anterior region focusing on the integument and the kidney-shaped glands in *L. riegeri* (F), with special emphasis on their row-like arrangement in *L. psammicola* (G). H, Schematic representation of the body wall musculature of *L. riegeri*. a (an), anus; ac, anterior cilium; afc, anteriofrontal cilia; afg, anterior portion of the frontal gland; amf, anterior point of muscular fusion; bc, basal cell; bm, extracellular matrix; br, brain; bsm, brain supportive musculature; cmds, circular muscle of the digestive system; dfg, duct of the frontal glands; dllm, dorsolateral longitudinal muscle; dlm, dorsal longitudinal muscle; e, egg; ep, epidermis cell; gd, glandular duct; hg, hindgut; ksg, kidney-shaped gland; lca, major caudal lobe; lci, minor caudal lobe; llm, lateral longitudinal muscle; lm, longitudinal muscle; lmds, longitudinal muscle of the digestive system; lr, rostral lobe; lra, major rostral lobe; lrl, lateral rostral lobe; ls, large surface vesicle; m1, type 1 mucous gland (*L. psammicola*); me, mesenchym; mg, male gonopore; mgg, male gonopore gland; mig, midgut; mo, mouth opening; np, neuropil; pc, postcerebral ganglion in *L. psammicola* (maybe synonymous with lateral ganglion in *L. riegeri*); pfg, posterior frontal gland; pg, postpharyngeal ganglion; phg, pharyngeal gland; pr, protonephridium; rs, seminal receptacle; spd, spermioduct; sph1-6, sphincters 1-6; ssm, star-shaped muscle; t, testis; tmr, transverse muscular ring complexes; vllm, ventrolateral longitudinal muscle; vlm, ventral longitudinal muscle. A, F, H, From Kerbl *et al.* (2015); C, D, E, from Rieger (1980), with permission.

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sparsely distributed monociliated sensory cells (Fig. 6.2.1 C) (Rieger 1980, Kerbl *et al.* 2015). An intertwining network of highly branched gliointerstitial cells (basal granule cells) may support the maintenance and function of the extracellular matrix (Fig. 6.2.1 C) (Rieger 1980, 1981). The entirely ciliated epidermis of *Lobatocerebrum* mostly resembles the ciliation pattern of free-living flatworms (as well as nemerteans, interstitial molluscs, cnidarians, or gnathostomulids), while meiofaunal annelids (except for Psammodrilidae) usually have cilia in a distinct pattern: the ciliation may be restricted to the ventral side, parts of the anterior region, (segmental) transverse rows, bands, or tufts (e.g., Worsaae and Kristensen 2005, Westheide 2008). Yet, the basal granule cells as found in *L. psammicola* (Fig. 6.2.1 C) (Rieger 1980, 1981) are quite common in annelids and usually absent in Platyhelminthes and many other invertebrates. Like glial cells, they are located above the basal lamina and between longitudinal muscle cells and epidermal cells like in other annelids (Rieger and Rieger 1976, Rieger 1981). TEM sections of *L. psammicola* also showed that the cuticularized ciliated epidermis continues into the foregut, presenting a densely ciliated pharynx and esophagus as found in several other annelid groups (Fig. 6.2.1 C) (Rieger 1980). All derivates of the epidermis (e.g., nervous system, epidermal glands) are clearly separated from mesodermal derivates (e.g., muscles, mesenchymal cells, gonads) in Lobatocerebridae by an extracellular matrix (Rieger 1980, 1988).

Circumferentially arranged peripheral nerves and longitudinal muscles are embedded into the layer of epithelial cells, which are separated by the extracellular matrix and large, nonmuscular mesenchymal filling cells (Fig. 6.2.1 C) from the gut epithelium. Only parts of the transverse muscle ring complexes are embedded into the epidermal layer, while the remaining parts are located more internal, internal to the extracellular matrix.

**Glands.** Lobatocerebridae have several types of broadly distributed epidermal unicellular glands as well as organ-associated, multicellular glandular complexes (Fig. 6.2.2). The glandular pores are all surrounded by a ring of microvilli, some of which penetrate the cuticle (Rieger 1981, Kerbl *et al.* 2015; Fig. 6.2.1 A, C–F). Whereas gland cell types with associated microvillar collars or specializations around the openings are common in many annelid taxa as well as in Cnidaria, Echinodermata, Enteropneusta, Gastrotricha, and Mollusca; free-living flatworms do not show such specializations (Rieger 1980, 1981). Together with the existence of a basal granule cell complex above the extracellular matrix, the epidermal glands further support the hypothesis about homologies in the body wall of *Lobatocerebrum* and annelids (Rieger, 1980).

There are several types of unicellular epidermal glands (Fig. 6.2.2 A–F), which can be distinguished based on their cellular characteristics and their vesicular and/or granular content: e.g., (1) Ciliated glands (Fig. 6.2.2 A, D, F) (also called regular scattered mucus glands by Rieger 1981) have the largest volume, and their cell membranes exhibit pairwise-arranged tubulin immunoreactive (IR) strands of cytoskeletal material. A circle of short tubulin IR structures around the gland opening was wrongly interpreted in Kerbl *et al.* (2015) as cilia with confocal laser scanning microscopy due to a strong IR signal (Fig. 6.2.2 A), but is now after better alignment with TEM shown to instead be thickened microvilli (Fig. 6.2.2 F; Fig. 6 A, D in Rieger 1981). The name "ciliated glands" is therefore misleading. The nucleus is located in the basal end of the cell close to the cell projection, which extends for several cell widths along the basal membrane and possibly connects to the peripheral nerves (Kerbl *et al.* 2015). The cell body is densely packed with spherical vesicles, which are not as electron-dense as the nucleus or the cell membrane. (2) Tubular glands (Fig. 6.2.2 B) are elongated, flask shaped, and basally projecting along the basal lamina with a continuous layer of tubulin IR elements close to their cell membrane, but without a ciliary ring around the opening. Their glandular content differs from the ciliated glands, being small, electron-dense, rod-shaped granules rather than spherical vesicles. Tubular glands are distributed randomly throughout the entire body length and body circumference, at least in *L. riegeri* (Kerbl *et al.* 2015). (3) Kidney-shaped gland cells (Fig. 6.2.2 C) do not have a ciliary ring around the opening and also lack the basal projections. Their vesicles resemble the ones of ciliated glands, and the dense packing affects the nucleus, which therefore appears to be remarkably sickle shaped. (4) Adhesive glands (Fig. 6.2.2 D, E) are unicellular glands with a ciliary ring around the opening, which is encircled by an anchor cell (Rieger 1991, Kerbl *et al.* 2015). The ciliary ring probably mechanically facilitates the release from the substrate, thereby forming an alternative system to the duo-gland-system employed by, e.g., Platyhelminthes. The granules differ between species, with *L. psammicola* (Fig. 6.2.2 D) having medium electron-dense granules with elongated, electron-dense inclusions in the center (Rieger 1991) and *L. riegeri* (Fig. 6.2.2 E) having several spherical inclusions (Kerbl *et al.* 2015). There also was a higher abundance of adhesive gland cells observed in *L. psammicola*, accumulating in the region between the male gonopore and the female gonad, why they may aid to copulation (Rieger 1991).

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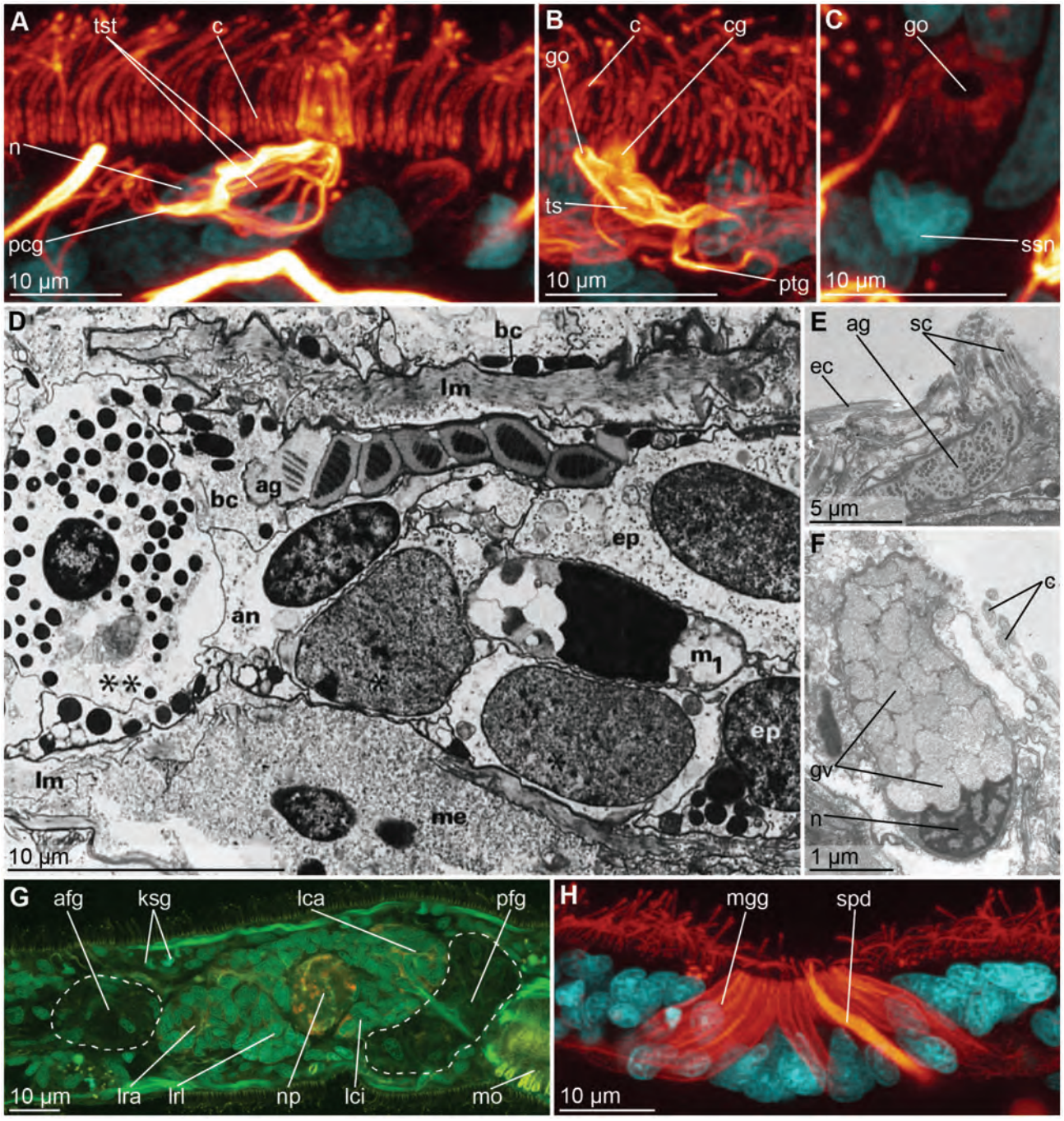


**Fig. 6.2.2:** Epidermal and organ-associated glands of *Lobatocerebrum*. A–C, Immunolabeling and confocal laser scanning microscopy of *Lobatocerebrum riegeri* (DAPI (4',6-diamidino-2-phenylindole) in cyan, acetylated α- tubulin in glow) of (A) ciliated gland, (B) tubular gland, and (C) kidney-shaped gland. D–F, Electron micrographs of (D) the epidermis with sections through epidermal cells and epidermal gland cells in *Lobatocerebrum psammicola*, (E) adhesive gland cell in *L. riegeri*, and (F) ciliated gland cell of *L. riegeri*. G, H, Immunolabeling and confocal laser scanning microscopy of *L. riegeri* (DAPI in cyan, acetylated α- tubulin in glow, phalloidin in green) of (G) two portions of frontal glands and (H) the male gonopore gland. afg, anterior frontal gland; ag, adhesive gland; bc, basal granule cell; c, cilium; cg, ciliated gland cell; ec, cilium of the epidermal cell; ep, epidermal cell; go, gland opening; gv, glandular vesicle; ksg, kidney-shaped gland; lca, major caudal lobe; lci, minor caudal lobe; lm, longitudinal muscle; lra, major rostral lobe; lrl, lateral rostral lobe; m1, type 1 mucous gland (*L. psammicola*); mgg, male gonopore gland; mo, mouth opening; n, nucleus; np, neuropil; pcg, projection of the ciliated gland; ptg, projection of the tubular gland; sc, shortened cilium; spd, spermioduct; ssn, sickle-shaped nucleus; ts, tubulin sheath; tst, tubulin-strand. D, From Rieger (1980) with permission; all other images from Kerbl *et al.* (2015).

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Several organs and structures also have associated multicellular glands: (i) Frontal glands (Fig. 6.2.2 G), (ii) pharyngeal glands (Fig. 6.2.2 G), and (iii) male gonopore glands (Fig. 6.2.2 H).

Frontal glands form a prominent group posterior to the lobular brain (and anterior to the pharynx) and a smaller group located anterior to the brain, both extending ventro-anteriorly through long gland necks into the rostrum. Their contents differ with elongated, rod-shaped granules found in the anterior frontal glands and spherical granules in the posterior frontal gland. The ducts of the anterior frontal glands appear to lead to the ventral side of the rostrum, while the ducts of posterior frontal glands extend ventral to the brain and toward the tip of the rostrum. Most of these ducts disembogue their secrete at the anterior tip of the rostrum, but their detailed tracing and precise opening are complicated by the strong labeling of other tubulin IR elements, such as nerve bundles, sensory cells, and unicellular epidermal glands (Kerbl *et al.* 2015).

Pharyngeal glands originate as epidermal glands but are later sunken beneath the epidermis, where they consequently are surrounded by extracellular matrix. Several individual gland cells constitute this glandular complex; the duct openings encircle the mouth opening, at the transition between epidermis and pharynx external to the stomatogastric nerve ring (Fig. 6.2.2 G). Their granular content is less electron-dense and larger than the granules of the posterior frontal glands. Different to the frontal glands, the entire cell wall and not only the gland neck contains tubulin IR elements (Kerbl *et al.* 2015).

The male gonopore glands (Fig. 6.2.2 H) comprise two different glandular types in *L. psammicola* (Rieger 1980, 1981, 1988, 1991), yet only one type was recovered in *L. riegeri* (Kerbl *et al.* 2015). These glands are arranged in an anterior and a posterior group around the male gonopore. Similar to the pharyngeal glands, the cells are sunken beneath the epidermis, with the cell bodies therefore surrounded by extracellular matrix. The granular content of these cells is similar to the ones of the pharyngeal glands in shape, size, and electron-density (Rieger 1980).

**Musculature.** In contrast to other annelids, the body wall muscles of *Lobatocerebrum* do not show any oblique striation (Fig. 9 in Rieger 1981). The longitudinal muscles of the body wall are arranged into 12 longitudinal muscle fiber bundles consisting of three to five individual muscle fibers, which extend from the anterior to the posterior end of the animal (Figs. 6.2.1 H and 6.2.3 A–L). All longitudinal muscle bundles are regularly distributed circumferentially, except around the larger body openings, such as the mouth opening, male gonopore, and anus, where the longitudinal bundles move closer together (Fig. 6.2.3 A–L) (Kerbl *et al.* 2015).

Internal muscle ring complexes are found perpendicular to the longitudinal muscles and are spaced equally apart along the body between the mouth opening and the anus (Kerbl *et al.* 2015), but are not present in the rostrum. Each individual "muscle ring" was found to consist of a few (three to eight) separate transverse fibers with distinct gaps in between (Kerbl *et al.* 2015), each transverse bundle extending between two and three longitudinal muscle bundles (Fig. 6.2.3 E, K, L). In histology sections, these ring complexes may appear as continuous internal circular muscles, which made it even harder to explain their inner position relative to the (external) longitudinal muscle fibers of the body wall (Rieger 1980, 1988, 1991, Haszprunar *et al.* 1991). However, a network of internal transverse muscle fibers found in a more recent immunohistochemical analysis (Kerbl *et al.* 2015) indicates that they are probably homologous to the transverse muscles in other annelids (see Tzetlin and Filippova 2005) rather than representing outer circular muscles, which have moved internally (or the longitudinal moved externally to these) during development.

In the rostrum, other diagonal fibers traverse directly through the rostrum, between the dorsal, ventral, or lateral longitudinal muscle bundles, and form a central star-shaped grid of muscle fibers (Fig. 6.2.3 F, G) (Kerbl *et al.* 2015). Two longitudinal pairs of muscles emerge from the ventral longitudinal muscle bundles, extend anteriorly, and branch between the caudal and rostral lobes of the brain (Fig. 6.2.3 A, C, H), probably supporting and/or stabilizing the brain's position within rostrum (Kerbl *et al.* 2015).

*Lobatocerebrum* does not have any specialized musculature related to male or female reproductive organs and seminal receptacles. The musculature of the intestinal system comprises a muscular grid of longitudinal and perpendicularly arranged circular muscle fibers lining the entire digestive tract, which often is rather extended, and thereby the muscles of the stomatogastric musculature are found closely adjacent to the outer transverse muscular ring complexes of the body wall (Figs. 6.2.1 G and 6.2.3 B, D, E). Five circular sphincters are found supporting the pharynx, and a sixth sphincter is located anterior to the dorsal anus (Fig. 6.2.3 D).

**Digestive system.** The digestive system consists of the ventral mouth opening, a highly ciliated and glandular pharynx, a short esophagus, and an intestine (Figs. 6.2.1 A, H and 6.2.3 B, D, E, I–L) separated into a midgut and a heavily ciliated hindgut (Fig. 6.2.3 D) and ending in a dorsal anus.

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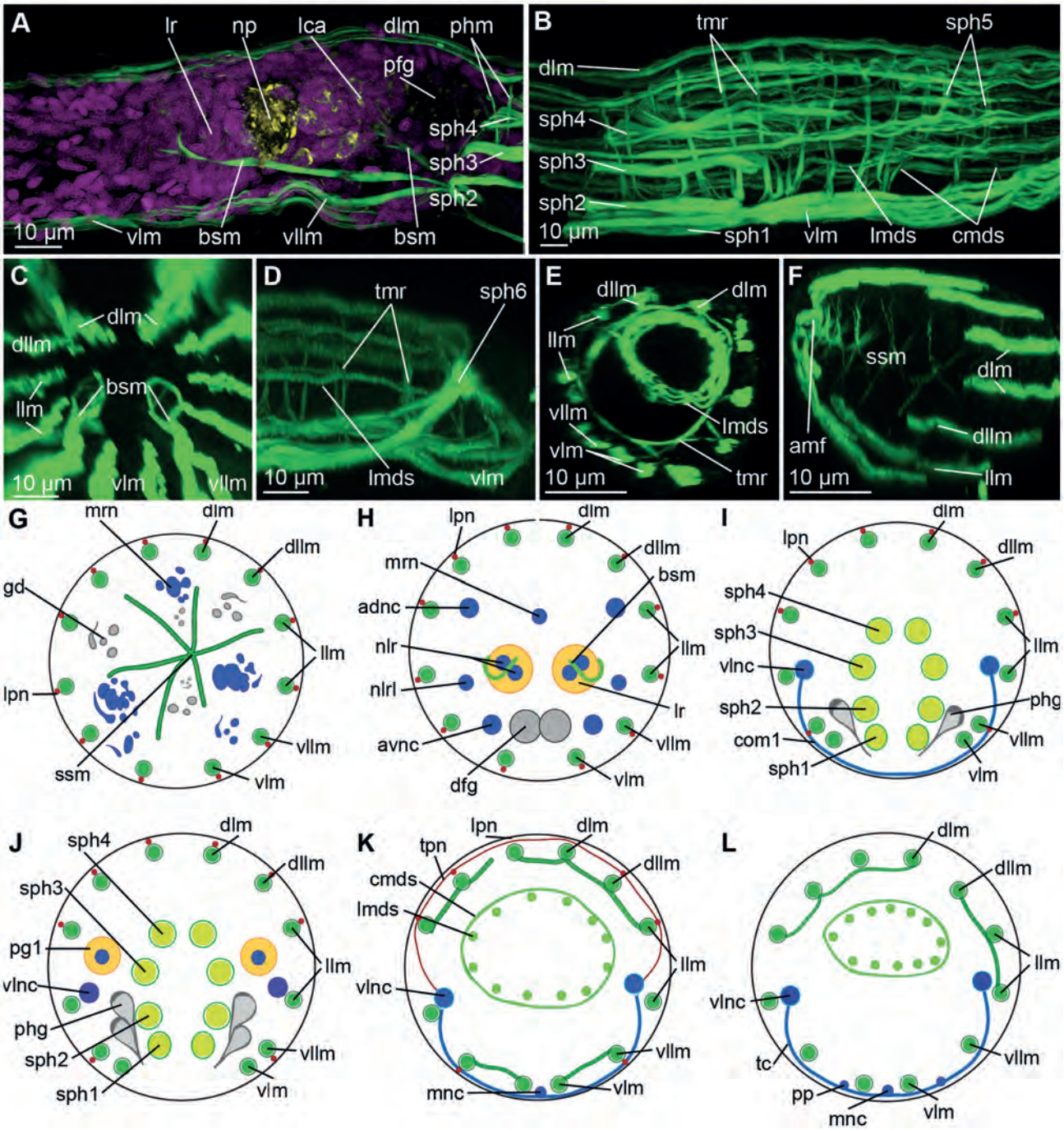


**Fig. 6.2.3:** Musculature of *Lobatocerebrum riegeri*. A–F, Immunolabeling and confocal laser scanning microscopy of (A) the brain supportive musculature (phalloidin in green, DAPI in purple, acetylated α-tubulin immunoreactivity in yellow), (B) the pharyngeal region (phalloidin in green), (C) the brain supporting musculature embracing the brain as observed from posterior to anterior, (D) the posterior end of the body with the posterior-most sphincter, (E) a cross-section through the fifth sphincter also showing the transverse muscle ring complexes, and (F) star-shaped muscles in the anterior tip of the animal. G–L, Schematic drawing of a cross-section through the body of *L. riegeri*, at the level of (G) the star-shaped muscles, (H) the brain supporting muscles anterior to the brain, (I) the pharynx, (J) the first postpharyngeal ganglion, (K) the third commissure, and (L) the terminal commissure. amf, anterior point of muscular fusion; an, anus; bsm, brain supportive musculature; cmds, circular muscle of the digestive system; dllm, dorsolateral longitudinal muscle; dlm, dorsal longitudinal muscle; gd, glandular duct; lca, major caudal lobe; llm, lateral longitudinal muscle; lm, longitudinal muscle; lmds, longitudinal muscle of the digestive system; lpn, longitudinal peripheral nerve; lr, rostral lobe; mnc, medioventral nerve cord; mrn, median rostral nerve; np, neuropil; pfg, posterior frontal gland; pg, postpharyngeal ganglion; phg, pharyngeal gland; phm, pharyngeal muscle; sph1-6, sphincters 1-6; ssm, star-shaped muscle; tc, terminal commissure; tmr, transverse muscular ring complexes; tpn, transverse peripheral nerve; vllm, ventrolateral longitudinal muscle; vlm, ventral longitudinal muscle; vlnc, ventrolateral nerve cord. All pictures from Kerbl *et al.* (2015).

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A basal granule cell system similar to that of the epidermis is also found in the intestine (Rieger 1981). The mouth opening is encircled by a nerve ring, surrounded by pharyngeal gland openings (Rieger 1980), which seem to be the only glandular system associated with the digestive system (Rieger 1980, Kerbl *et al.* 2015; Figs. 6.2.1 A and 6.2.3 I, J). The ciliation is densest at the pharynx, whereas the posterior region of the esophagus is only heavily ciliated on the ventral side (Rieger 1981, Kerbl *et al.* 2015).

The midgut is constituted by glandular cells with large inclusions and small granules and with dense microvillar brushes on their apical surfaces. These cells are absent in the ciliated hindgut (Rieger 1981).

The anterior region of the hindgut is constituted mainly of palisade epithelial cells with long and densely packed cilia, whereas the posterior hindgut epithelium is dominated by interdigitated ciliated cells (Rieger 1981).

**Excretory system.** *Lobatocerebrum psammicola* was suggested to have three pairs of U-shaped protonephridia (based on the description of three protonephridia: one left of pharynx-gut-transition, one on the right side of the animal between pharynx and testis, and another one right of the testis) based on squeezed preparations and live observations of cyrtocyte-like structures (Rieger 1980, 1991). *Lobatocerebrum psammicola* was hence suggested to have at least three pairs of protonephridia (Fig. 6.2.1 D) (Rieger 1980), while only one nephridium located posterior to the male gonad was mentioned for *L. riegeri* (which most likely corresponds to *L.* sp. II as described in Rieger 1980). Rieger's (1980, 1988) live observations indicated one flame bulb cell per cyrtocyte, and ultrathin sections showed 5 to 10 cilia within the canal (Rieger 1980, 1988, 1991).

**Body cavities.** Lobatocerebridae are acoelomate, and none of the previous studies found coelomic cavities. The parenchymal cells between the epidermis and the gut epithelium can be differentiated into two or three different mesenchymal cell populations (Fig. 6.2.4 B, C): (i) cells associated with the basal matrix of the epidermis, (ii) cells associated with the basal matrix of the gut epithelium, and (iii) cells between the derivates of ecto- and endoderm (Fig. 6.2.4 C). These parenchymal cells are voluminous and elongated-cylindrical but spatially constricted in the median and the posterior part of the body due to the presence of the spacious digestive system. Due to this spatial constraint, the parenchymal cells in this region are in contact with both epidermis and gut epithelium.

**Nervous system and sensory organs.** The central nervous system in Lobatocerebridae consists of the large, eponymous lobular brain, with several nerve bundles emerging anteriorly, laterally, and posteriorly (Fig. 6.2.5 A–F) and the ventral nervous system with one pair of ventrolateral nerve cords and one medioventral nerve bundle, which are connected by five commissures (Fig. 6.2.5 A, D, G). A segmental arrangement of the five commissures cannot be ascertained (which is confirmed by Rieger 1980, 1981, 1988, 1990 and Kerbl *et al.* 2015), since it is not possible to correlate their location and number with any other morphological character of these animals and only the two postpharyngeal commissures are accompanied by paired ganglia. There are several individual longitudinal nerves distal to the longitudinal muscle bundles and transverse nerves, which are located at commissures and in the posterior region of the animal. Additionally, it seems that a thin nerve net is formed in the region around the male gonopore, which also includes a nerve ring around the gonopore itself (Fig. 6.2.5 H). All components of the nervous system are intraepidermal, except for the sunken-in brain, which is surrounded by the basal lamina.

The brain (Fig. 6.2.5 B, C, E, F) is located in the posterior region of the rostrum, anterior to the pharynx. Several ganglionic lobes (consisting of an internal neuropil and an external, densely packed somata layer) are formed around the central neuropil (Rieger 1980, Kerbl *et al.* 2015): (i) anterior to the neuropil, one pair of rostral lobes (lobus rostralis [Rieger 1980], probably substructured into major, minor, and lateral rostral lobes [Kerbl *et al.* 2015]); (ii) posterior to the neuropil, one pair of major caudal lobes; and (iii) one pair of minor caudal lobes (probably separated into median and lateral lobe). All lobes are associated with nerve bundles emerging from a condensed bundle of transverse nerve fiber, located dorsally in the ovoid-shaped neuropil. This bundle probably resembles the dorsal commissure of the dorsal root of the circumesophageal connective in other annelid groups (Orrhage and Müller 2005). The lobe-associated nerve bundles are supplemented by additional bundles, resulting in 9–15 nerve fiber bundles visible in cross-sections of the rostrum (Fig. 6.2.5 A, D, E) (Kerbl *et al.* 2015). Lateral projections of the neuropil emerge independently. The neuropil consists of the aforementioned mediodorsal nerve bundle, one thick dense median nerve bundle that shows resemblance to the median commissure in annelid brains, and several thinner ventral commissures. The somata of nerve cells forming the brain, which are identified mainly by the compact arrangement of their similar-sized nuclei (as detected with DAPI) around the neuropil, are additionally delineated from the mesodermal derivates by the extracellular matrix. Several of the neural somata are labeled with FMRFamide-like or serotonin-like immunoreactivity in the brain and along the rostral nerves, although the distribution does not seem to be linked to any specific brain region or lobe (Kerbl *et al.* 2015).

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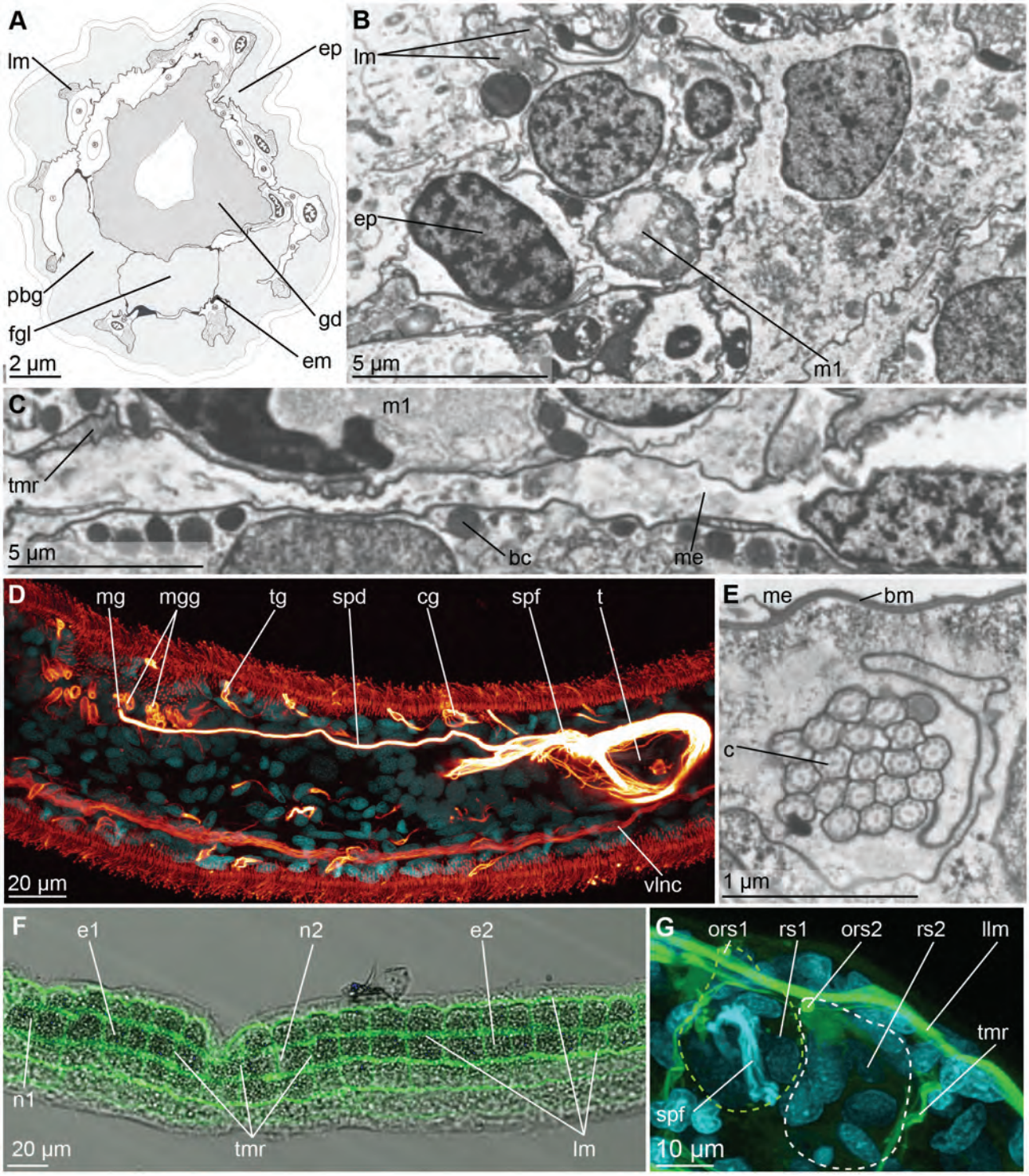


**Fig. 6.2.4:** Connective tissue and reproductive organs of *Lobatocerebrum*. A, Schematic drawing of a body cross-section of *Lobatocerebrum psammicola*. B, C, Electron micrographs of mesenchymal cells of *L. psammicola* (B) in front of the brain from cross-sections and (C) in the midgut region from frontal sections. D, Immunolabeling and confocal laser scanning microscopy of male reproductive system in *Lobatocerebrum riegeri* (DAPI in cyan, acetylated α-tubulin immunoreactivity in glow). E, Electron micrograph of a cross-section through the spermioduct in *L. psammicola*. F, G, Immunolabeling and confocal laser scanning microscopy of *L. riegeri* of (F) female reproductive system and (G) seminal receptacles (transmitted light, DAPI in cyan, phalloidin in green). bc, basal granule cell; bm, basal membrane; c, cilium; cg, ciliated gland; e1 and e2, egg 1 and egg 2; em, extracellular matrix; ep, epidermal cell; fgl, frontal gland; gd, gut epithelium; llm, lateral longitudinal muscle; lm, longitudinal muscle; m1, type 1 mucous gland (*L. psammicola*); me, mesenchymal cell; mg, male gonopore; mgg, male gonopore gland; n1 and n2, nucleus of egg 1 and egg 2; ors1 and ors2, opening of seminal receptacle 1 and 2; pbg, postbuccal ganglion; rs1 and rs2, seminal receptacle 1 and 2; spd, spermioduct; spf, sperm filaments; t, testis; tg, tubular gland; tmr, transverse muscular ring. A, From Rieger (1988) with permission; B, C, E from Rieger (1980), with permission; D, F, G, from Kerbl *et al.* (2015).

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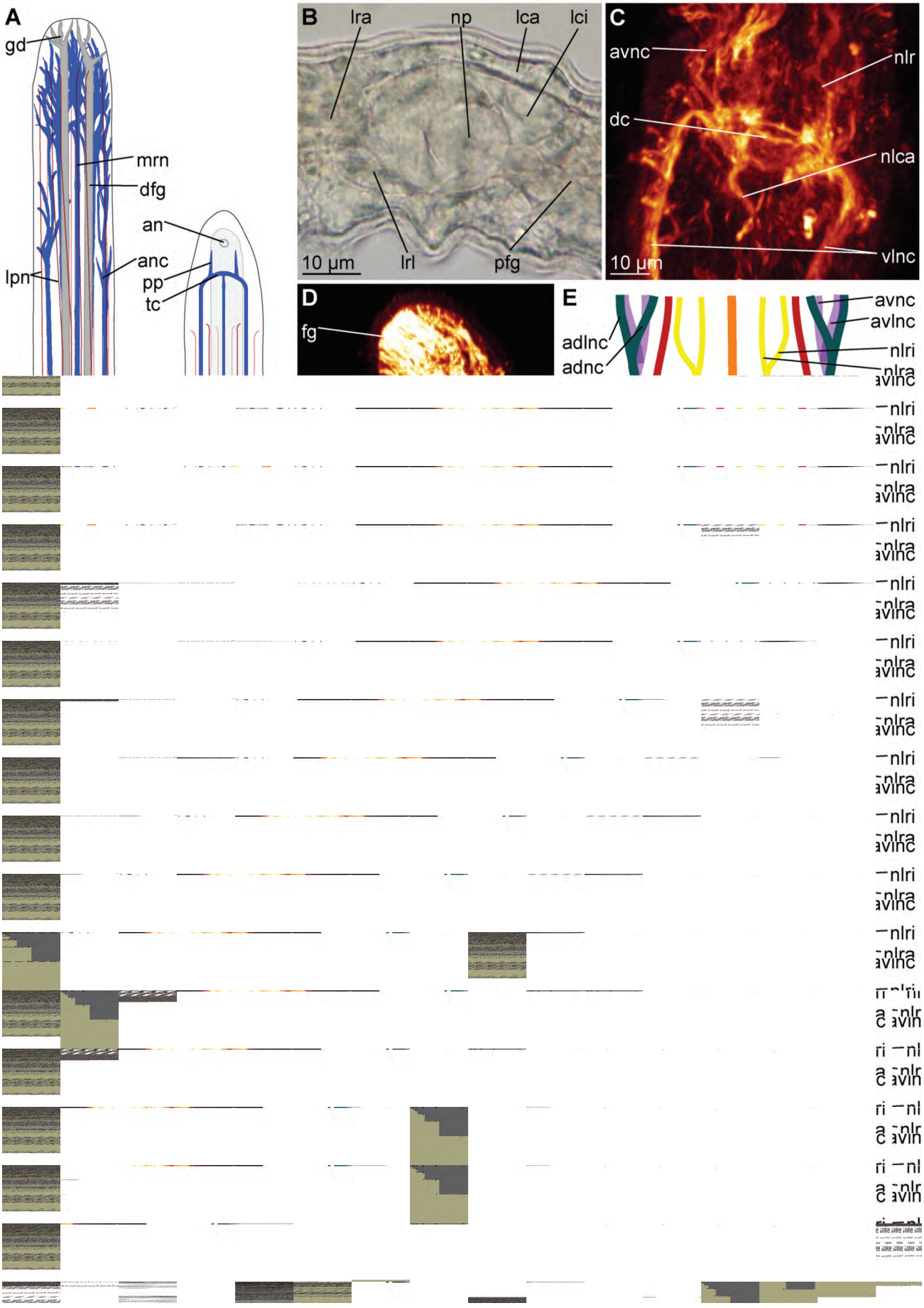


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The most prominent nerves extending from the neuropil are the ventrolateral nerve cords (Fig. 6.2.5 A, C–E), which extend ventrolaterally between the lateral longitudinal muscle bundles. One thin medioventral nerve is formed by two nerve bundles, which diverge from the lateral cords at the first postpharyngeal commissure and fuse into one median structure at the second commissure. The medioventral nerve further extends parallel to the ventrolateral cords, with several FMRFamide-like and serotonin-like IR somata randomly scattered alongside the ventrolateral nerve cords. Ganglia are only found dorsoposterior to the two postpharyngeal commissures (Fig. 6.2.5 G). In total, five commissures are found along the body: the two ganglionated commissures posterior to the pharynx (postpharyngeal commissures, Fig. 6.2.5 G), one commissure between the pharynx and the male gonopore, one commissure anterior to the ovary, and the terminal commissure connecting the two lateral nerve cords with the medioventral nerve.

Several longitudinal and circular peripheral nerves are present in Lobatocerebridae (Fig. 6.2.5 A). The longitudinal nerves are located parallel and external to the longitudinal muscle bundles (Rieger 1980, 1981, 1988, Kerbl *et al.* 2015). The circular peripheral nerves are located external to the longitudinal muscles and are either formed as complete circles or associated with commissures.

The stomatogastric nervous system is constituted by a thin nerve ring at the base of the pharynx, and a few associated perikarya internal to the openings of the pharyngeal gland ducts, without any observed neural accumulations along the stomach or the intestine.

Lobatocerebridae do not have any specialized sensory organs such as eyes or nuchal organs but do possess several, seemingly randomly scattered, epidermal sensory cells with one single cilium, often surrounded by a microvillar ring (Fig. 6.2.5 H) (Kerbl *et al.* 2015). However, their connection to the nervous system could not be detected.

Additionally, nine tubulin IR neurite bundles extend anteriorly from the brain and fan out along the anterior-ventral side of the rostrum. Some of these processes possibly originate from single monociliated sensory cells (Kerbl *et al.* 2015), yet neither ultrastructural (Rieger 1980, 1981, 1988, 1991) nor immunohistochemical (Kerbl *et al.* 2015) investigations could show an equivalent number of sensory cells (or sensory organs) relative to the density of nerve fibers (Fig. 6.2.5 A, D, E) (Kerbl *et al.* 2015). However, following and untangling the ends of these nerve fiber bundles (and thereby their points of innervation or origin) are further complicated by the strong tubulin IR of ciliated epidermis and the frontal gland ducts, which also extend to the anterior tip of the rostrum (Rieger 1980, Kerbl *et al.* 2015).

**Reproductive organs and gametes.** The hermaphroditic Lobatocerebridae have an unpaired male gonad, which is connected to the dorsal male gonopore via a thin, ciliated spermioduct (male channel, Fig. 6.2.4 D, E). The ciliation is strongest in the part of the funnel, which leads gametes from the unpaired testes to the gonopore, and resembles the coelomoduct-solution in several bilateral groups. Numerous glandular necks of two glandular types open in the depression around the male gonopore. Furthermore, a nerve ring around the male gonopore and a weak nerve net extending from it was detected, whose connection to either the peripheral or the central nervous system has not been found so far (Fig. 6.2.5 H). The unpaired testis is located posterior to the male gonopore and has a bag-shaped lumen, with

◂ **Fig. 6.2.5:** Nervous system of *Lobatocerebrum riegeri*. A, Schematic drawing of the nervous system. B, Light microscopic image of the brain. C, Immunolabeling and confocal laser scanning microscopy of the neuropil and emerging nerves (acetylated α-tubulin immunoreactivity in glow). D, Overview of the nervous system (acetylated α-tubulin immunoreactivity in glow). E, Schematic reconstruction of the brain with the respective lobes and emerging nerves (mvn not separated from vlnc yet, therefore indicated as thin grey line). F–H, Immunolabeling and confocal laser scanning microscopy of (F) a median section through the brain (acetylated α-tubulin immunoreactivity in glow, DAPI in cyan), (G) the two postpharyngeal ganglia (acetylated α-tubulin immunoreactivity in yellow, serotonin-immunoreactivity in red, DAPI in cyan), and (H) the nerve net around the male gonopore (acetylated α-tubulin immunoreactivity in yellow, serotonin-like immunoreactivity in pink). adlnc, anterior dorsolateral nerve cord; adnc, anterior dorsal nerve cord; afg, anterior frontal gland; an, anus; avlnc, anterior ventrolateral nerve cord; avnc, anterior ventral nerve cord; avc, anteroventral commissure of the neuropil; br, brain; c1–4, commissure 1-4; dc, dorsal commissure of the neuropil; dfg, ducts of the frontal glands; e1–3, eggs 1–3; fg, frontal gland; gd, glandular ducts; lca, major caudal lobe; lci, minor caudal lobe; lcil, lateral minor caudal lobe; lcim, median minor caudal lobe; ln, lateral nerve emerging from the neuropil; lpn, lateral peripheral nerve; lpnp, lateral nerve emerging from the neuropil; lr, rostral lobe; lra, major rostral lobe; lri, minor rostral lobe; lrl, lateral rostral lobe; mc, median commissure of the neuropil; mg, male gonopore; mgg, male gonopore gland; mlca, median nerve innervating the major caudal lobe; mo, mouth opening; mrn, median rostral nerve; mvn, medioventral nerve; nlca, nerve innervating the major caudal lobe; nlci, nerve innervating the minor caudal lobe; nlcil, nerve innervating the lateral minor caudal lobe; nlr, nerve innervating the rostral lobe; nlra, nerve innervating the major rostral lobe; nlri, nerve innervating the minor rostral lobe; nlrl, nerve innervating the lateral rostral lobe; np, neuropil; nrmg, nerve ring around the male gonopore; pfg, posterior frontal gland; pg1 and 2, postpharyngeal ganglion 1 and 2; phg, pharyngeal gland; pp, posterior projection; rs, seminal receptacle; snr, stomatogastric nerve ring; spc, antiseroton IR perikaryon of the epidermis; spd, spermioduct; ss, sensorium; t, testis; tc, terminal commissure; tpn, transverse ring of the peripheral nervous system; vc, ventral commissure of the neuropil; vlnc, ventrolateral nerve cord. A, C–H, From Kerbl *et al.* (2015).

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a thin epithelium separating male gametes from the surrounding tissues (Fig. 6.2.4 D, E). Sperm is arranged as loose bundles in the testis and more densely packed and folded in the several seminal receptacles (Fig. 6.2.4 D, G). The spermatozoa are filamentous without any obvious separation into the head with acrosome, midpiece with mitochondria, and tail with flagellum (Rieger 1980, 1988, 1991).

The oocytes are located close to the basal membrane of the gut, yet no ovarium has been detected (Fig. 6.2.4 F). They have an irregular shape, which is likely predefined by the available space between the organs and the epidermis (Fig. 6.2.4 F). Mature eggs are located more posterior than earlier developmental stages. The eggs are suggested to elongate during maturation, based on electron microscopic studies (Rieger 1980).

### Reproduction and development

Lobatocerebridae are hermaphroditic and possess seminal receptacles to store foreign sperm. Due to the scarcity of animals from only few reported localities worldwide, no studies have yet described their copulation, development, or life cycle. It is unknown where fertilization takes place, but possibly externally using the stored sperm in connection with egg laying. No cocoons have been observed. The preserved material includes only adult and juvenile specimens; however, it is assumed that these animals, similar to other meiofaunal taxa, lack a larval stage and have direct development. The juvenile and adult stages differ only in the addition of reproductive organs, with the organ systems otherwise similarly arranged (Kerbl *et al.* 2015).

### Biology and ecology

#### Distribution

Lobatocerebridae were first described from the shallow waters off the coast of North Carolina, USA (meiofaunal samples from 50 m depth). However, the earliest studies (Rieger 1980, 1981) mention two more species from the deep waters off North Carolina (approximately 800 m depth) and the shallow coast off Eilat, Israel, respectively. Additional records of *L. psammicola* along the Atlantic Ocean coasts include the Øresund (Denmark [Kristensen 1983], Gran Canaria [Spain] and Elba [Italy, W. Sterrer, unpublished], and the Atlantic coast of Panama [Laumer *et al.* 2015]). Since genetic material and detailed morphological assessments are lacking for these few specimens reported, it cannot be reevaluated whether any of these findings may instead represent *L. riegeri* or an undescribed species.

**Habitat.** Lobatocerebridae are found in subtidal marine habitats with coarse sand mixed with fine silt (badly sorted sediment), but with limited organic and terrestrial matter. Although found at shallow depths, they are never abundant and may be mistaken for Platyhelminthes, juvenile nemerteans, or gnathostomulids, which might explain their understudied nature, few recordings, and lack of reports out of the Atlantic Ocean and the Red Sea.

**Feeding.** Although no food uptake could be observed in living specimens, the apparent lack of structures such as jaws, teeth, muscular bulbs, or muscular diaphragms such as found in other meiofaunal annelids (e.g., *Dinophilus* [Jennings and Gelder 1969, Purschke 1985], *Nerilla* [Gelder and Uglow 1973], *Ophryotrocha* [Purschke 1985, 1987, Paxton 2004, Macnaughton *et al.* 2010], and *Psammodrilus* [Worsaae *et al.* 2018]) suggests the implementation of the epidermal cilia to transport food particles to the mouth opening and further on into the digestive system. The musculature of the digestive system is probably supported by the body wall muscles in moving its content back and forth and thereby mixes the food with enzymes produced by glands from the gut epithelium.

### Phylogeny and taxonomy

#### Phylogeny

Rieger (1980, 1981, 1991) described the family Lobatocerebridae as probably related to Annelida, but also having affinities to Platyhelminthes. Due to the many unique traits and the mixture of annelid traits (e.g., the structure of the male gonoduct, a metameric flamebulb unit [nephridia], the cuticular fine structure, the epidermal gland cell fine structure, the basal granule cell system above the basal lamina, and the hindgut-anus system) and turbellarian traits (e.g., the muscle cell cytology, the complete ciliation, the acoelomate body cavity, and the unpaired middorsal gonopore), it was suggested to be a separate phylum Lobatocerebromorpha (Haszprunar *et al.* 1991). A phylogenetic analysis based on morphological characters could not resolve its exact position but regarded it a "basal trochozoan" (Zrzavý 2003).

Finally, a recent transcriptomic analysis managed to include and nest *Lobatocerebrum* deeply within Annelida, strongly supporting its annelid affinity (Laumer *et al.* 2015). The exact position within Annelida is still

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debatable, yet in some of the analyses, *Lobatocerebrum* was found to group with Sipuncula, although with moderate support (Laumer *et al.* 2015).

Although the unsegmented body of the two groups could represent a synapomorphy of Lobatocerebridae and Sipuncula, the similarities in the internal morphology are limited, as is apparent in, e.g., studies of the ventral nerve cords: Adult sipunculids express one midventral nerve cord, whereas lobatocerebrids have three separate cords. Moreover, while several commissures can be detected during early development prior to fusing of the cords in sipunculids (Wanninger *et al.* 2005, Kristof *et al.* 2008), *Lobatocerebrum* shows only two ganglionated commissures (and three unganglionated), which cannot be correlated to any other organ system (Kerbl *et al.* 2015). Additionally, Lobatocerebridae show a ventromedian nerve, which does not seem to be present in developmental stages of Sipuncula prior to fusion of their cords.

Although similarities between sipunculids and Lobatocerebridae are limited, there are some general similarities found between *Lobatocerebrum* and other (meiofaunal) annelids such as Dinophilidae, Microphthalminae, or Diurodrilidae, e.g., an acoelomate condition, partial to complete ciliation, a highly glandular epidermis, a gliointerstitial system with basal granule cells, a ventral nervous system with paired separate cords and a median nerve cord with few ganglionated commissures (e.g., Fransen 1980, Rieger and Purschke 2005, Worsaae and Kristensen 2005, Kerbl *et al.* 2015). None of the previously mentioned annelid groups have been shown to be closely related to neither *Lobatocerebrum* nor each other, and convergences in the body plans of meiofaunal annelids have been documented before (Andrade *et al.* 2015, Struck *et al.* 2015). Since Lobatocerebridae most likely is secondarily miniaturized, many similarities between it and other meiofaunal taxa possibly are a result of convergent adaptation to the confined interstitial environment.

Worth mentioning as a side track, the neuromuscular system of the orthonectid *Intoshia linei* (Slyusarev and Starunov 2016), a possibly derived annelid, shows a somewhat similar arrangement of circular muscles internal to longitudinal muscles as otherwise only found in *Lobatocerebrum*. Future developmental studies of the transverse muscle ring complexes or of the ventral cords and commissures might reveal information of systematic importance.

Although molecular phylogenomics have now characterized Lobatocerebridae as annelids, none of their morphological characters by themselves support its annelid affinity. However, the combination of morphological traits sets it apart from interstitial members of Platyhelminthes, Mollusca, Nemertea, and Gnathifera (Rieger 1980, Kerbl *et al.* 2015) and indicates an annelid relationship of the family.

## Taxonomy

### Family Lobatocerebridae Rieger, 1980 (Figs. 6.2.1–6.2.5)

#### *Lobatocerebrum* Rieger, 1980

**Diagnosis:** Small, elongated, acoelomate, unsegmented marine interstial annelid with large, lobular dorsal brain. Without chaetae and reduced blood vascular system. Pairs of metamerically arranged protonephrida. Ciliated and completely cuticularized body wall, epidermis scattered with different types of mucous and adhesive glands. Hermaphrodites. Anterior, dorsolateral male gonopore. Female gonad ventroposterior. Dorsal to lateral seminal vesicles anterior to the dorsal anus.

**Type species:** *Lobatocerebrum psammicola* Rieger, 1980

**Distribution and habitat:** *Lobatocerebrum* consists of two species, reported from the East and West Atlantic as well as the Red Sea.

#### *Lobatocerebrum psammicola* Rieger, 1980.

**Type locality:** Shallow waters (30 m) off Beaufort, North Carolina, USA.

**Habitat:** heterogenous medium-coarse sandy sediment. Also found in coral rubble sand (not well-sorted, mixed fine and coarse sediment) at Bocas del Toro, Atlantic coast of Panama (Laumer *et al.* 2015). Dr. W. Sterrer also found lobatocerebrids in fine sand sediments below *Zostera* meadows of Gran Canaria, Canary Island, Western Atlantic, and in Southern Italy, Mediterranean Sea (W. Sterrer personal communication).

#### *Lobatocerebrum riegeri* Kerbl, Bekkouche, Sterrer & Worsaae, 2015.

**Type locality:** Subtidal (9 m) off Eilat, Israel.

**Habitat:** coarse calcareous sand.

**Remarks:** The differences between the described and undescribed species are minute, and they differ only in the ultrastructure of the epidermal glands and their granules and vesicles, the length of the entire organism or of specific organs, and the relative placement of the organs within the organism. There exist two described species (*L. psammicola* Rieger, 1980, from the shallow waters [30 m] off Beaufort, North Carolina, and *L. riegeri* Kerbl, Bekkouche, Sterrer & Worsaae, 2015, from the subtidal [9 m] off Eilat, Israel) and at least one more undescribed species (*L.* sp. I), which was found and recorded by Rieger (1980) from a collection of fine, silty sediment at 800-m depth off Beaufort, North Carolina. The second undescribed species mentioned in his articles (*L.* sp. II, Rieger 1980, 1981, 1991)

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most likely is *L. riegeri*, which was collected at the same locality in similar habitat; however, molecular support is not available. Specimens found in Panama are suggested to be *L. psammicola* due to light microscopic observation; however, more detailed anatomical analyses are needed for final confirmation. Due to the overall lack of molecular fingerprints from the different localities, the existence of cryptic species cannot be ruled out, and the number of species might increase in this family following further investigations.

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## References

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "Archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Fransen, M.E. (1980): Ultrastructure of colomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphology* 95:235–249.

Gelder, S.R. & Uglow, R.F. (1973): Feeding and gut structure in *Nerilla antennata* (Annelida: Archiannelida). *Journal of Zoology (London)* 171:225–237.

Hausen, H. (2005): Comparative structure of the epidermis in polychaetes (Annelida). *Hydrobiologia* 535/536: 25–35.

Haszprunar, G., Rieger, R.M., & Schuchert, P. (1991): Extant "problematica" within or near the Metazoa. In: Simonetta, A.M. & Conway Morris, S. (eds). *The Early Evolution of Metazoa and the Significance of Problematic Taxa*. Cambridge University Press, Cambridge: 99–105.

Jennings, J.B. & Gelder, S.R. (1969): Feeding and digestion in *Dinophilus gyrociliatus* (Annelida: Archiannelida). *Journal of Zoology (London)* 158: 441–451.

Kerbl, A., Bekkouche, N., Sterrer, W. & Worsaae, K. (2015): Detailed reconstruction of the nervous and muscular system of Lobatocerebridae with an evaluation of its annelid affinity. *BMC Evolutionary Biology* 15: 277.

Kristensen, R.M. (1983): Loricifera, a new phylum with Aschelminthes characters from the meiobenthos. *Journal of Zoological Systematics and Evolutionary Research* 21 (3): 163–180.

Kristof, A., Wollesen, T. & Wanninger, A. (2008): Segmental mode of neural patterning in Sipuncula. *Current Biology* 18: 1129–1132.

Laumer, C.E., Bekkouche, N., Kerbl, A., Goetz, F., Neves, R.C., Sørensen, M.V., Kristensen, R.M., Hejnol, A., Dunn, C.W., Giribet, G. & Worsaae, K. (2015): Spiralian phylogeny informs the evolution of microscopic lineages. *Current Biology* 25: 2000–2006.

Macnaughton, M.O., Worsaae, K. & Eibye-Jacobsen, D. (2010): Jaw morphology and ontogeny in five species of *Ophryotrocha*. *Journal of Morphology* 271: 324–339.

Martinez, A., Worsaae, K. & Purschke, G. (2017): Protodrilidae Hatschek, 1888. In: v. Beutel, R.G., Kristensen, N.P., Leschen, R., Purschke, G., Westheide, W. & Zachos, F. (eds.) *Handbook of Zoology Online*. De Gruyter, Berlin. https://www.degruyter.com/view/Zoology/bp_029147-6_8

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

Paxton, H. (2004): Jaw growth and replacement in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Zoomorphology* 123:147–154.

Purschke, G. (1985): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). I: The pharynx of the Dinophilidae. *Zoomorphology* 105:223–239.

Purschke, G. (1987): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in polychaeta (Annelida). IV. The pharynx and jaws of the Dorvilleidae. *Acta Zoologica (Stockholm)* 68: 83–105.

Rieger, R.M. (1980): A new group of interstitial worms, Lobatocerebridae nov. fam. (Annelida) and its significance for Metazoan phylogeny. *Zoomorphology* 95: 41–84.

Rieger, R.M. (1981): Fine structure of the body wall, nervous system, and digestive tract in the Lobatocerebridae Rieger and the organization of the gliointerstitial system in Annelida. *Journal of Morphology* 167: 139–165.

Rieger, R.M. (1988): Comparative ultrastructure and the Lobatocerebridae: keys to understand the phylogenetic relationship of Annelia and the acoelomates. In: Westheide, W. & Hermans, C.O. (eds). *The Ultrastructure of Polychaeta*. *Mikrofauna Marina* 4: 373–382.

Rieger, R.M. (1991): Neue Organisationstypen aus der Sandlückenraumfauna: die Lobatocerebriden und *Jennaria pulchra*. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 84: 247–259.

Rieger, R.M. & Rieger, G.E. (1976): Fine structure of the archiannelid cuticle and remarks on the evolution of the cuticle within the Spiralia. *Acta Zoologica (Stockholm)* 57:53–68.

Slyusarev, G.S. & Starunov, V.V. (2016): The structure of the muscular and nervous system of the female *Intoshia linei* (Orthonectida). *Organisms Diversity & Evolution* 16(1): 65–71.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25(15): 1993–1999.

Tzetlin, A.B. & Filippova, A.V. (2005): Muscular system in polychaetes (Annelida). *Hydrobiologia* 535/536: 113–126.

Wanninger, A., Koop, D., Bromham, L., Noonan, E. & Degnan, B.M. (2005): Nervous and muscle system development in *Phascolion*

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*strombus* (Sipuncula). *Development, Genes and Evolution* 215: 509–518.
Westheide, W. (2008): *Polychaetes: Interstitial Families*. 2nd ed. The Linnean Society of London (Field Studies Council Shrewsbury), London.
Westheide, W. & Rieger, R.M. (1978): Cuticle ultrastructure of hesionid polychaetes (Annelida). *Zoomorphologie* 91: 1–18.
Worsaae, K. (2014): Nerillidae Levinsen, 1883. In: v. Beutel, R.G., Kristensen, N.P., Leschen, R., Purschke, G., Westheide, W. & Zachos, F. (eds.) *Handbook of Zoology Online*. De Gruyter, Berlin. https://www.degruyter.com/view/Zoology/bp_029147-6-10
Worsaae, K. & Kristensen, R.M. (2005): The evolution of interstitial Polychaeta (*Annelida)*. *Hydrobiologia* 535/536: 317–338.
Worsaae, K., Giribet, G. & Martínez, A. (2018): The role of progenesis in the diversification of the interstitial annelid lineage Psammodrilidae. *Invertebrate Systematics* 32(4):774–793.
Zrzavý, J. (2003): Gastrotricha and metazoan phylogeny. *Zoologica Scripta* 32: 61–81.

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# 7 Pleistoannelida

## 7.1 Sedentaria: Orbiniida

Wilfried Westheide

### 7.1.1 Dinophilidae Verrill, 1892

#### Introduction

Dinophilids include some of the smallest annelid species known, with a body length between 1 and 2 mm and exhibit an extremely low degree of external structural diversity (Westheide 1990, 2008). Nevertheless, they were already well known to marine zoologists on both sides of the Atlantic in the second half of the nineteenth century (Weldon 1886, Korschelt 1887, Harmer 1889, Schimkewitsch 1895, Moore 1899), with early comprehensive investigations into their morphology and embryology (Nelson 1904, 1907) constituting highlights of invertebrate zoological research at the time.

Dinophilidae contains the two strictly marine genera *Dinophilus* O. Schmidt, 1857 and *Trilobodrilus* Remane, 1925. The closeness of the relationship between these two taxa has never been questioned and continues to be corroborated by a growing number of synapomorphies, e.g., the fine structure of muscle cells in the ventral pharynx (Purschke 1985).

The monotypic genus *Apharyngtus* Westheide, 1971 displays significant similarities to the two first taxa but lacks a ventral muscular pharynx and the specific unpaired male copulatory organ (Westheide 1971). Recent molecular investigations place *Apharyngtus* in the immediate phylogenetic neighborhood of the dinophilid taxa (Struck *et al*. 2015) but indicate that they do not form a monophyletic taxon. The erection of a new family taxon Apharyngtidae thus seems to be necessary (see Chapter 7.1.2).

#### Morphology

##### External morphology

The long fusiform body is almost cigar shaped (Fig. 7.1.1.1). It has a body length between 1 and 2 mm and a width of about 200 µm, with the exception of the extremely tiny male (50 µm) of *Dinophilus gyrociliatus* (see further in the chapter). The anterior end consists of a bluntly conical almost trilobed prostomium, rounded at the front and tapering behind to a well-defined neck. It is followed by a peristomial section with two apodous rings (Eibye-Jacobsen 1994) and a few simple, irregularly annulated segments without appendages or chaetae. Posterior most, there is a simple pygidial appendage (tail, stylus) with unclear boundary, which is slightly differently shaped in the two genera (Nelson 1907).

The body surface is covered by a species-specific pattern of cilia with an obligatory complete ciliary tract on the ventral side (Fig. 7.1.1.3 A), which is used for continuously sliding within the interstices of the substrate by the *Trilobodrilus* species. The preoral section of this tract covers the ventral side of the head and passes into the ciliated lining of the Y-shaped mouth (Fig. 7.1.1.5 B), where it sweeps food particles into the esophagus on a continuous basis. The postoral tract of the ventral band begins at the posterior end of the oral opening and continuous backward to the pygidium, where it is reduced to one third of its width in the middle of the body.

The head and trunk are partly or completely encircled by transverse ciliary rings and they are covered by stiff adjoined ciliated tufts (spines or sensory bristles). In *Trilobodrilus* species, with the exception of *Trilobodrilus hermaphroditus* (see Riser 1999), those rings are restricted to the head. In *Dinophilus*, the rings enable the animals to rotate slowly when they swim. In *T. hermaphroditus*, 21 rings are present in the trunk area; the first peristomial ring encircles the body completely, and the 20 following rings mostly are dorsally open (Müller 1999). The number of transverse rings in *Dinophilus taeniatus* doubles during maturation. The juveniles possess seven transverse rings embracing their bodies; an adult animal has a total of 12–14 ciliary bands (Fig. 7.1.1.3 A) (Kerbl 2016). The rings are formed by rows of multiciliated cells that each beat rhythmically in a backward direction. All dinophilids possess four conspicuous groups of tufts upon the apical margin of the head. The two ventral tufts are slightly closer to each other than the dorsal pair (Figs. 7.1.1.2 A, B and 7.1.1.3 A, C). The species show additional small tufts differently scattered over the head and the trunk; e.g., *Trilobodrilus itoi* has a middorsal ciliary tuft in the gapped portion of the second ciliary ring on the head (Kajihara *et al*. 2015). The anterior part of the prostomium shows two ciliary rings. The first one is an almost complete thickset row of cilia. It is V shaped on the middorsal ridge (Fig. 7.1.1.3 A) and it is located in front of the eyes. The second prostomial ring consists of two rows of cilia that are widely separated dorsally.

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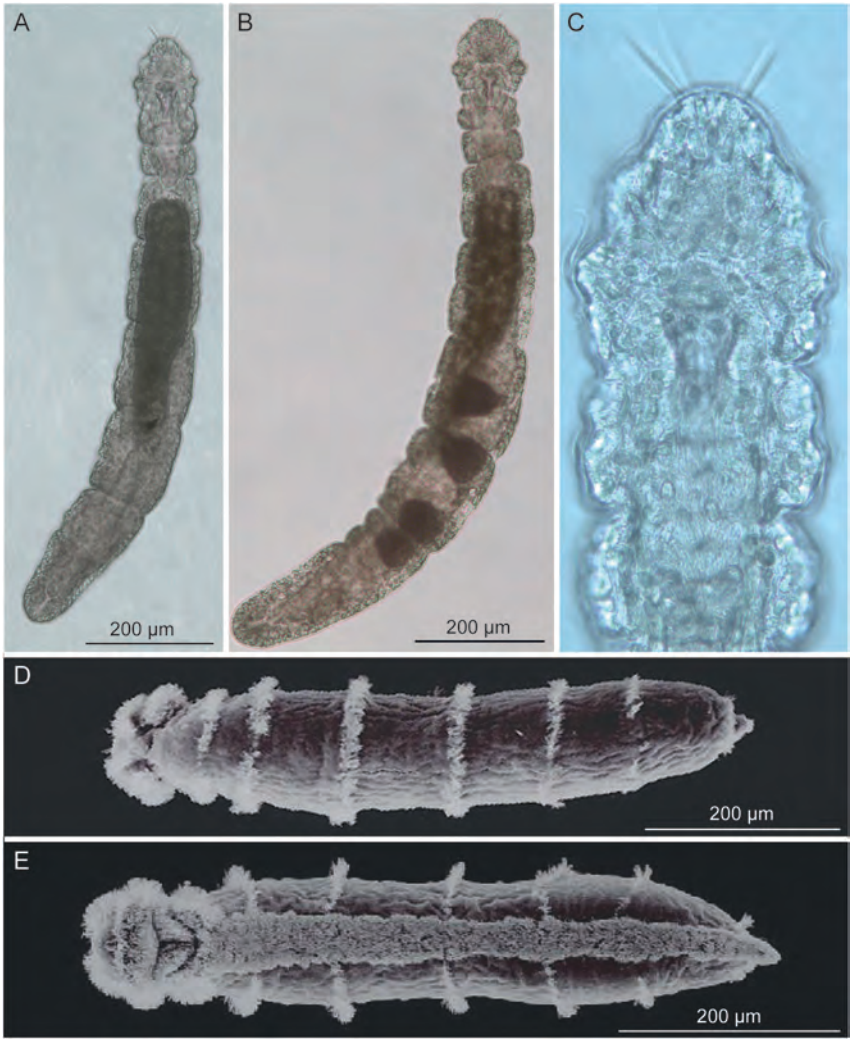


**Fig. 7.1.1.1:** A–C, *Trilobodrilus axi*. Micrographs of live specimens. A, Mature male. B, Mature female. C, Anterior end. Head with stiff adjoined ciliary tufts. D, E, *Dinophilus gyrociliatus*. Female. Scanning electron micrographs. Dorsal view (D). Ventral view (E). A–C, G. Purschke. D, E, W. Mangerich & W. Westheide.

All species exhibit an indistinctly bordered pair of ciliated pits laterally positioned on the head that are nuchal organs. These are especially obvious in the *Trilobodrilus* species (Fig. 7.1.1.2 A, B) (Rieger and Rieger 1975, Purschke 1984, 1985, 1997). Innervation occurs by nerves emerging from the circumesophageal commissure.

Only in *Dinophilus* do two pigmented eyes occur in the head (Fig. 7.1.1.3 C). They consist each of one pigmented supportive cell, two rhabdomeric sensory receptor cells in an everse design (Korschelt 1882, Eakin *et al*. 1977). In addition, a lens-like structure as part of the pigment cell is present as well. These features are indicative for adult annelid eyes rather than for larval eyes (Purschke *et al*. 2014).

Monomorphic *Dinophilus* species display a vivid orange color (Fig. 7.1.1.6 C). *Dinophilus gyrociliatus* and the transparent *Trilobodrilus* species are more or less colorless, with creamy white oocytes in the mature females.

**Segmentation.** Various numbers of segments have been attributed to *Dinophilus* and *Trilobodrilus* species because of the indistinct outer metameric articulation of live specimens. The literature is therefore divided regarding the number of segments (see Müller and Westheide 2002). Only after confocal laser scanning microscopy analyses (Müller 1999 Orrhage and Müller 2005) (Figs. 7.1.1.3 and 7.1.1.5) began to be used in morphological investigations, making it possible to count the exact number of ganglia and commissures in the nervous system, to visualize nephridia, and to better identify ciliary rings (Fig. 7.1.1.5 A), was it possible to ascertain the true metameric pattern of these tiny annelids.

▸ **Fig. 7.1.1.2:** A, B, *Trilobodrilus* sp. Details of the head and anterior trunk: dorsal view (A) and lateral view (B). C, *Dinophilus taeniatus*. Schematic sagittal section of encysted female. A, B, After Rieger and Rieger (1975); C, after Jägersten (1944a).

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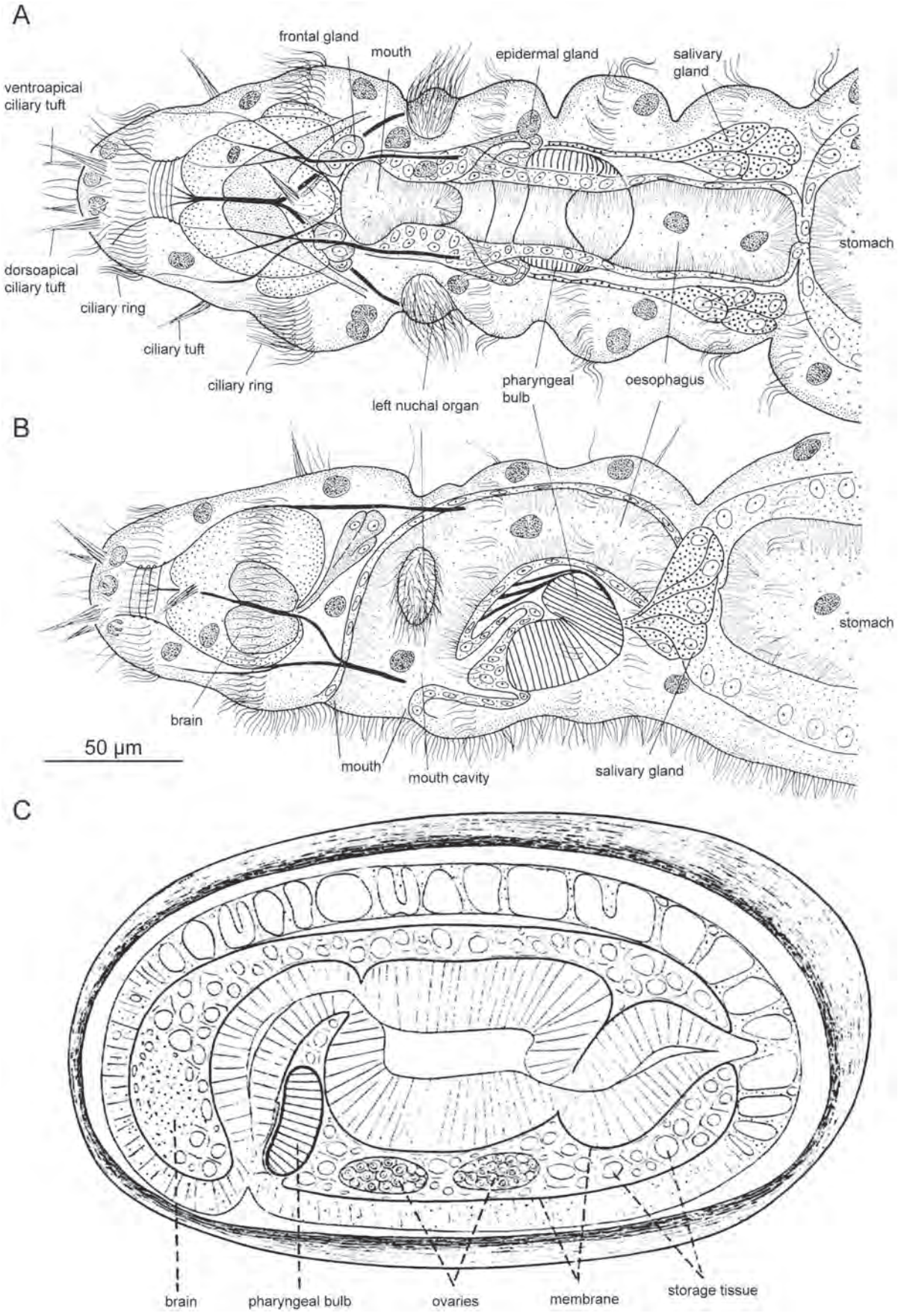


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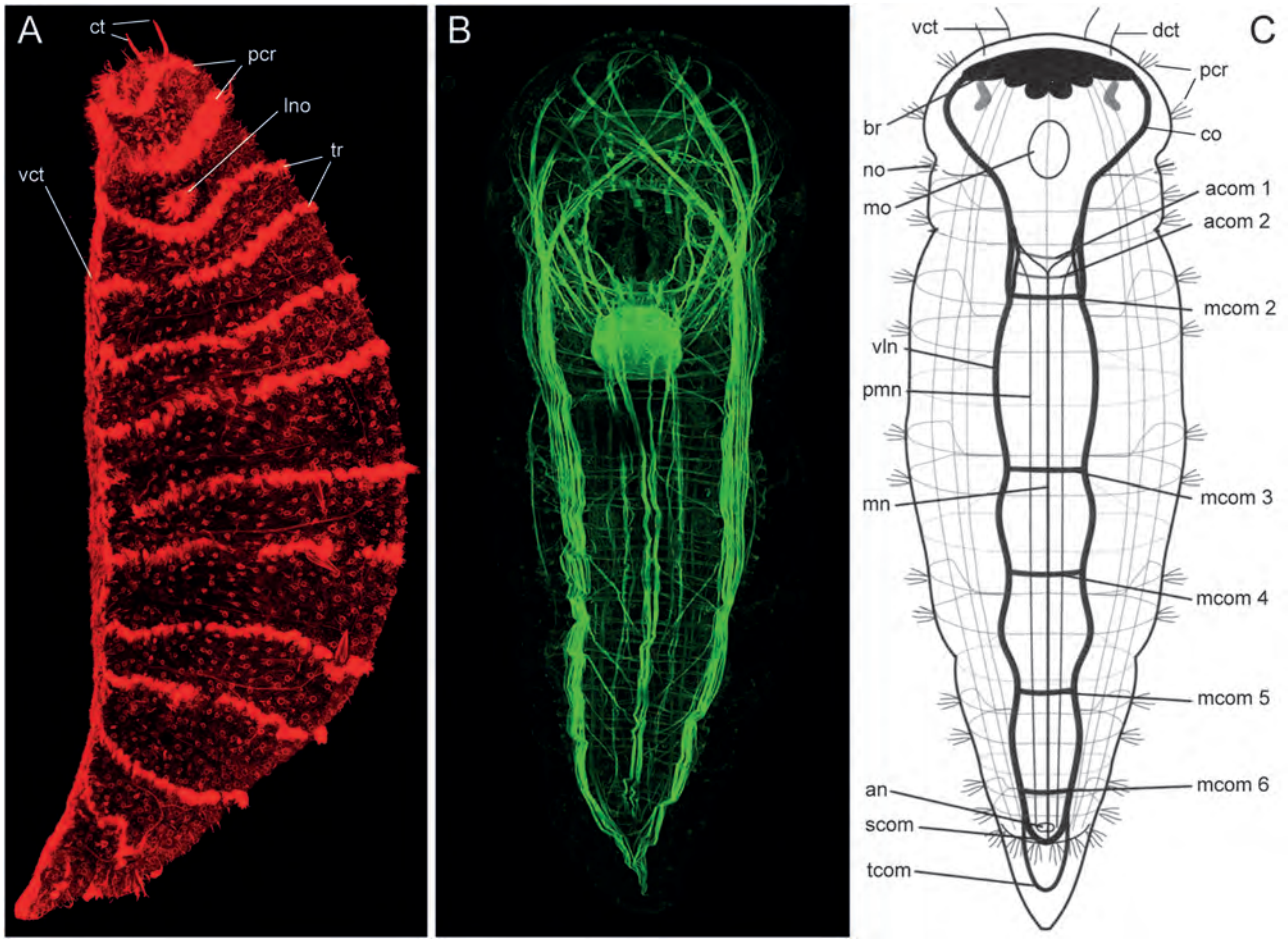


**Fig. 7.1.1.3:** *Dinophilus taeniatus*. A, Lateral view. Outer ciliary pattern. Trunk with transverse ciliary rings (tr) and ventral ciliary tract (vct). Surface covered with epidermal gland openings situated between the ciliary rings. Terminal ciliated tufts (ct) and prostomial rings (per). Nuchal organ of the left body side (lno). B, Pattern of phalloidin-labeled muscle fibers in a juvenile specimen. Pharyngeal bulb centrally located. C, Antiacetylated α-tubulin-IR. Nervous system. Prostominum with ventral (vct) and dorsal stiff dorsal (dct) ciliary tufts and ciliary rings (per). Mouth opening (mo). Circumesophageal connective (co) lateral (rem), paramedian (pmn) and median (mn) nerve cords. Subrectal (scom), terminal (tcom) and transverse commissures (com). Originals: A, Kerbl.

On the basis of such analyses, we now know that individuals of *Dinophilus* and *Trilobodrilus* possess six trunk segments.

### Anatomy

**Epidermis and Cuticle.** The epidermis is a transparent epithelium, which is completely covered with a relatively thin uniform cuticle (Brandenburg 1970a). The latter does not possess a collagenous grid or is composed of three layers (Brandenburg 1970a, Rieger and Rieger 1976). The outer palisade-like layer is covered by flat microvillar tips (Fig. 7.1.1.4). This specific cuticular structure is probably unknown in other annelid species (Purschke 1984, 1985). The cuticula of the pharyngeal sac is somewhat differently structured. Larger gland cells open between the epidermis cells. In light microscopy of *Trilobodrilus* species, two types of conspicuous epidermal glands can be distinguished: spherular inclusions forming enveloped polygonal fields and spindle-shaped glands (Westheide 1967, Rao 1973). The size and structure of the spherular inclusions (Fig. 7.1.1.5 C, D) are discussed to be of taxonomic value (Kajihara *et al.* 2015). Nelson (1907) described different types of epidermal, mostly mucous, glandular cells in a *Dinophilus* species.

**Musculature.** The body wall musculature comprises layers of circular, diagonal, and longitudinal muscles cells and is basically similar in *Trilobodrilus* and *Dinophilus* (Müller 1999, Kerbl 2016). Most prominent are the longitudinal fibers: there are two pairs of dorsolateral and ventrolateral longitudinal strands and an additional ventromedian bundle. These are interconnected by thinner circular and diagonal fibers (Fig. 7.1.1.3 B). The prostomium and the

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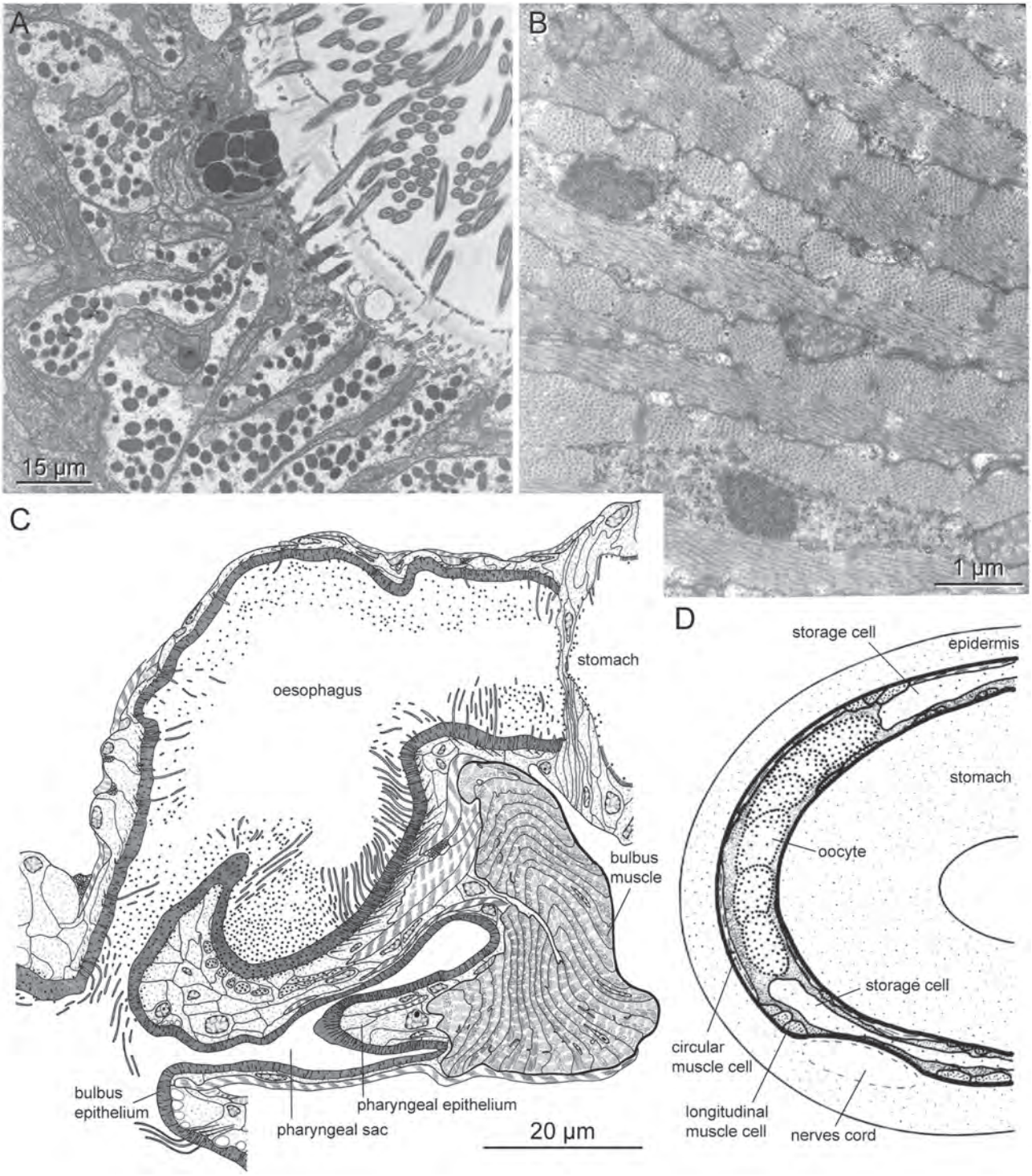


**Fig. 7.1.1.4:** Pharyngeal bulb. Coelom. A, Esophageal epidermis with salivary gland cells. B, Sagittal section through plate muscle cells of pharyngeal organ in *Dinophilus gyrociliatus*. C, Sagittal section of mouth opening in *Trilobodrilus axi* with pharyngeal organ. D, Cross-section of body trunk. Female *D. gyrociliatus*. A–C, After Purschke (1984); D, after Fransen (1980).

foregut display a relatively complicated arrangement of muscle cells, including the highly specialized plate muscle cells of the pharynx (Fig. 7.1.1.4 B) (see digestive system, p. 218). The main function of the musculature is generally seen as maintaining and changing the shape of the body rather than locomotion.

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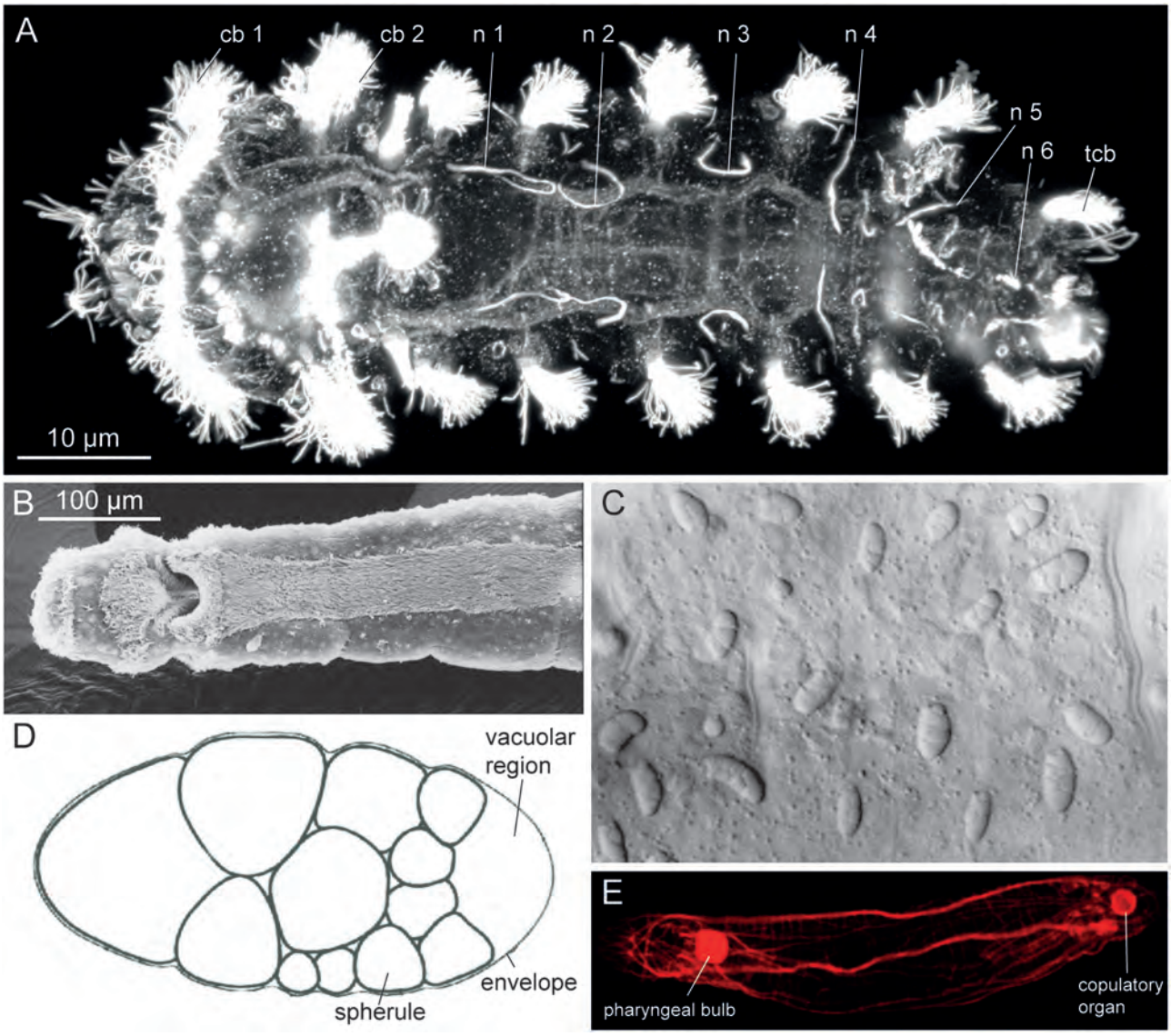


**Fig. 7.1.1.5:** A, *Dinophilus taeniatus*. Acetylated α-tubulin-IR. Ventral view of a young female. Nervous system. Ciliary rings (cb). Paired nephridia (n). B, *Trilobodrilus axi*. Ventral view of the anterior body with mouth opening and ventral ciliation. C, Light microscopical photo of spherular epidermal inclusions in *T. axi*. D, Schematic drawing of epidermal inclusion and terminology for the components. E, Musculature in *T. axi*. A, A. Kerbl (2016); B, E, G. Purschke; C, W. Westheide; D, Kajihara *et al*. (2015).

**Digestive system.** The triradiate mouth opening lies directly behind the prostomium (Fig. 7.1.1.1). There is a basket-like muscle sack surrounding the bulb (Kerbl 2016). It leads into the esophagus and empties into a capacious stomach, which joins the intestine. The anus opens dorsally. The esophageal cuticle is densely ciliated, except for a deep ventral fold, known as the pharyngeal sac. The most prominent structure of the anterior intestinal system is the ventral pharyngeal organ (Ohm 1963). This solid, kidney-shaped bulbus (length about 50–60 µm) is slightly bent dorsally in an upward direction. The most characteristic feature of the bulbus is the density of its plate-shaped muscle cells, 27 in *D. gyrociliatus* and 28 in *Trilobodrilus axi*. The muscle cells are obliquely striated, displaying a family-specific arrangement of opposing systems of myofilaments lying virtually at right angles to each other and approximately 45° to the sagittal axis (Fig. 7.1.1.4 B) (Jägersten 1947, Rieger and Rieger 1975, Purschke 1985). These cells are surrounded by a distinct extracellular lamina, to which dorsolateral and ventrolateral extrinsic pro- and retractor muscles adhere. Posterior to the mouth opening, there is a pair of ventral ciliary fields, which are considered serving as sensory organs (Kerbl 2016). A total of 25 to 30 paired salivary

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glands on each side are present behind the pharyngeal organ. Strands of thin processes of the gland cells run anterior and open into the pharyngeal fold (Figs. 7.1.1.2 A and 7.1.1.4 A).

Food uptake occurs mostly by grazing bacteria, foraminiferans, and diatoms (Jennings and Donworth 1986) from the "aufwuchs" of sand grains and other solid structures, by the abrading action of the pharyngeal organ (Jennings and Gelder 1969). The monomorphic species feed principally on diatoms.

Movement of the bulb is promoted by muscles, which extend between the pharynx and the epidermal neck region. Additionally, the pharyngeal bulb is connected to various muscles in the prostomial area. The action of the pharyngeal organ is described as extrusion through the mouth opening, with the food then converged back and forth along the substratum in order to dislodge particles (Westheide and Schmidt 1974). Generally, dislodged particles are maintained close to the mouth by mucus discharged from cephalic glands. Food particles can also be collected into the mouth by the movements of the esophageal cilia, enabling the animals to take up larger numbers of minute planktonic cells.

The uptake and incorporation of the dissolved amino acid glycine by *T. axi* have been demonstrated clearly (Tempel and Westheide 1980), although not in very high quantities. As indicated by autoradiography, uptake occurs primarily across the body surface from the interstitial water of coarse-grained tidal beaches.

**Nervous system.** The ladder-like central nervous system begins anteriorly with a compact dorsal brain and a pair of circumesophageal connectives that encircle the mouth and the pharyngeal organ that split into a dorsal and a ventral root typical of polychaetes (Weldon 1886, Nelson 1904, Kotikova 1973, Windoffer and Westheide 1988a,b, Beniash *et al*. 1992, Windoffer 1992, Müller and Westheide 2002, Orrhage and Müller 2005, Fofanova *et al*. 2014, Kerbl 2016). The brain continues with a ventral nerve cord containing widely spaced main nerves equipped with ganglia and transverse commissures (Fig. 7.1.1.3 C). Sophisticated immunohistological labeling and confocal laser scanning microscopy have permitted an almost complete reconstruction of the anatomy of the nervous system in both male and female individuals of *D. gyrociliatus*, *T. axi*, *D. taeniatus*, and *T. hermaphroditus* (Müller 1999, Müller and Westheide 2002, Kerbl 2016). All nerves are intraepidermal.

The ventral nervous system consists of five longitudinal nerve cords: one pair forming the median nerve by fusion and one pair of paramedian nerves and one pair of main ventral nerves situated more laterally (Müller 1999, Müller and Westheide 2002, Orrhage and Müller 2005, Kerbl 2016). They are accompanied by additional longitudinal nerves: one unpaired dorsal, one pair of dorsolateral, and two pairs of lateral nerves in *D. gyrociliatus*. They are connected by one (in monomorphic *Dinophilus* and *Trilobodrilus*) or three commissures (in dimorphic species) per segment. The 18 commissures occur in groups of three (segments 1 to 4) and two commissures (segments 5 to 6). The posterior body end comprises two commissures, which are closely adjacent to each other: a dorsal subrectal and a ventral terminal one (Fig. 7.1.1.3 C). There are six pairs of ganglia indicating six trunk segments. Prominent lateral nerves emerge from the ventrolateral nerve cord, which accompany the transverse ciliary rings; they consist of four to five individual fibers. A stomatograstric system forms a ring around the pharynx.

**Body cavities and coelom.** A typical blood vascular system does not exist. Beauchamp (1910) stated that the partially obliterated and highly restricted coelom functions as a hemocoel. Much of its coelomic space is occupied by voluminous glycogen-rich filling cells (up to 25 µm in diameter) derived from the coelomic epithelium and called coelenchyma (Fig. 7.1.1.4 D). Dinophilids are virtually acoelomate animals (Fransen 1980). A continuous lining of the coelom therefore does not exist and the coelomic fluid may bathe the musculature, and even the epidermis and the gut epithelium.

**Excretory system and nephridia.** Excretory organs are protonephridia, the fine structure of which is still incompletely elucidated. According to Ruebush (1940), there are five pairs in the female of a monomorphic species, only four in the male (Shearer 1911); they are absent in the segment containing the genital ducts. There are six pairs in adult *D. gyrociliatus* females (Fig. 7.1.1.5 A). The multiciliated terminal cell is of the flame bulb type. It possesses a filtration system formed by microvillar rods and bridged by an extracellular matrix, which presumably functions as a macromolecular filter (Brandenburg 1970b).

**Reproductive organs and gametes.** The male reproductive system (Jägersten 1944a) consists of testes, vesiculae seminales, and an unpaired copulatory organ. The testes extend, on each side, up to the first segment as paired lobes united posteriorly below the gut or it is an unpaired ventrally situated sac. The ovoid vesiculae accumulate sperm via small openings (Fig. 7.1.1.7 A).

The spermatozoa of dinophilids belong to the highly modified type (Fig. 7.1.1.7 C); they display an extremely elongated filiform structure (Franzén 1977, Westheide 1984, Scharnofske 1986), with a length of about 90 µm in *T. axi*. One pair of seminal vesicles is present in the

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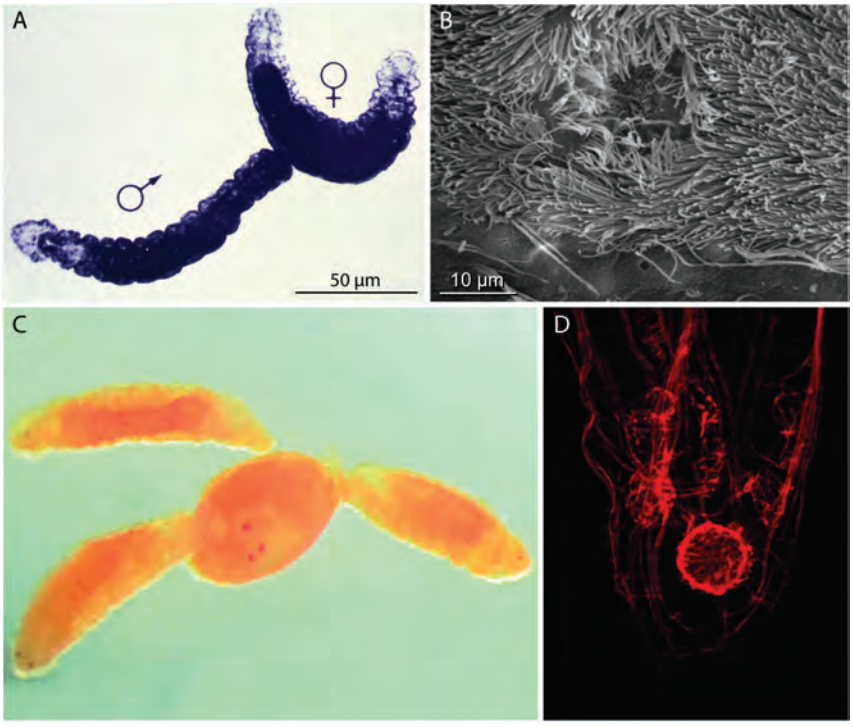


**Fig. 7.1.1.6:** Reproduction. A, B, D, *Trilobodrilus axi*. A, Copulation. Male being pulled around by the female. B, Genital opening within ventral ciliary tract of a male. C, Copulation of three males and one female in *Dinophilus taeniatus*. D, Musculature of posterior end with male genital organ. A, Schmidt and Westheide (1972); B, D, original: G. Purschke; C, original. T. Mayorova.

posterior part of the monomorphic *Dinophilus* males (Ruebush 1940); two pairs are found in *T. axi* (Fig. 7.1.1.7 A). Each vesicle is part of a ciliated spermioduct with an outer muscular layer. The two ducts of each side in *T. axi* join so that, as in *Dinophilus*, only two canals discharge sperm into the copulatory organ. In the dwarf male of *D. gyrociliatus*, vesicles and spermioducts of this type do not occur, but instead, there are two strange spherical, monociliated organs that connect the testes and the copulatory organ (Scharnofske 1984).

The anatomy of the prominent unpaired copulatory organ is basically the same in *Trilobodrilus* and *Dinophilus* (Fig. 7.1.1.7 B). A somewhat urn-shaped, ventrally open musculature comprises a complex inner layer and an outer muscular sheath. It is surrounded by a collar of large gland cell bodies (Westheide 1988). Their apical projections penetrate the musculature and, together with supporting cells, build up the penial cone or penis proper (Fig. 7.1.1.7 B). Position, organization, and ultrastructure give evidence that the copulatory organ differentiates out of an invagination of epidermis and underlying body musculature. In both genera, when the copulatory organ is at rest, the penis proper projects into a pocket-like chamber of the ventral body surface in the posteriormost segment. Spermioducts and spherical organs, respectively, penetrate the peripheral musculature and empty into an atrium-like lateral fold of this chamber that surrounds the penial apex. The chamber space continues into the penial cone, thus forming a central dorsoventrally directed lumen, into which different penial glands discharge (Fig. 7.1.1.8 B). Apically arranged gland cell projections within the penis proper contain characteristic needle-like secretory products that together form a conical structure having the appearance of a bundle of stylets. In the somewhat simpler *D. gyrociliatus* male, only these needle-like secretory structures seem to exist (Fig. 7.1.1.8 B). No such glandular product, however, could be definitely found by Scharnofske (1984) in the male organ of *Trilobodrilus* individuals (Westheide 1988).

**Dwarf male of *D. gyrociliatus*.** The dwarf male of the dimorphic *D. gyrociliatus* is unique. It is the smallest annelid hitherto known and one of the smallest invertebrates (about 50 µm in length and between just 15 and 20 µm in width). The typical pigmented prostomial eyes of the genus are not developed. An intestinal tract is completely lacking.

Its extremely simple organization is entirely devoted to locomotion and reproduction – a kind of mobile male sexual organ. The animal contains about 300 cells (Scharnofske 1984), 68 of which belonging to the nervous system and include two glial cells (Windoffer 1992, Windoffer and Westheide 1988a,b). Forty neuronal cells project into the epidermal epithelium and are considered to be receptor cells. Twentytwo cells are

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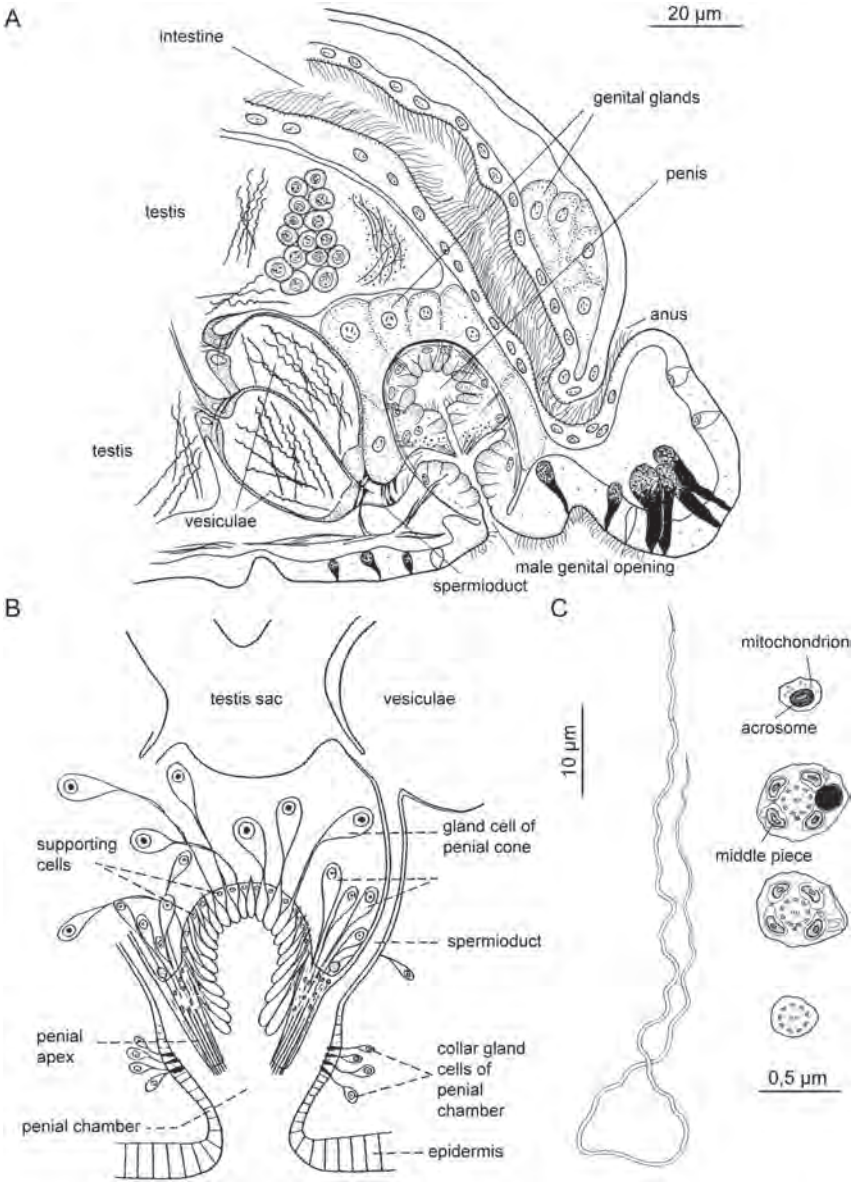


**Fig. 7.1.1.7:** Male genital organs. A, Schematic sagittal reconstruction of male posterior end in *Trilobodrilus axi*. B, Schematic reconstruction of male genital organs in *Dinophilus*. C, Sperm. Reconstructed cell and transmission electron microscopy cross-sections. A, After Westheide and Schmidt (1974); B, Jägersten (1944b); C, Franzén (1977).

equipped with motile cilia and form the single small dorsal and two larger symmetrically positioned ventral ciliary fields of locomotion (Fig. 7.1.1.8 C). The unipolar, bipolar, or pseudo-unipolar receptor cells can be divided into different types. The two penis ganglia are associated with the copulatory organ, and the two frontal ganglia form the brain; in addition, there is a much smaller pair of ventral ganglia. The ganglia are connected by commissures and paired nerve cord (Fig. 7.1.1.8 A). There is only one pair of nephridia in a dwarf male located in the anterior third of the body. The almost egg-shaped individual is not segmented but appears to be "laced up" along the middle of its body. It possesses three voluminous frontal gland cells of up to 10 µm in diameter; caudally, six pairs of glands occur, with each pair consisting of two types of cells. The ciliary pattern consists of three ciliary fields, an apical bundle, a frontal ring, and a ventral band, which widens at the caudal end.

The musculature in its entirety consists of 34 symmetrically arranged cells. Five pairs form the two ventrolaterally longitudinal muscles and the dorsal longitudinal muscles. All the longitudinal muscle cells – except one – run along the testis and over the various penis muscles. There are 10 circular muscle cells – five on each side, which are connected with each other dorsolaterally and ventrally.

Sperm develop and are collected in two voluminous bean-shaped paired cavities (testes) (Nachtsheim 1919), from which two short well-developed spermioducts with solid walls (vasa deferentia) open into the penial sac of

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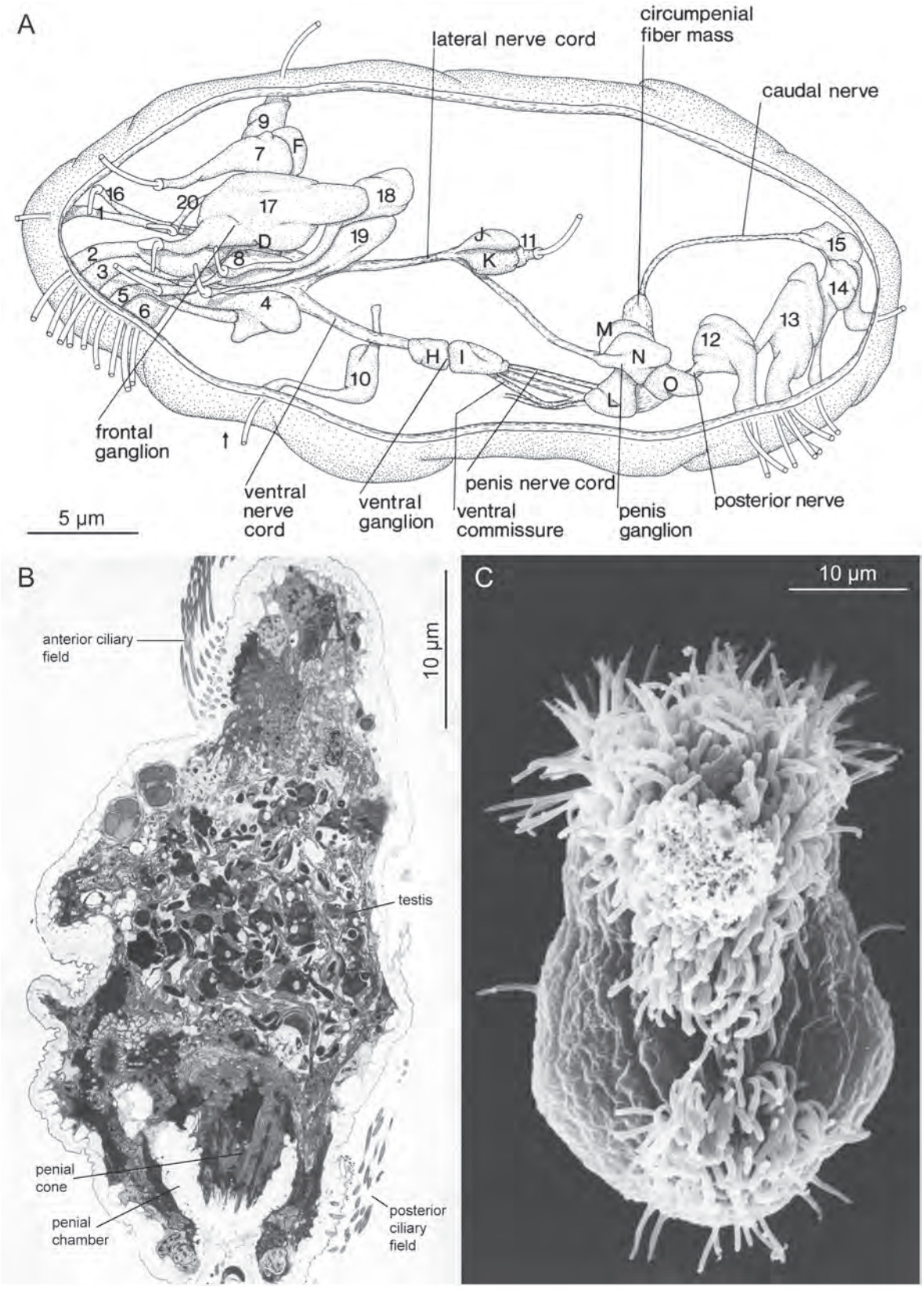


**Fig. 7.1.1.8:** *Dinophilus gyrociliatus*. Dwarf male. A, Lateral reconstruction of the nervous system. B, Longitudinal transmission electron microscopy (TEM) section through the testis, copulatory organ, and penial chamber. C, Lateral TEM photo. A, C, after Windoffer and Westheide (1988a); B, after Scharnofske (1984).

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the copulatory organ proper (see previous discussion). The penial cone is similar in construction to the corresponding organ in dimorphic species. Nachtsheim (1919) observed a lifespan of approximately 10 days in the dwarf males, which is considerably shorter than that in the females (2 to 3 months).

**Ovaries.** Ovaries are positioned ventral to the intestinal tract and develop out of paired coelomic sacs. They extend from one of the middle segments to the posterior end. Each sac has two sections merging caudally, finally forming a joint envelope for the growing oocytes encircled by a thin epithelial layer and an outer muscular coat (Nachtsheim 1919, Ruebush 1940). According to Eckelbarger (1983), a peculiar process of fusion between certain oocytes and their sister oocytes during early oogenesis takes place within the ovary.

Small female gonopores at the ventral body side have been described for some *Dinophilus* species (Korschelt 1882, Ruebush 1940) but have not been proved in others. Mostly, eggs are released through an indistinct opening ventrally in the posterior part of the body (Fig. 7.1.1.9 A, B) or by a momentary rupture of the integument.

After being spawned, the individual eggs of dinophilids release a mucopolysaccharide that appears bloated immediately after exposure to seawater (Fig. 7.1.1.9 D–F). Thus, eggs discharged side by side stick together and are covered by a jelly-like cocoon surrounding the eggs. The number of eggs in a cocoon varies with the individual and with the number of previous egg layings. Ruebush (1940) counted 14 to 16 eggs in the first cocoon and 6 to 8 eggs in the second and in the third of a monomorphic species.

In *T. axi*, females release three to eight eggs at a time; their development lasts 13 to 19 days at 15–18°C (Ax 1968, Westheide and Schmidt 1974).

### Reproduction and development

No asexual reproduction has been reported for any true dinophilid species. With the exception of *T. hermaphroditus* Riser, 1999, dinophilids are gonochoristic. The *Dinophilus* species can be separated into monomorphic and sexually dimorphic forms with extremely small males (see taxonomy). In general, one cannot determine the sex using external features alone. One exception is the male in *Trilobodrilus*, which has a large gap in the ventral ciliated tract, where it surrounds the genital opening (Fig. 7.1.1.6 B).

Several accounts of sperm transfer in dinophilids exist (Ruebush 1940), all agreeing that the process occurs histolytically by direct hypodermic injection and that no female organs or ducts are involved (Jägersten 1944b). The most detailed descriptions – including several vivid photos – are probably the paper by Traut (1966) and the film by Schmidt and Westheide (1972) on copulation in *D. gyrociliatus* (Fig. 7.1.1.9). At the outset of the process, the dwarf male presses the ventral side of its body against the female and performs a slight bend ventrally. The opening of the penial pocket is then placed on the surface of the

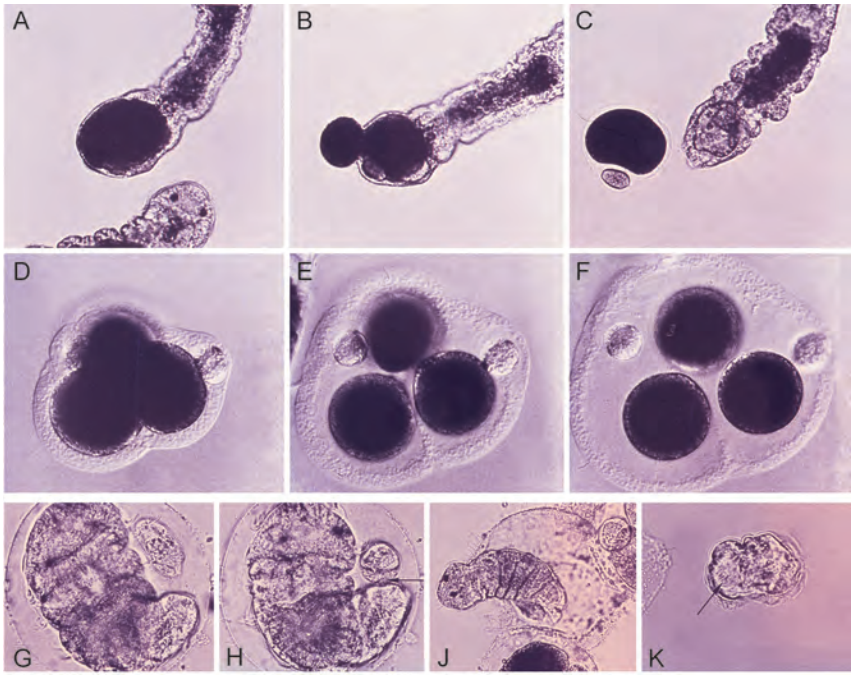


**Fig. 7.1.1.9:** Successive motion pictures showing reproduction in *Dinophilus gyrociliatus*. A, B, Female releasing eggs through an indistinct opening in the posterior end. C, Cocoon with one female and one male egg. D–F, Bloating of mucopolysaccharides of the jelly-like cocoon after exposure to seawater. G, H, Hypodermic injection within a cocoon. J, Hatching female. K, Free-swimming male. A, Schmidt and Westheide (1972).

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female´s body and retracted after two or three seconds. The margin of the penial pocket adheres to the female, probably supported by glands opening outside the penis near the aperture of the genital chamber, resulting in the male sometimes being pulled around by the female (Ax 1968) (Fig. 7.1.1.6 A). During its first phase of copulation, a hole is punctured in the female epidermis without any detectable mechanical influence of the penis. Through this hole, sperm now flows rapidly into the female, assisted by repeated pumping movements of the penis. The entire procedure may not take longer than 25 to 30 seconds.

The process of copulation and the hypodermic injection of sperm into the females of monomorphic species are similar to that described in *D. gyrociliatus*. In monomorphic species, there is no definite place on the female body for the injection; copulation may take place in all parts of the body except the head (Ruebush 1940). Obviously, there is no relation between the female´s maturity and the copulation; the process is not prevented by a previous copulation. Punctuary may succeed after several attempts at penetration. In *D. taeniatus*, more than one male may be involved in the process of injecting sperm into a female (Fig. 7.1.1.6 C).

In *D. gyrociliatus*, the dimorphism of mature individuals (see previous discussion) is reflected in the dimorphism of the ova (Grün 1972). Small eggs of about 40 µm in diameter give rise to dwarf males, while large eggs of about 80 µm in diameter develop into the normal-sized females (Schmidt and Westheide 1972) (Fig. 7.1.1.9 C). Deposited cocoons contain male and female eggs in an average ratio of 1 to 3. At least cocoons contain one male and one female egg. There are no free-swimming larval stages; the young animals hatch after 6 days. Hatching females have five segments; the sixth segment develops soon after (Kerbl 2016). Their life cycle takes a maximum of 3 weeks, including 1 week of embryonic development inside the cocoon.

In *D. gyrociliatus*, dwarf males are already mature when hatching. They may copulate within the cocoon or outside it, either with sister or nonsister individuals after chance meetings. The development of *D. gyrociliatus* is slightly shorter than in the monomorphic species; normally, it requires 10 to 12 days compared to 3 weeks in *D. taeniatus* (populations of Greenland and the White Sea).

**Life cycles**

In the *T. axi* populations of Sylt (North Sea), spawning is mainly controlled by temperature; successful reproduction occurs only at temperatures above the critical level between 3 and 6°C (Schmidt and Westheide 1971). For the reproductive periods of *Trilobodrilus heideri*, see von Nordheim (1984).

The annual life cycle of the monomorphic *D. taeniatus* on the Yorkshire coast (England) is completely different. Free-swimming animals occur October–June, showing a maximum in March–April, and then decline as water temperatures increase (Jennings and Donworth 1986); see also Jägersten (1944a, 1951) for the Swedish West coast. Decline is due to death of adult individuals and a unique obligatory encystment stage of the immature progeny for up to 8 months. The cyst is an egg-shaped state (Fig. 7.1.1.2 C), which is a rigid capsule reaching a size of 800 µm in length. Partial dedifferentiation within the cysts is followed by redifferentiation and excystment October–January as water temperatures decrease and the number of planktonic diatoms flourish. Excystment is temperature dependent and is inhibited by summer temperatures. Excysted worms feed and reproduce until May. The females deposit a maximum of four cocoons in a sequence over 2 to 3 months, with up to 16 eggs per cocoon. The sexual reproduction takes place in winter months, when diatoms are abundant and macroherbivorous competitors are absent.

**Sex determination**

The genom of *D. gyrociliatus* is subdivided into a large number of chromosomes, which relatively are smaller in size than those of other polychaetes. This may be probably due to the limited quantity of DNA of its genome, which is the lowest observed hitherto in invertebrates; the haploid content in DNA was measured as 0.07 pg. The karyotype of the female consists of 2n = 24 chromosomes, and the male has 2n = 23.

The unique characteristics of the eggs and the sexual dimorphism in the species have created much interest in the sex determination of this species, and a number of determination mechanism have been discussed (Mecznikow 1866, von Malsen 1906, Conklin 1906, Korschelt 1887, Nachtsheim 1914, 1919, Shearer 1912, Tzonis 1938, Sella and Ramella 1999). After detection of the regular occurrence of a univalent sex chromosome in male meiosis, sex determination is considered to take place in the gametes; most probably it is chromosomal and syngamic of the X0–XX type. Large eggs are then fertilized selectively by female-determining spermatozoa (Martin and Traut 1987). The chromosomal X0–XX sex determination in *D. gyrociliatus* is the only case of a marine polychaete (Simonini *et al.* 2003). Sex ratio is affected by variations in numerous maternal and environmental factors (Traut 1969a, 1970, Prevedelli and Zunarelli Vandini 1999). Also, diet affects sex ratio: individuals that are fed with cereals show a clear displacement of sex ratio toward males (Prevedelli and Zunarelli Vandini 1999). Parthenogenetic development, however, does not seem to occur (Nachtsheim 1919, Zunarelli Vandini 1956).

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## Biology and ecology

### Distribution

Dinophilids have a worldwide distribution. Monomorphic *Dinophilus* seem to prefer shallow older seas of the arctic, subarctic, and boreal coasts of, e.g., Newfoundland, Greenland, Sweden, Denmark, Great Britain, and Russia; the dimorphic species occurs in both boreal and subtropical waters (Kerbl *et al*. 2016).

*Trilobodrilus* species are typical interstitial meiofauna organisms, which are restricted to coarse, generally well-sorted clean, sandy habitats. Individual species occur in eulitoral (e.g., *T. axi*) or sublitoral (e.g., *T. heideri*) sediments down to several meters depth. Typical subtidal localities are the so-called *Amphioxus* sands. Generally, the trilobodrilids penetrate such sediments no deeper than about 10 cm. Fine sandy beaches and organic rich mudflats in wadden-sea sediments are avoided. For this reason, only a few localities with rich populations of *T. axi* are found along the European Atlantic coast line. These include the North Sea island of Sylt, Germany (Schmidt 1969), and Arcachon, France (Westheide 1972–1973), where, in the spring and summer, extremely high density groups of up to 600 individuals per 50 cm³ (Schmidt 1969) inhabit the surface layer of sandy beaches across a 2-m-wide band in the eulitoral area of the beach slope. Similarly, high-density habitats of an undescribed *Trilobodrilus* species have been observed to occur on the Oregon coast (Coos Bay) of North America (Westheide and Purschke unpublished observation). Beaufort, North Carolina (Rieger and Rieger 1975), and Puget Sound, Washington (Wieser 1957), were additional localities of *Trilobodrilus*. *Trilobodrilus* species are, however, conspicuously absent from equally suitable sandy beaches of warm and tropical areas; among other beaches, those along the Tunisian coastline of the Mediterranean Sea (Westheide 1972), the Galapagos archipelago (Schmidt and Westheide 1977), the island of Mahé (Seychelles), the coastlines of Florida, and the beaches of the island of Phuket (Thailand) have been investigated thus far, with the exception of *Trilobodrilus indicus* collected in intertidal sands from the Bay of Bengal (Rao 1973). Nevertheless, *T. axi* appears to be highly resistant to cold temperatures. In experiments with supercooled water without ice formation, individuals of this species show no damage after 5 hours at –12°C (Westheide and von Basse 1978).

*Dinophilus* species rarely live within litoral sediments. They are generally present epibenthically on a variety of seaweeds at a few meters depth, as well as on rocks and stones. *Dinophilus gyrociliatus* can most easily be found in the surface layer of detritus at the bottom of seawater aquarium tanks.

## Phylogeny and taxonomy

### Historical phylogeny

Since the description of the genus *Dinophilus* by Oskar Schmidt in 1848, its phylogenetic position in the animal kingdom has been a matter of controversy (Schroeder and Hermans 1975). It was initially assigned to the Plathyhelminthes on account of its external resemblance to smaller turbellarians (Schmidt 1857). The presence of a proboscis caused Beneden (1851) and Verrill (1892) to place *Dinophilus* within the nemerteans.

Still utterly confusing was the classification of *Dinophilus* by Schultze (1851) in his "Naturgeschichte der Turbellarien," where he suggested "neben der Ordnung der Nemertinen noch als besondere Ordnung die Mikrostomeen und *Dinophilus* unter dem Namen Arhynchia (Rüssellose) im Gegensatz zu den Nemertinen, den Rhynchocoela." In the nomenclatoral appendix of his Turbellaria II Rhabdocoelida, Graff (1913) mentioned *Dinophilus borealis*, 1862 as a possible synonym of *Plagiostomum vittatum*. As late as 1901, a species clearly belonging to the Nemertea was described by E. Schultz as *Dinophilus rostratus*. Schmarda (1861) was the first to assign the taxon to the Annelida, and since then, embryological and morphological findings (Prowazek 1900, Nelson 1904, 1907) – in particular the typical spiral cleavage process with a paired meioblast forming the mesoderm – have left no doubts to its annelid affiliation. Despite this, the possibility of an additional close relationship to the rotifers (von Graff 1882, Lang 1884, Nachtsheim 1919) continued to be discussed until Nelson (1904), among others, insisted that "the cleavage pattern has presented such startling and accurate resemblance" to annelids that any other relationship within invertebrate animals was deemed impossible.

Over the following period, two different ideas of dinophilid evolution were discussed. The taxon was proposed to date back to an early stem species within the annelid tree (Bubko 1973). Mamkaev and Selivanova (1979) and other, mainly Russian, zoologists classed Dinophilidae as a higher taxon in its own right, isolated from the true Polychaeta.

A similar line of thoughts was the basis of Hatschek`s (1893) incorporation of *Dinophilus* into the "1. Subclasse Archiannelida" of his "System der Anneliden," an idea that determined the phylogenetic position of the Dinophilidae for a considerable time. Toward the second half of the twentieth century, however, the so-called archiannelids were no longer regarded as a

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primitive taxon but instead as secondary altered and simplified polychaetes (Remane 1932), which are especially adapted for interstitial life (Hermans 1969, Jouin 1971). Finally, Westheide (1985) demonstrated that a monophyletic taxon Archiannelida with the inclusion of Dinophilidae has become obsolete. The traditional Archiannelda concept has now been rejected on the basis of molecular investigations (Struck *et al*. 2002, 2015, Andrade *et al*. 2015).

Mecznikow (1866) probably was the first who considered *Dinophilus* to be a stationary larva, but one in which the development ends and which has become correspondingly modified. Because of the strong resemblance between dinophilids and polytrochous larvae (Weldon 1886), especially larvae of eunicemorphic polychaetes, another group of systematists regarded the taxon as gradually reduced Dorvilleidae. The idea of a close relationship of dinophilids and eunicids became especially convincing when Åkesson (1977) demonstrated reciprocal infection with the coelomic parasitic and host-specific coccidian of the genus *Grellia*, between the two taxa. Westheide (1982, 1984, 1985) and Westheide and Riser (1983) constructed a hypothetical reduction series that saw *Dinophilus* and *Trilobodrilus* feature as the morphological endpoint of a series of taxa, which evolved by neotenous (progenetic) evolution (Westheide 1987). Since dinophilid taxa were regarded as derived members of Dorvilleidae, Eibye-Jacobsen and Kristensen (1994) completely eliminated the taxon Dinophilidae.

Molecular systematic investigations, however, did not confirm these morphology-based hypotheses (Struck *et al*. 2002, 2015, Andrade *et al*. 2015), failing to detect a close relationship between dinophilid and eunicid polychaetes. Today, progenesis is still considered the evolutionary background of dinophilid evolution. Kerbl *et al*. (2016) presented morphological evidence for pedomorphosis: The female *D. gyrociliatus* resemble prehatching stages of *D. taeniatus*, indicating that *D. gyrociliatus* may have originated through progenesis from a juvenile ancestor similar to *D. taeniatus*. It was found that the myogenesis, ciliogenesis, and neurogenesis in adult *D. gyrociliatus* resemble the architecture in juvenile *D. taeniatus*. According to Struck *et al*. (2015), the taxon Dinophilidae seems to be robustly situated in the new sendentariate taxon Orbiniida (Struck *et al*. 2015) in the close vicinity of *Apharyngtus punicus* Westheide, 1971 and *Diurodrilus subterraneus* Remane, 1925. David and Halanych (2017) have described the mitochondrial genome of *Dinophilus gyrociliatus* and have used it for demonstrating the position of the species within the pleistoannelid relationship system. There it forms the sister group of *Urechis caupo*.

Phylogenetic analyses reveal the family of the Dinophilidae to be monophyletic (Kajihara *et al*. 2015, Vang 2015) and to consist of three independent clades. The genus *Dinophilus*, however, is paraphyletic. Since *Trilobodrilus* is the sister taxon of the clade containing monomorphic *Dinophilus* species, Vang (2015) proposes the erection of a new generic taxon (*Durinus*) within Dinophilidae.

**Taxonomy**

The nine *Dinophilus* species presented by Nelson (1907) were mainly distinguished from each other on the basis of their ciliary pattern (Ruebush 1940), the description of which, however, suffered from observational deficiencies. Five of the species listed by Nelson were dimorphic, only *D. gyrociliatus* O. Schmidt, 1848 is currently generally accepted.

Vang (2015) listed 17 other species names, four of which are classified as "not accepted," one is the planktonic plathyhelminth species *Alaurina composita* Metschnikoff, 1861, and four are identical with *D. gyrociliatus*. Vang (2015) set about the old suspicion that several of the monomorphic *Dinophilus* actually comprise a single species. After carrying out both morphological and molecular analyses, he now accepts the following four monomorphic species: *Dinophilus taeniatus* Harmer, 1889, *Dinophilus gardineri* Moore, 1900, *Dinophilus jagersteni* Jones & Ferguson, 1957, and *Dinophilus kinkaidi* Jones & Ferguson, 1957. According to his unexpected molecular results, all monomorphic *Dinophilus* from Europe – from West Greenland to the White Sea in Russia – are to be accepted as the same species. It has been deemed that the species should be named *D. taeniatus* Harmer, 1899 (see Donworth 1986) despite the fact that the synonymous, but rarely used, name *Dinophilus vorticoides* Schmidt, 1848 has priority.

The taxonomic situation in the taxon *Trilobodrilus* (Remane 1925) is undisputed. Kajihara *et al*. (2015) list six species: *T. heideri* Remane, 1925, *Trilobodrilus nipponicus* Uchida & Okuda, 1943, *T. axi* Westheide, 1967, *T. indicus* Rao, 1973, *T. hermaphroditus* Riser, 1999, and *T. itoi* Kajihara *et al*., 2015 (see previous discussion). Two new species from California increase the number of valid species to eight (Kerbl *et al*. 2018).

**Family Dinophilidae Verrill, 1892**

**Type genus:** *Dinophilus*

**Diagnosis:** Small polychaetes with six segments, including an anterior peristomial body part consisting of two rings. Lacking any parapodial lobes and chitinous chaetae or tentacular appendages, except an unpaired pygidial lobe in *Dinophilus* (Fig. 7.1.1.1 D, E).

**Genus *Dinophilus taeniatus* Harmer, 1889**

(other monomorphic species, see Vang 2015)

Strongly colored, with monomorphic sexes, with an obligatory extended encystment stage (Fig. 7.1.1.2 C) within a relatively long life cycle.

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**Genus *Dinophilus gyrociliatus* O. Schmidt, 1857**
Sexually dimorphic species with a rapid life cycle without any cysts; dwarf males developing from male eggs of considerably smaller size.

**Genus *Trilobodrilus* Remane, 1925**
**Diagnosis:** Posterior part of prostomium slightly swollen, giving a trilobed appearance. No pigmented eyes. With compound refractive epidermal glands throughout the body.
**Type species:** *Trilobodrilus heideri* Remane, 1925
8 species:
*Trilobodrilus heideri* Remane, 1925
*Trilobodrilus nipponicus* Uchida & Okuda, 1943
*Trilobodrilus axi* Westheide, 1967
*Trilobodrilus indicus* Rao, 1973
*Trilobodrilus hermaphroditus* Riser, 1999
*Trilobodrilus itoi*, Kajihara, Ikoma, Yamasaki & Hiruta, 2015
*Trilobodrilus ellenscripsae* Kerbl, Nereide, Gonzales Rouse 6 Worsaae, 2018
*Trilobodrilus windansea* Kerbl, Nereide, Gonzales Rouse 6 Worsaae, 2018

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## References

Åkesson, B. (1977): Parasite-host relationship and phylogenetic systematics. The taxonomic position of dinophilids. In: Sterrer, W. & Ax, P. (eds.) The meiofauna species in time and space. Workshop Symposium, Bermuda 1975. *Mikrofauna des Meeresbodens* 61: 19–28.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "Archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32(11): 2860–2875.

Ax. P. (1968): Das Fortpflanzungsverhalten von *Trilobodrilus* (Archiannelida, Dinophilidae). *Marine Biology Berlin* 1: 330–335.

de Beauchamp, P. (1910): Sur la présence d'un hemocoele chez *Dinophilus*. *Bulletin de la Société Zoologique de France* 35: 18–35.

van Beneden, P.J. (1851): Notices sur un nouveau Nemertien de la côte d´Ostende. *Bulletin de l'Académie Royale de Belge* 18, 1.

Beniash, E.A., Yerlikova, N.N. & Yevdonin, L.A. (1992): Some characteristics of the *Dinophilus vorticoides* anatomy of the nervous system. In: Bushinskaja, G.N. (ed.) *Polychaeta and their ecological significance. Explorations of the Fauna of the Seas* 43(51). Russian Academy of Science, St. Petersburg: 5–8.

Brandenburg, J. (1970a): Die Cuticula des *Dinophilus* (Archiannelida). *Zeitschrift für Morphologie der Tiere* 68: 300–307.

Brandenburg, J. (1970b): Die Reusenzelle (Cyrtocyte) des *Dinophilus* (Achiannelida). *Zeitschrift für Morphologie der Tiere* 68: 83–92.

Bubko, O.V. (1973): On systematic position of Oweniidae and Archiannelida (Annelida). *Zoologicheskij Zhurnal* 52: 1286–1296 [in Russian].

Conklin, E.G. (1906): Sex differentiation in *Dinophilus*. *Science* 24: 294–296.

David, K.T. & Halanych, K.M. (2017): Mitochondrial genome of *Dinophilus gyrociliatus* (Annelida:Dinophilidae). *Mitochondrial DNA Part B: Resources* 2, 2, 831–832.

Donworth, P.G. (1986): A reappraisal and validation of the species *Dinophilus taeniatus* Harmer 1889 and of taxonomically significant features in monomorphic dinophilids (Annelida, Polychaeta). *Zoologischer Anzeiger* 216: 32–38.

Eakin, R.M., Martin, G.G. & Reed, C.T. (1977): Evolutionary significance of fine structure of Archiannelida eyes. *Zoomorphology* 88: 1–18.

Eckelbarger, K.J. (1983): Evolutionary radiation in polychaete ovaries and vitellogenetic mechanisms: their possible role in life history patterns. *Canadian Journal of Zoology* 61: 487–504.

Eibye-Jacobsen, D. (1994): On the nature of the two anterior asetigerous rings in Dorvilleidae and Dinophilidae (Annelida, Polychaeta). In: Danvin, J.-C., Laubier, L. & Reish, D.J. (eds.) *Actes de la 4ème conference internationale des Polychètes. Mémoires du Muséum national d´Histoire naturelle* 162: 93–100.

Eibye-Jacobsen, D. & Kristensen, R.M. (1994): A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta* 7: 257–262.

Fofanova, E.G., Nezlin, L.P. & Voronezhskaya, E.F. (2014): Ciliary and nervous structures in juvenile females of the annelid *Dinophilus gyrociliatus* (O. Schmidt, 1848) (Annelida: Polychaeta). *Russian Journal of Marine Biology* 40: 43–52.

Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphologie* 93: 235–249.

Franzén, Å. (1977): Ultrastructure of spermatids and spermatozoa in Archiannelida. *Zoon* 5: 97–105.

von Graff, L. (1882): *Monographie der Turbellarien. I. Rhabdocoelida*. Verlag von Wilhelm Engelmann, Leipzig.

von Graff, L. (1913): *Turbellaria II. Rhabdocoelida. Das Tierreich*. R. Friedländer & Sohn, Berlin 35: 1–484.

Grün, G. (1972): Über den Eidimorphismus und die Oogenese von *Dinophilus gyrociliatus* (Archiannelida). Zeitschrift für *Zellforschung und mikroskopische Anatomie* 130: 70–92.

Harmer, S.F. (1889): Notes on the anatomy of *Dinophilus*. *Journal of the Marine Biological Association of the united Kingdom* 1: 119–143.

Hatschek, B. (1893): System der Anneliden, ein vorläufiger Bericht. *Lotos, Naturwissenschaftliche Zeitschrift* 13: 123–126.

Hermans, C.O. (1969): The systematic position of the Archiannelida. *Systematic Zoology* 18: 85–102.

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Jägersten, G. (1944a): Zur Kenntnis der Morphologie, Enzystierung und Taxonomie von *Dinophilus*. *Konglia Svenska Vetenskaps-Akademiens Förhandlingar* 21: 1–90.

Jägersten, G. (1944b): Über den Bau des Kopulationsapparates und des Kopulationsmechanismus bei *Dinophilus*. *Zoologische Bijdragen, Uppsala* 22: 61–86.

Jägersten, G. (1947): On the structure of the pharynx of the Archiannelida with special reference to there-occurring muscle cells of aberrant type. *Zoologisk Bijdragen Uppsala* 25: 551–570.

Jägersten, G. (1951): Life cycle of *Dinophilus*, with special reference to the encystment and its dependence on temperature. *Oikos* 3: 143–165.

Jennings, J.B. & Donworth, P.J. (1986): Observations on the life cycle and nutrition of *Dinophilus taeniatus* Harmer, 1889 (Annelida: Polychaeta). *Ophelia* 25: 119–137.

Jennings, J.B. & Gelder, S.R. (1969): Feeding and digestion in *Dinophilus gyrociliatus* (Annelida: Archiannelida). *Journal of Zoology, London* 158: 441–451.

Jouin, C. (1971): Status of the knowledge of the systematics and ecology of Archiannelida. In: Hulings, N.C. (ed.) Proceedings of the First International Conference on Meiofauna. *Smithsonian Contributions to Zoology* 76: 47–56.

Kajihara, H., Ikoma, M., Yamasaki, H.& Hiruta, S.F. (2015): *Trilobodrilus itoi* sp. now., with a re-description of *T. nipponicus* (Annelida: Dinophilidae) and a molecular phylogeny of the genus. *Zoological Science* 32: 405–417.

Kerbl, A. (2016): Neuromuscular structure, evolution and development in meiofaunal annelides with special focus on *Dinophilus gyrociliatus*/Dinophilidae). Department of Biology, University of Copenhagen. PhD thesis.

Kerbl, A., Fofanova, E.G., Mayorova, T.D., Voronezhskaya, E.E., Worsaae, K. (2016): Comparison of neuromuscular development in two dinophilid species (Annelida) suggests progenetic origin of *Dinophilus gyrociliatus*. *Frontiers in Zoology* 13:49: 1–39.

Korschelt, E. (1882): Über Bau und Entwicklung des *Dinophilus apatris*. Inaugural Dissertation, *Zeitschrift für wissenschaftliche Zoologie* 37: 315–333.

Korschelt, E. (1887): Die Gattung *Dinophilus* und der bei ihr auftretende Geschlechtsdimorphismus. Eine kritische Zusammenfassung neuerer und älterer Forschungsergebnisse. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 2: 955–967.

Kotikova, E.A. (1973): New data concerning the nervous system of Archiannelida. *Zoologicheskii Zhurnal* 52: 1611–1615 [in Russian].

Lang, A. (1884): Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrenzenden Meeresabschnitte. Eine Monographie. In: Zoologische Station zu Neapel (ed.) *Fauna und Flora des Golfes von Neapel*. W. Engelmann, Leipzig: 1–688.

von Malsen, H. (1906): Geschlechtsbestimmende Einflüsse und Eibildung des *Dinophilus apatris*. *Archiv für mikroskopische Anatomie und Entwicklungsgeschichte* 69: 63–99.

Mamkaev, V. & Selivanova, R.V. (1979): Elektronenmikroskopische Untersuchungen an *Dinophilus vorticoides* O. Schmidt. *Trudy Zoologisches Institut Leningrad* 84: 73–83 [in Russian].

Martin, F. & Traut, W. (1987): The mode of sex determination in *Dinophilus gyrociliatus* (Archiannelida). *International Journal of Invertebrate Reproduction and Development* 11: 159–171.

Mecznikow, E. (1866): *Apsilus lentiformis*, ein Räderthier. *Zeitschrift für wissenschaftliche Zoologie* 16: 346–356.

Moore, A. (1899): *Dinophilus gardineri* (Sp. nov.). *The Biological Bulletin* 1: 15–18.

Müller, M.C.M. (1999): Das Nervensystem der Polychaeten: Immunhistochemische Untersuchungen an ausgewählten Taxa. University of Osnabrück, PhD thesis.

Müller, M.C.M. & Westheide, W. (2002): Comparative analysis of the nervous system in presumptive progenetic dinophilid and dorvilleid polychaetes (Annelida) by immunohistochemistry and CLSM. *Acta Zoologica (Stockholm)* 83: 33–48.

Nachtsheim, H. (1914): Das Problem der Geschlechtsbestimmung bei *Dinophilus*. Berichte der Naturforschenden Gesellschaft, Band 21, Freiburg Breisgau.

Nachtsheim, H. (1919): Zytologische und experimentelle Untersuchungen über die Geschlechtsbestimmung bei *Dinophilus apatris* Korsch. *Archiv für mikroskopische Anatomie* 93: 17–140.

Nelson, J.A. (1904): The early development of dinophilids: a study in cell-lineage. *Proceedings of the Academy of Natural Science of Philadelphia* 56: 687–737.

Nelson, J.A. (1907): The morphology of *Dinophilus conklini* n.sp. *Proceedings of the Academy of Natural Science of Philadelphia* 59: 82–143.

von Nordheim, H. (1984). Life histories of subtidal interstitial polychaetes of the families Polygordiidae, Protodrilidae, Nerillidae, Dinophilidae, and Diurodrilidae from Helgoland (North Sea). *Helgoländer Meeresuntersuchungen* 38: 1–20.

Ohm, G. (1963): Über den Bau des Pharynx einiger Archianneliden. *Zoologischer Anzeiger* 171: 179–203.

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

Prevedelli, D. & Zunarelli Vandini, R. (1999): Survival, fecundity and sex ratio of *Dinophilus gyrociliatus* (Polychaeta: Dinophilidae) under different dietary conditions. *Marine Biology* 133(2): 231–236.

Prowazek, S. (1900): Zur Entwicklungsgeschichte des Wurmes *Dinophilus apatris*. *Naturwissenschaftliche Wochenschrift* 15: 1–37.

Purschke, G. (1984): Vergleichende anatomische und ultrastrukturelle Untersuchungen ventraler Pharynxapparate bei Polychaeten und ihre phylogenetische Bedeutung. University of Göttingen, PhD thesis.

Purschke, G. (1985): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). I. The pharynx of Dinophilidae. *Zoomorphology* 105: 223–239.

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

Purschke, G., Bleidorn, C., Struck, T. (2014). Systematics, evolution and phylogeny of Annelida – a morphological perspective. *Memoirs of Museum of Victoria* 71: 247–269.

Rao, C.G. (1973): *Trilobodrilus indicus* n. sp. (Dinophilidae, Archiannelida) from Andhra coast. *Proceedings of the Indian Academy of Science* 77: 101–108.

Remane, A. (1925): Diagnosen neuer Archianneliden (zugleich 3. Beitrag zur Fauna der Kieler Bucht). *Zoologischer Anzeiger* 65: 15–47.

Remane, A. (1932): Archiannelida. In: Grimpe, G. (eds.) *Die Tierwelt der Nord- und Ostsee. Lieferung XXII, Teil VI*. Akademische Verlagsgesellschaft Leipzig: 1–36.

Rieger, R.M. & Rieger, G.E. (1975): Fine structure of the pharyngeal bulb in *Trilobodrilus* and its phylogenetic significance within Archiannelida. *Tissue and Cell* 7: 267–279.

Rieger, R.M. & Rieger, G.E. (1976): Fine structure of the archiannelid cuticle and remarks on the evolution of the cuticle within the spiralia. *Acta Zoologica (Stockholm)* 57: 53–68.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Riser, N.W. (1999): Description of a new species of dinophilid polychaete, with observations on other dinophilids and interstitial polychaetes in New England. *Northeastern Naturalist* 6: 211–220.

Ruebush, T.K. (1940): Morphology, encapsulation and osmoregulation of *Dinophilus gardineri* Moore. *Transactions of the American Microscopical Society* 59: 205–223.

Scharnofske, P. (1984): Anatomie, Ultrastruktur und Funktion der männlichen Geschlechtsorgane der Dinophilidae und Histriobdellidae (Annelida, Polychaeta). University of Göttingen, PhD thesis.

Scharnofske, P. (1986): Ultrastructure of sperm morphology of *Trilobodrilus* axi and *T. heideri* (Dinophilidae, Polychaeta). *Helgoländer Meeresuntersuchungen* 40: 419–430.

Schimkewitsch, W. (1895): Zur Kenntnis des Baues und der Entwicklung des *Dinophilus* vom Weißen Meere. *Zeitschrift für Wissenschaftliche Zoologie* 59: 46–79.

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

Schmidt, E.O. (1848): *Neue Beiträge zur Geschichte der Würmer gesammelt auf einer Reise nach den Färör im Frühjahr 1848*. F. Manke, Jena.

Schmidt, O. (1857): Zur Kenntnis der Turbellaria Rhabdocoela und einiger anderer Würmer des Mittelmeeres. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* 23: 347–351.

Schmidt, P. (1969): Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrands der Nordsee-Insel Sylt. II. Quantitative Verteilung und Populationsdynamik einzelner Arten. *Internationale Revue der gesamten Hydrobiologie* 54(1): 95–174.

Schmidt, P. & Westheide, W. (1971): Der Einfluss der Temperatur auf die Oocytenentwicklung und Eiablage bei dem interstitiellen Archianneliden *Trilobodrilus axi*. *Marine Biology* 10: 94–100.

Schmidt, P. & Westheide, W. (1972): *Dinophilus gyrociliatus* (Polychaeta). Nahrungsaufnahme und Fortpflanzung. *Encyclopedia Cinematographica E* 1750: 1–16.

Schmidt, P. & Westheide, W. (1977): Interstitielle Fauna von Galapagos. XVII. Polygordiiae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae. *Mikrofauna des Meeresbodens* 62: 1–38.

Schroeder, P.C., & Hermans, C.O. (1975): Annelida: Polychaeta. In: Giese, A.C. & Pearse, J.S. (eds.): *Reproduction of Marine Invertebrates*. Vol. 2. Academic Press, New York, san Francisco, London: 1–213.

Schultz, E. (1901): *Dinophilus rostratus* nov. spec. Wissenschaftliche Meeresuntersuchungen, Kiel. Abteilung Helgoland. *Neue Folge* 5: 3–8.

Schultze, M.S. (1851): *Beiträge zur Naturgeschichte der Turbellarien I*. C.A. Koch´s Verlagshandlung, Greifswald.

Sella, W. & Ramella, L. (1999): Sexual conflict and mating systems in the dorvilleid genus Ophryotrocha and the dinophilid genus *Dinophilus*. *Hydrobiologia* 402: 203–213.

Shearer, C. (1911): The problem of sex determination in *Dinophilus gyrociliatus*. *Journal of the Marine Biological Association* 9: 156–160.

Shearer, C. (1912): The problem of sex determination in *Dinophilus gyrociliatus*. The sexual cycle. *Quarterly Journal of Microscopical Sciences. N.S.* 57: 329.

Simonini, R., Molinari, F., Pagliai, A.M., Ansaloni, I. & Prevedelli, D. (2003): Karyotype and sex determination in *Dinophilus gyrociliatus* (Polychaeta: Dinophilidae). *Marine Biology* 142(3): 441–445.

Struck, T.H., Westheide, W. & Purschke, G. (2002): Progenesis in Eunicida ("Polychaeta", Annelida) – separate evolutionary events? Evidence from molecular data. *Molecular Phylogenetics and Evolution* 25: 695–697.

Struck, T.H., Golombek, A., Weigert, A. Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Tempel, D. & Westheide, W. (1980): Uptake and incorporation of dissolved amino acids by interstitial Turbellaria and Polychaeta and their dependence on temperature and salinity. *Marine Ecology – Progress Series* 3: 41–50.

Traut, W. (1966): Über die Kopulation bei *Dinophilus gyrociliatus* (Archiannelida). *Zoologischer Anzeiger* 177: 402–411.

Traut, W. (1969a): Zur Sexualität von *Dinophilus gyrociliaus* (Archiannelida). Der Einfluss von Außenbedingungen und genetischen Faktoren auf das Geschlechtsverhältnis. *Biologisches Zentralblatt* 88: 496–495.

Traut, W. (1969b): Zur Sexualität von *Dinophilus gyrociliatus* (Archianneldia). Der Bau des Ovars und die Oogenese. *Biologisches Zentralblatt* 88: 695–714.

Traut, W. (1970): Zur Sexualität von *Dinophilus gyrociliatus* (Archiannelida). III. Die Geschlechtsbestimmung. *Biologisches Zentralblatt Band* 89: 137–161.

Tzonis, K. (1938): Beeinflussung der Geschlechtsverhältnisse bei *Dinophilus apatris* Korsch. durch Außenbedingungen. Zoologische Jahrbücher. *Allgemeine Zoologie und Physiologie der Tiere* 58: 539–550.

Vang, Á. (2015): Taxonomy and phylogeny of *Dinophilus taeniatus* (Dinophilidae, Annelida). University of Copenhagen, Master thesis.

Verrill, A.E. (1892): Dinophilidae of New England. *Transactions of the Connecticut Academy of Arts and Sciences* 8: 457–488.

Weldon, W.F.R. (1886): On *Dinophilus gigas*. *Quarterly Journal of Microscopical Science* 27: 109–121.

Westheide, W. (1967): Die Gattung *Trilobodrilus* (Archiannelida, Polychaeta) von der deutschen Nordseeküste. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 16: 207–215.

Westheide, W. (1971): *Apharyngtus punicus* nov. gen. nov. spec.: Ein aberranter Archiannelide aus dem Mesopsammal der tunesischen Mittelmeerküste. *Mikrofauna des Meeresbodens* 6: 223–249.

Westheide, W. (1972): La faune des Polychètes et des Archannélides dans les plages sableuses à ressac de la côte méditerranéenne de la Tunisie. *Bulletin d'Institut Océanographic et de Pêche, Salammbô* 2: 449–468.

Westheide, W. (1972–1973): Documents faunistique et écologiques. Nouvelles récoltes d´Annélides interstitielles dans les plages sableuses du Bassin d´Arcachon. *Vie et Milieu* 23, fasc. 2 ser. A: 365–370.

Westheide, W. (1982): *Ikosipodus carolensis* gen. et sp. n., an interstitial neotenic polychaete from North Carolina, U.S.A. and its phylogenetic relationships within Dorvilleidae. *Zoologica Scripta* 11: 117–126.

Westheide, W. (1984): The concept of reproduction in polychaetes with small body size: adaptations in interstitial species. *Fortschritte der Zoologie* 29: 265–287.

Westheide, W. (1985): The systematic position of Dinophilidae and the archiannelid problem. In: Conway Morris, S., George, J.D.,

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Gibson, R. & Platt, H.M. (eds.) *The Origin and Relationships of Lower Invertebrates*. Clarendon Press, Oxford: 310–326.
Westheide, W. (1987): Progenesis as a principle in meiofauna evolution. *Journal of Natural History* 21(4): 843–854.
Westheide, W. (1988): Genital organs. In: Westheide, W. & Hermans, C.O. (eds.) The Ultrastructure of Polychaeta. *Microfauna Marina* 4: 263–279.
Westheide, W. (1990): Polychaetes: interstitial families. In: Kermack, D.M., Barnes, R.S.K. (eds.) *Synopsis of the British Fauna No. 44*. Universal Book Services. DR. W. Backhuys, Oegstgeest: 1–152.
Westheide, W. (2008): *Polychaetes: Interstitial Families*. 2nd ed. Linnean Society of London and the Estuarine and Coastal Science Association, London: 1–169.
Westheide, W. & von Basse, M. (1978): Chilling and freezing resistance of two interstitial polychaetes from a sandy tidal beach. *Oecologia (Berlin)* 33: 45–54.
Westheide, W. & Riser, N.W. (1983): Morphology and phylogenetic relationships of the neotenic interstitial polychaete *Apodotrocha progenerans* n. gen., n. spec. (Annelida). *Zoomorphology* 103: 67–87.
Westheide, W. & Schmidt, P. (1974): *Trilobodrilus axi* (Polychaeta). Nahrungsaufnahme und Fortpflanzung. *Encyclopedia Cinematographica E* 1955: 1–12.
Wieser, W. (1957): Archiannelids from the intertidal of Puget Sound. *Transactions of the American Microscopical Society* 76: 275–285.
Windoffer, R. (1992): Immunohistochemische und elektronenmikroskopische Untersuchungen am Nervensystem zweier *Dinophilus*-Arten mit unterschiedlichem Lebenszyklus. University of Osnabrück, PhD thesis.
Windoffer, R. & Westheide, W. (1988a): The nervous system of the male *Dinophilus gyrociliatus* (Annelida: Polychaeta). I. Number, types and distribution pattern of sensory cells. *Acta Zoologica* 69: 55–64.
Windoffer, R. & Westheide, W. (1988b): The nervous system of the male *Dinophilus gyrociliatus* (Annelida: Polychaeta). II. Electron microscopical reconstruction of nervous anatomy and effector cells. *Journal of Comparative Neurology* 272: 475–488.
Zunarelli Vandini, R. (1956): A possible way of origin of parthenogenetic strains of *Dinophilus apatris* (= *D. gyrociliatus*). *Experimentia* 21: 368–369.

Wilfried Westheide

## 7.1.2 *Apharyngtus* Westheide, 1971

### Introduction

In the course of extensive meiofauna collections on the Mediterranean coast of Tunisia (Westheide 1970, 1972a,b), a very small and hitherto unknown polychaete species was discovered at various localities on the western coast of the Bay of Tunis (Figs. 7.1.2.1 and 7.1.2.2 A, B). It was found exclusively on the upper shoreline of fine sandy beaches at a depth of 5–15 cm. Data on the ecology and biology of *Apharyngtus* are still lacking.

The original description (Westheide 1971) left the family taxon open. Correspondence in habitus with similarly sized Dinophilidae (ciliated, slightly ventrally flattened, appendage-less body without chaetae) initially suggested that the new species could be a representative of a new dinophilid taxon (Westheide 1982, 1985, Westheide and Riser 1983). A first cladistic analysis using morphological characters found *Apharyngtus* and Dinophilidae as part of the eunicid family taxon Dorvilleidae (Eibye-Jacobsen and Kristensen 1994). However, this hypothesis was not generally accepted and remained a matter of scientific debate (Rouse and Pleijel 2001).

### Morphology

*Apharyngtus punicus* is just 610–940 µm in length and under 100 µm wide. The elongate body is divided into a characteristically shaped prostomium, a mouth segment, various indistinct body segments, and a posterior pygidium (Figs. 7.1.2.1 and 7.1.2.2 A, B). Appendages, chaetae, and other segmental structures are entirely absent. The prostomium is 60–80 µm long and divided into an approximately semicircular front section and a less broad base. Ciliary fields and rings are present on its ventral side (Fig. 7.1.2.2 C, D). Behind the mouth opening, parallel bands of highly effective locomotor cilia extend along the ventral body side (Fig. 7.1.2.2 A, B, E).

The ventral mouth opening leads into an equally densely ciliated esophagus, which extends through the subsequent segment as an elongated sac (Figs. 7.1.2.1 and 7.1.2.3). The cilia around the mouth opening stir up grains of sand, diatoms, as well as bacteria and convey them into the esophagus (Fig. 7.1.2.2 C, D). The esophagus is connected to the midgut by a narrow opening, where a sphincter-like structure allows food particles to pass into the gut (Fig. 7.1.2.3). Sand and coarse detritus are expelled back out through the mouth opening. The midgut leads into a densely ciliated hindgut, from which an elongate (approximately 40 µm), internally ciliated anal opening leads out of the pygidium dorsally (Fig. 7.1.2.1).

The esophagus possesses no notable, conspicuous muscular structures. The large pharynx bulb typically found in Dinophilidae (Rieger and Rieger 1975, Purschke 1985) is absent, meaning that the most critical morphological correspondence with Dinophilidae is lacking.

Transmission electron microscopy analyses (Glenn-Kaiser unpublished observation) revealed the cuticle to be a relatively thin, largely undifferentiated fibrillary layer permeated only by fine epidermal processes. Neither a coelom nor a blood vascular system was detected, but

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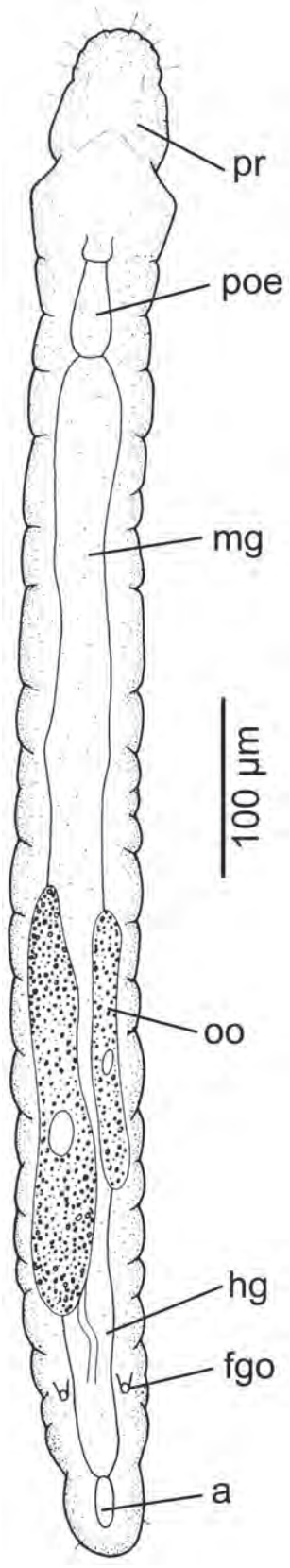


**Fig. 7.1.2.1:** *Apharyngtus punicus*. Habitus of a mature female. a, anus; fgo, female genital opening; hg, hindgut; mg, midgut; oo, oocyte; poe, posterior esophagus; pr, prostomium. From Westheide (1971).

parts of the body are conspicuously filled with coelenchyme cells. The animals possess paired protonephridia. Initial confocal laser scanning microscopic observations revealed a basiepithelial nervous system, which comprises a prostomial brain and a ventral nerve cord with a pair of widely separated main trunks (Glenn-Kaiser unpublished observation). It remained unresolved whether additional longitudinal nerves or ganglia are present. The musculature primarily comprises longitudinal fibers (Fig. 7.1.2.3).

### Reproduction and development

The species is gonochoristic and the two sexes are virtually monomorphic (Fig. 7.1.2.2 A, B). Females possess elongated, yolk-rich egg cells, which are found in the rear section of the body. A pair of female genital pores was observed at the transition to the pygidium (Figs 7.1.2.1 and 7.1.2.2 E). In males, an elongated ciliary field has been observed on the pygidium, which is supplied with numerous gland cell openings (Fig. 7.1.2.2 B). Spermatozoa are filiform and about 70–90 µm long.

### Phylogeny and taxonomy

Although molecular investigations revealed a certain degree of proximity between this species and Dinophilidae, they were also unambiguous in ruling out its membership of this taxon: *Apharyngtus* is the sister group of Diurodrilidae, and this clade is the sister group of a clade comprising Orbiniidae and Parergodrilidae (Struck *et al*. 2015). Within Orbiniida Nerillidae, Dinophilidae, Diurodrilidae, and *Apharyngtus* are the closest related taxa. A relationship to Eunicida could be corroborated neither for Dinophilidae nor for *Apharyngtus*. Therefore, the morphological similarities to the developmental stages of the former have to be interpreted as convergent (Struck *et al*. 2002, 2015).

Curiously enough, the first time the taxon was found again after its initial description was during investigations of the meiofauna of New Zealand, where Riser (1984) discovered the species to be abundant at Pakiri Beach on the North Island. The species was not encountered again in the Mediterranean region until L. Schärer and R.M. Rieger discovered it in Corsica in 1996 during a zoological excursion from Innbruck University, Austria. In 2007, A. and W. Westheide collected the species in larger numbers in the bottom sediment of a small lagoon on the east coast of the island of Corsica South of Bastia and finally made the

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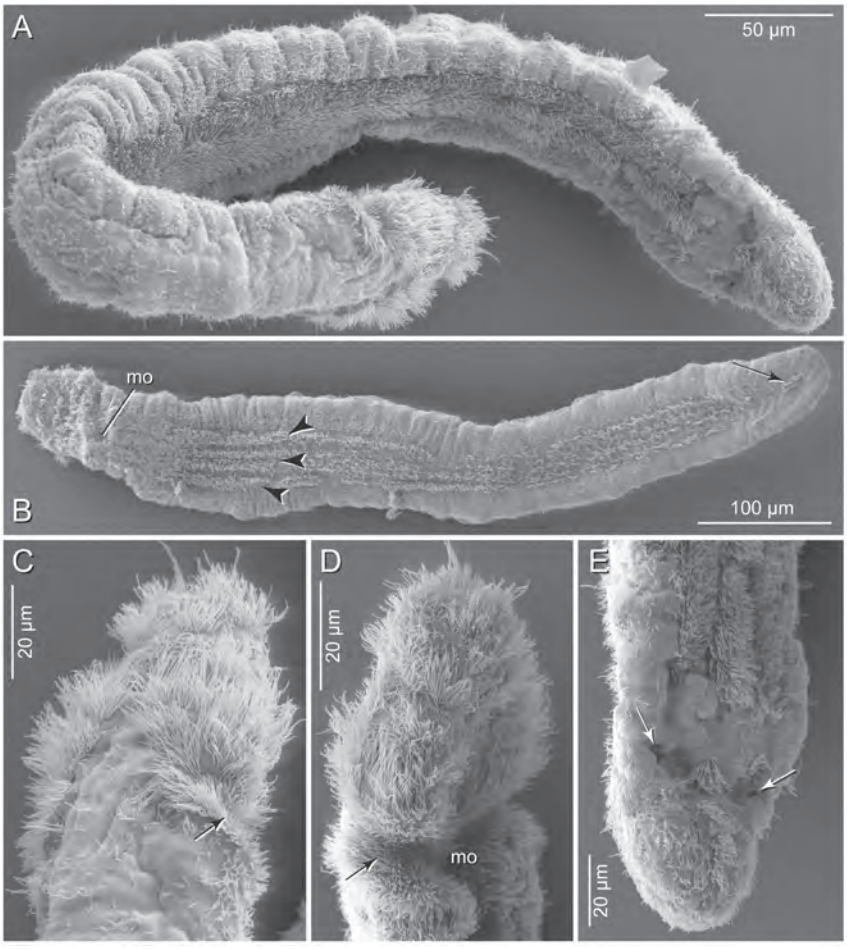


**Fig. 7.1.2.2:** *Apharyngtus punicus*. Scanning electron microscopy (SEM) micrographs. A, Habitus of a mature female; body with numerous cilia, ventral ciliary band. B, Male in ventral view; note tripartite ventral ciliary band (arrowheads); arrow points to putative male opening. C, D, Ciliation of prostomium and peristomium. C, Dorsolateral view; arrow points to ciliated furrow leading to the mouth. D, Ventrolateral view; arrow points to furrow leading to the mouth (mo). E, Posterior end of female, ventral view with paired genital pores (arrows); note end of midventral ciliary band in front of genital region. mo, mouth. SEM micrographs, W. Mangerich, Osnabrück.

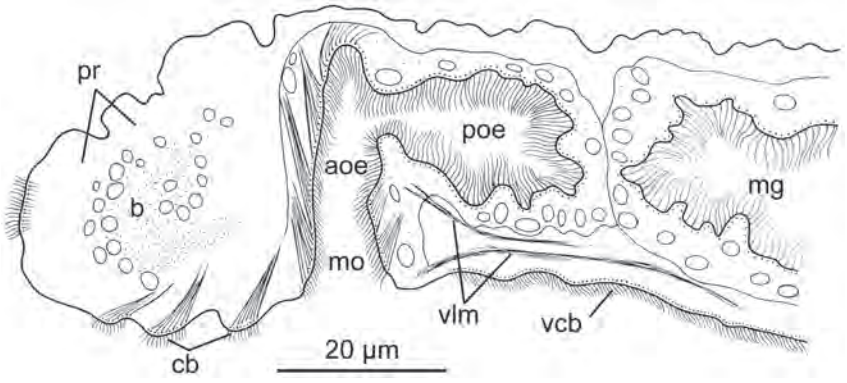


**Fig. 7.1.2.3:** *Apharyngtus punicus*. Sagittal section of anterior end; prostomium (pr) with intraepithelial brain (b), esophagus divided into ascending anterior (aoe) and horizontal posterior part (poe). aoe, anterior esophagus; b, brain; cb, prostomial ciliary band; mg, midgut; mo, mouth; poe, posterior esophagus; pr, prostomium; vcb, ventral ciliary band; vlm, ventral longitudinal musculature. From Westheide 1971.

material accessible for molecular phylogenetic analysis (Struck *et al*. 2015).

***Apharyngtus* Westheide, 1971**

**Type species:** *Apharyngtus punicus* Westheide, 1971

**Synonyms:** none

**Diagnosis:** Small, elongated, segmented body with prostomium and pygidium, without appendages, parapodia, and chaetae. Prostomium comprising two parts. Wide ciliated mouth opening, esophagus divided in anterior and posterior part, no muscular pharynx. Body divided into 18–20 indistinct annuli. Epidermis with numerous locomotory cilia, specific arrangement on prostomium and mouth region; ventral ciliary band tripartite extending from mouth to genital openings; gonochoristic, ♀♀ with paired gonoducts and genital openings; ♂♂ with unpaired elongated, glandular, ciliated opening (Westheide 1971).

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### References

Eibye-Jacobsen, D. & Kristensen, R.M. (1994): A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta* 23: 107–131.

Purschke, G. (1985): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida).1. The pharynx of the Dinophilidae. *Zoomorphology* 105: 223–239.

Rieger, R.M. & Rieger, G.E. (1975): Fine structure of the pharyngeal bulb in *Trilobodrilus* and its phylogenetic significance within Archiannelida. *Tissue and Cell* 7: 267–279.

Riser, N.W. (1984). General observations on the intertidal interstitial fauna of New Zealand. *Tane* 30: 239–250.

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

Struck, T.H., Westheide, W. & Purschke, G. (2002): Progenesis in Eunicida ("Polychaeta", Annelida) – separate evolutionary events? Evidence from molecular data. *Molecular Phylogenetics and Evolution* 25: 190–199.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Westheide, W. (1970). Zur Organisation und Ökologie des interstitiellen Polychaeten *Hesionides gohari* Hartmann-Schröder (Hesionidae). *Mikrofauna des Meeresbodens* 3: 1–37.

Westheide, W. (1971): *Apharyngtus punicus* nov. gen. nov. spec., ein aberrnater Archiannelide aus dem Mesopsammal der tunesischen Mittelmeerküste. *Mikrofauna des Meeresbodens* 6: 1–19.

Westheide, W. (1972a). La faune des polychètes et des archiannélides dans les plages sableuses à ressac de la côte méditerranéenne de la Tunisie. *Bulletin de l'Institut d'Océanographique et de Pêche de Salammbô* 2: 449–468.

Westheide, W. (1972b). Räumliche und zeitliche Differenzierungen im Verteilungsmuster der marinen Interstitialfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 65: 23–32.

Westheide, W. (1985): The systematic position of the Dinophiliidae and the Archiannelid problem. In: Morris, C.S., George, D., Gibson, R. & Platt, H.M. (eds.) *The Origins and Relationships of Lower Invertebrates*. Oxford University Press, Oxford: 310–326.

Westheide, W. & Riser, N.W. (1983): Morphology and phylogenetic relationships of the neotenic interstitial Polychaete *Apodotrocha progenerans* n.gen. n.sp. (Annelida). *Zoomorphology* 103: 67–87.


Günter Purschke

## 7.1.3 Parergodrilidae Reisinger, 1925

### Introduction

Parergodrilidae is a small taxon of exclusively meiofaunal polychaetes with body lengths ranging from 0.8 to 2.8 mm. Until recently, only two species have been recognized: one terrestrial, *Parergodrilus heideri* Reisinger, 1925 and one marine, *Stygocapitella subterranea* Knöllner, 1934 (Rouse and Pleijel 2001, Westheide 2008). However, at least the marine species consists of a complex of several cryptic species (Schmidt and Westheide 2000, Struck *et al*. 2017). All known species have an oligochaete-like appearance without anterior or posterior appendages. The parapodia are reduced to two ventrolaterally arranged rows of simple chaetae of different types (Fig. 7.1.3.1). Although superficially similar to another terrestrial polychaete species, *Hrabeiella periglandulata* Pizl & Chalupsky, 1984, there is no evidence for a close relationship, either from molecular or from morphological data (Rota 1998, Purschke 1999, 2006, Rota *et al*. 2001, Struck *et al*. 2002, Jördens *et al*. 2004); instead, the similarities must be interpreted as having convergently evolved, due to similar selection pressures in similar habitats, as suggested previously by Purschke (1999). *Parergodrilus* occurs in the leaf litter of beech and other forests, whereas *Stygocapitella* lives in damp sands in the upper eulittoral or supralittoral zones of sandy beaches. Development is direct in the gonochoristic species. Due to their aberrant morphology and occurrence, it is not surprising that they were first detected and described by nonpolychaetologists (Reisinger 1925, Knöllner 1934). Whereas *Stygocapitella* had been found to be worldwide distributed, with the exception of tropical regions, *Parergodrilus* originally seemed to be restricted to Europe, but recent records from Korea and the USA indicate a much wider distribution for this taxon as well (Purschke 1999, Rota and Jong 2015).

Surprisingly, the first species was found in Austrian forests by Reisinger in 1925 and named *P. heideri*. Reisinger (1925) described a high but superficial resemblance to Enchytraeidae (Clitellata), but he recognized similarities to either Rotatoria or Archiannelida. The first view was obviously influenced by the absence of males. About 10 years later, the second species, *S. subterranea*, was described from a sandy beach in the Baltic near Kiel, Germany, by Knöllner (1934) and considered to be a capitellid polychaete. In 1958, the two species were found and studied again, and this extensive morphological investigation led Karling (1958) to conclude that the two species must be closely related and should comprise one family, Stygocapitellidae, and all specimens of *Parergodrilus* represented females. So far, males were unknown in *P. heideri*, and the species was considered to be hermaphroditic (Reisinger 1925). Subsequently, Reisinger (1960) started a reinvestigation and found and described male individuals in *P. heideri*, albeit occurring in considerably lower numbers than females (ratio 1:8 to 1:15). In this study, Reisinger (1960) transferred the two species into the taxon Parergodrilidae for nomenclatural reasons

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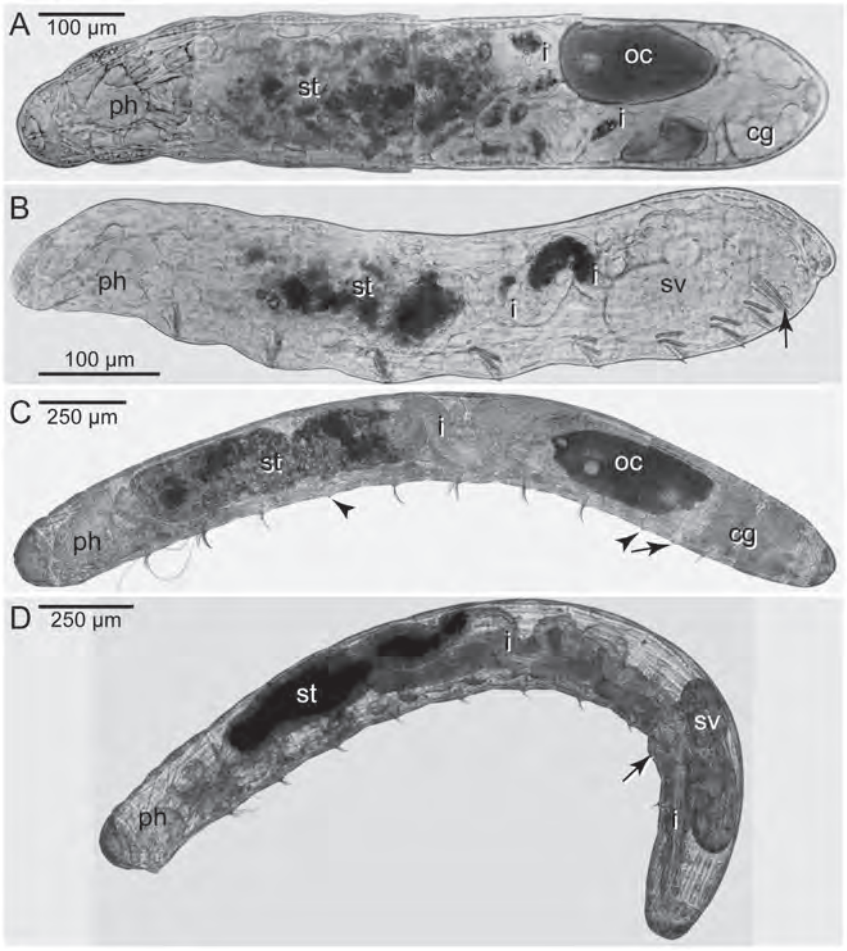


**Fig. 7.1.3.1:** Parergodrilidae. Habitus, Light microscopy of living adult individuals. A, B, *Parergodrilus heideri* (from Germany). A, Female with two vitellogenic oocytes (oc). B, Male; arrow points to genital chaetae. C, D, *Stygocapitella subterranea*. C, Female with vitellogenic oocyte (oc); arrow: female genital opening; arrowheads point to lost chaetae (from Nahant, Massachusetts, USA). D, Male; arrow points to prostate gland opening (from North Sea Island of Sylt, Germany). cg, cocoon gland; i, intestine; ph, pharynx; sv, seminal vesicle; st, stomach.

and considered them to be a taxon within the sedentariate polychaetes. However, their exact systematic position remained unresolved and controversial until molecular studies had been applied to solve this problem. Today, it is generally accepted that Parergodrilidae and Orbiniidae are sister taxa within Orbiniida (Struck *et al*. 2015). Because of their aberrant structure, previously unresolved phylogenetic position, and biology, parergodrilids have received high interest and are comparatively well-known polychaetes (reviews by Purschke 1999, Rouse and Pleijel 2001, Westheide 1990, 2008).

## Morphology

### External morphology

With a cylindrical body without any appendages, parergodrilids somewhat resemble oligochaetes on first sight (Fig. 7.1.3.1 A–D). As such, it is not surprising that they were not found and described by polychaetologists. However, due to the limited number of segments, they are comparatively stout, and with body dimensions of 0.75 mm (♂♂)–1 mm (♀♀) by 0.1 mm (*P. heideri*) and 1.5–2.6 mm by 0.2–0.25 mm (*Stygocapitella* spp.), they are much shorter than typical oligochaetes. Like oligochaetous clitellates, the body surface is without locomotory cilia in parergodrilids, and sensory cells form indistinct buds with cilia arising slightly above the cuticle (Purschke 1999, Fig. 6).

The body of *Stygocapitella* spp. comprises prostomium, peristomium, 13 segments, and pygidium (Karling 1958, Reisinger 1960, Westheide 2008, Struck *et al*. 2017). Up to 10 segments bear chaetae, and except for the peristomium and the last segment, each segment is composed of two to three more or less distinct rings (Figs. 7.1.3.1 A–D and 7.1.3.2 A). The chaetae are arranged in pairs of ventrolateral bundles, and typical parapodia are lacking. Known species possess either 8 or 10 chaetigers. Chaetae may be of three types and occur from the second segment onward in a specific pattern (Fig. 7.1.3.3 A–H) (Karling 1958, Reisinger 1960, Riser 1980, Purschke 1999, Westheide 2008): Bilimbate chaetae are present in each segment and in each species (Struck *et al*. 2017). In addition, two bilimbate chaetae with long whip-like

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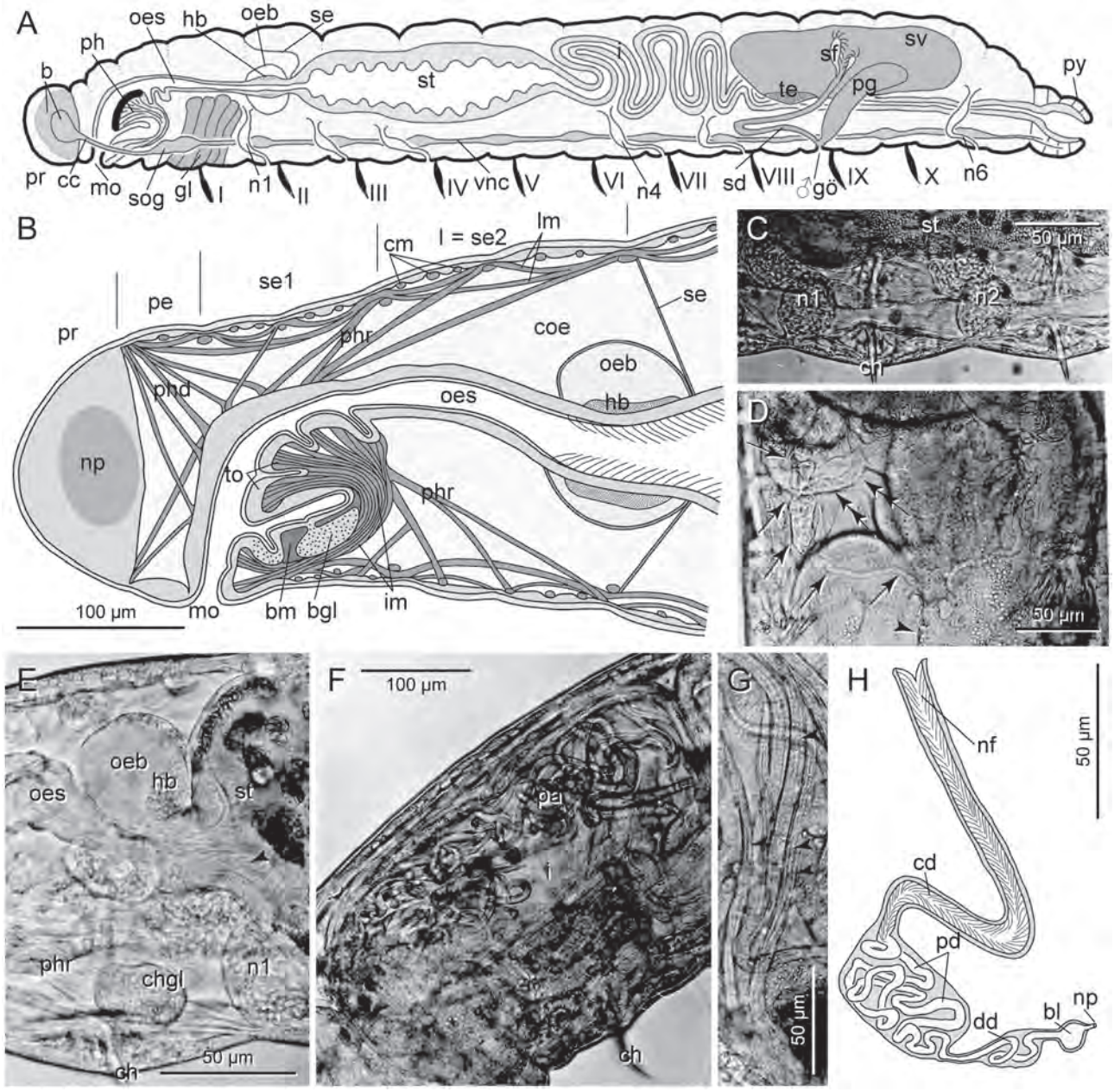


**Fig. 7.1.3.2:** Parergodrilidae. Morphology. A, B, D, F–H, *Stygocapitella subterranea*. C, E, *Parergodrilus heideri*. A, ♂; internal organization with alimentary canal, central nervous system, nephridia, and genital organs. Roman numerals refer to chaetigerous segments. B, Anterior end, ventral pharynx comprising tongue-like organ (to), bulbus muscle (bm), bulbus gland (bgl), investing muscle (im), and various retractor muscles (phr) and dilator muscle fibers (phd); septum (se) between the first and second chaetiger; esophageal bulb (oeb) with heart body (hb). C, The two pairs of nephridia (n1, n2) with highly coiled duct, lateral view. D, Fourth pair of nephridia (double arrow points to long ciliated duct, arrows to proximal duct, arrowhead to opening, ventral view). E, Esophageal bulb with heart body; arrowhead points to ciliation of posterior esophagus. F, Coiled intestine (i) with numerous apicomplexan parasites (pa). G, Enlargement of parasites; arrowheads refer to longitudinal striation. H, Reconstruction of nephridium. ♂go, male opening; b, brain; bgl, bulbus gland; bl bladder, bm bulbus muscle, cc circumesophageal connective; cd, ciliated duct; chgl, chaetal gland; ch, chaeta; cm, circular muscle; dd, distal duct; gl, anterior male gland; hb, heart body; i, intestine; im, investing muscle; lm, longitudinal muscle; mo, mouth; n1–n6, nephridia 1–6; nf, funnel of nephridium; np, nephridiopore; np, neuropil; oeb, esophageal bulb; oes, esophagus; pa, parasite; pd, proximal duct; pe, peristomium; pg, prostate gland; ph, pharynx; phd, pharynx dilator; phr, pharynx retractor; pr, prostomium; py pygidium; sd, spermioduct; se, septum; sf, seminal funnel; sg1, segment 1; sog, subesophageal ganglion; st, stomach; sv, seminal vesicle; te, testes; to, tongue-like organ. A, redrawn after Reisinger (1960); B–H, originals.

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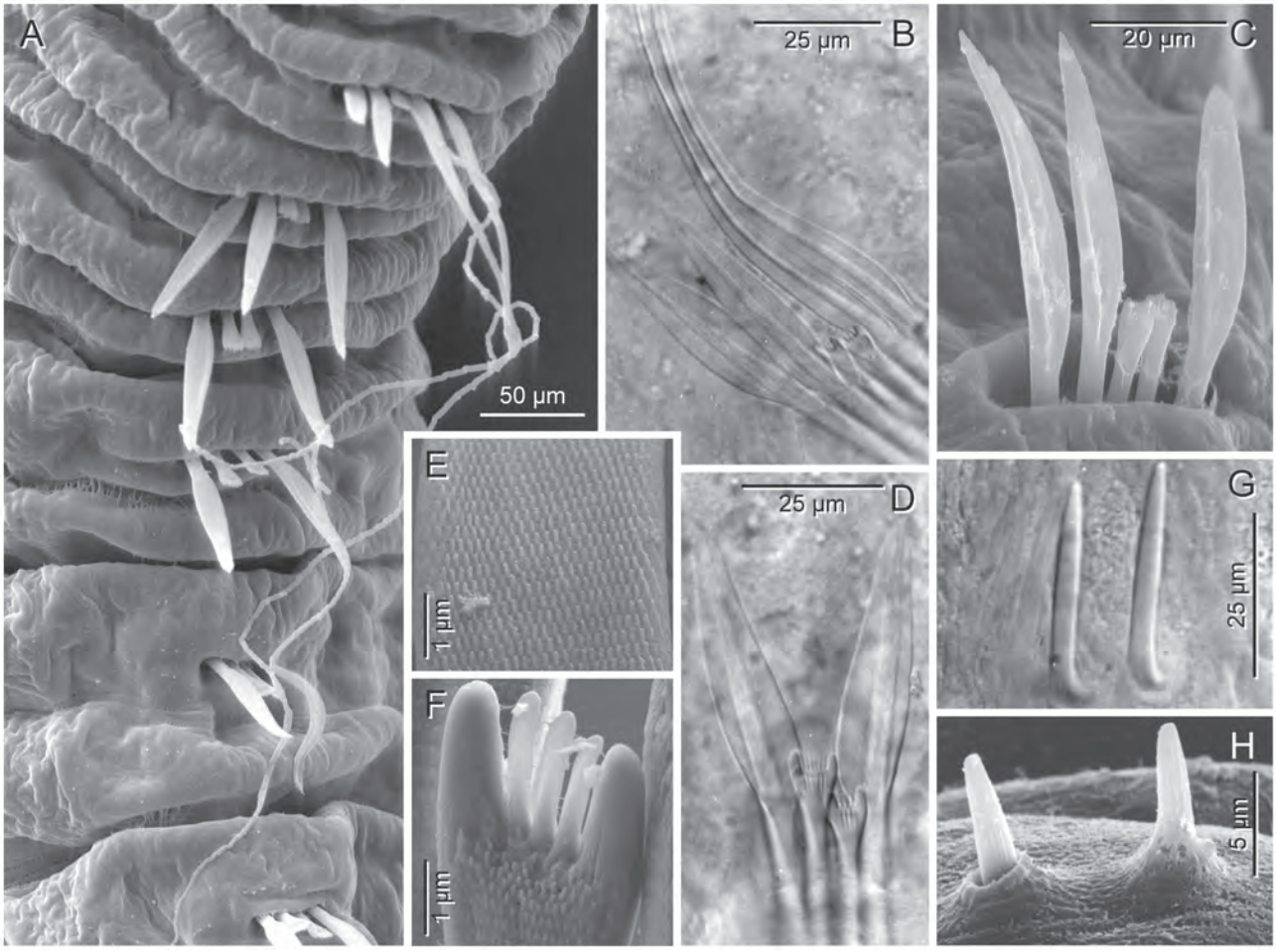


**Fig. 7.1.3.3:** Parergodrilidae. Morphology of the chaetae. A–F, *Stygocapitella subterranea*. A, Ventrolateral view of left row of chaetal bundles in the first six chaetigers. B, First chaetiger with two bilimbate chaetae, two forked chaetae, and two bilimbate chaetae with whip-like extensions. C, Second chaetiger consisting of three bilimbate and two forked chaetae. D, Fourth chaetiger with two bilimbate and two forked chaetae. E, Bilimbate chaeta, surface structure. F, Forked chaeta with three spines between the stronger outer prongs. G, H, *Parergodrilus heideri*. G, Entire chaetae of squeezed specimen. H, Chaetal bundle protruding from body surface. A, C, E, F, H, scanning electron microscopy micrographs; B, D, G, Light microscopic interference contrast images – originals.

distal extensions are present on the first chaetiger (Fig. 7.1.3.3 A, B). The bilimbates show a fine striation pattern under the light microscope, which likely represents internal structures, since these chaetae show a different structure when viewed with scanning electron microscopy (SEM): Their surface shows a regular pattern of tiny teeth (230 nm by 70 nm; Fig. 7.1.3.3 B–E). All but one species possess forked chaetae, with two to six spines between the stronger outer prongs; the number of spines is not species specific and is difficult to determine with light microscopy (Fig. 7.1.3.3 D, F). Known species differ in the number of bilimbates and presence or absence of forked chaetae.

In *P. heideri*, the body comprises different numbers of segments in females and males (Karling 1958, Reisinger 1960). In addition to prostomium, peristomium, and pygidium, there are eight chaetigers in females and 10 in males, the last two of which are more or less reduced and fused except for the chaetae. Most likely, there is an anterior achaetigerous segment as well (Reisinger 1960). Each chaetiger bears a pair of ventrolateral bundles of chaetae (Fig. 7.1.3.3 G, H) (Reisinger 1925, 1960, Rota 1997, 1998). Each bundle comprises two short chaetae (25–30 µm); they are simple pointed rods with an enlarged and slightly bent base. In males, the last two pairs of bundles (Fig. 7.1.3.1 B) may be referred to as genital chaetae (Reisinger 1960), but only the innermost chaetae of the posterior pair open into the genital atrium (Purschke 2002). These chaetae are similar in structure and size to the others except for the innermost posterior chaetae, which are about twice the size (Reisinger 1960, Purschke 2002). If viewed under SEM, the chaetae show fine longitudinal ridges (Fig. 7.1.3.3 H).

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## Anatomy

**Epidermis and Cuticle.** The epidermis of Parergodrilidae is covered by a strong cuticle (up to 2 µm thick) composed of a basal cuticle and a thin epicuticle. In *Stygocapitella*, the epicuticle is covered by a dense layer of epicuticular projections (70 by 30 nm), giving the cuticle an appearance as observed in clitellates (Purschke 1986, 1987). These projections are absent in *Parergodrilus* (Rota 1998). The basal cuticle includes regularly arranged layers of parallel collagen fibers. It is traversed by only very few microvilli. As mentioned earlier, there are no ciliated epidermal cells, as might be expected for polychaetes of this small size. As discussed by Purschke (2002), this feature and the structure of the cuticle are very likely to be related to the terrestrial or semiterrestrial habitat. As well as supportive cells, the epidermis comprises different gland cells distributed over the body in a specific pattern (Reisinger 1925, 1960, Karling 1958). In *P. heideri*, there are large paired multicellular glands situated dorsally.

**Musculature.** The musculature of the body wall consists of a network of regularly arranged circular and longitudinal muscle fibers (Reisinger 1925, 1960, Karling 1958) (Fig. 7.1.3.2 B). The circular fibers are ventrally interrupted where the nerve cord bulges into the body cavity. There are two to seven muscle fiber rings per segment (Fig. 7.1.3.2 B). The main longitudinal fibers are attached to the body wall at the segment borders, and smaller longitudinal fibers run to the median segmental furrows. In addition, there are transversal and chaetal muscle fibers. The muscle fibers are typical obliquely striated or of the smooth fiber type.

**Digestive system.** The alimentary canal consists of a ventral pharynx, esophagus, stomach, coiled intestine, and a short hindgut (Reisinger 1925, 1960, Karling 1958, Michel 1988) (Fig. 7.1.3.2 B). The ultrastructure is known only for the ventral pharynx (Purschke 1987). The alimentary canal is ciliated throughout its length, except for the stomodaeum. At the borders between chaetiger 1 and 2, the esophagus leads to a spacious stomach, which extends toward chaetiger 5/6 in *S. subterranea* (Fig. 7.1.3.2 A). The anterior part of the intestine is highly coiled and leads to a straight tube in chaetiger 8, where the genital organs are usually situated. In *P. heideri*, the transition stomach/intestine lies in chaetiger 4/5 and the genital organs start in chaetiger 6. The anus is located terminally on the pygidium. The ventral pharynx is comparatively complex (Purschke 1987). Although modified, it may be assigned to the same type as occurring in Orbiniidae and many other polychaetes (type 1 of Tzetlin and Purschke 2005). In parergodrilids, the muscle bulb is more or less reduced and replaced by a large multicellular gland comprising different gland cells. The bulbus muscle consists of transverse fibers and interstitial cells with a tonofilament system oriented perpendicular to the myofilaments. This structure is absent in *P. heideri*. The most conspicuous structure is a tongue-like organ possessing a strong pistil-shaped cuticle. This projection serves as an attachment structure for the elaborate musculature. The whole structure is united and enveloped by the investing muscle fiber system. Various additional fibers, mainly retractors, attach to the pharynx (Fig. 7.1.3.2 B). The ectodermal esophagus extends into the first chaetiger and continues into the entodermal part, which is densely ciliated. In this area, a large contractile blood vessel is present, containing the heart body (Fig. 7.1.3.2 A, B, E). This blood vessel has been called an esophageal bulb by Karling (1958). The stomach contains detritus-like ingested material, diatoms, as well as small sand particles, whereas the intestine usually appears to be empty. In *S. subterranea*, almost 100% of most populations appears to be infected by an as yet undescribed apicomplexan species, which occasionally occurs in high numbers (observations on various beaches on the North Sea Island of Sylt and Canoe Beach, Nahant, MA, USA; Fig. 7.1.3.2 F, G). These look thread like and show a characteristic longitudinal striation pattern.

**Nervous system and sensory organs.** Although located deep within the body, the nervous system still has a basiepithelial position and is built up of a prostomial brain communicating through the circumesophageal connectives with the ventral nerve cord (Purschke 1999). In *Stygocapitella*, the prostomium is comparatively large and houses the entire brain, which is not delimitated from the epidermis by an extracellular matrix (ECM), whereas in *P. heideri*, the prostomium is too small and the brain bulges backward into the following segments (Fig. 7.1.3.2 A, B). It forms two pairs of posterior lobes of somata, as present in other polychaetes with a small or reduced prostomium (see Purschke 2016). The brain is almost internalized but anteriorly is in broad contact with the epidermis. It is covered by a continuous ECM overlain by a thin coelothel in *P. heideri*. In the ventral cord, a ganglion can be distinguished in each segment. The ventral nerve cord appears as a uni-neuralian cord (see Purschke 2016), with the longitudinal tracts closely apposed, but at least in *S. subterranea,* a median nerve and two main cords can be distinguished if viewed in more detail (Purschke unpublished data). Each segment is innervated by three ring nerves emanating from the ventral nerve cord. An additional pair of minute longitudinal lateral nerves connecting the ring nerves has also been described (Reisinger

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1960). So far, a division of the circumesophageal connectives into dorsal and ventral roots has not been observed, but detailed investigations on the nervous system applying staining with antibodies have not been carried out so far. In the brain and ventral cord, the somata are located as typical for annelids (Purschke 2016): dorsal and lateral in the brain and lateral and ventral in the ventral cord.

Sense organs are poorly developed in Parergodrilidae; pigmented eyes are absent and nuchal organs are present only in *Stygocapitella*. Since the latter are internalized, they were unknown for a long time (Purschke 1986). The nuchal organs are situated laterally at the border between the prostomium and the peristomium. They communicate with the exterior via a small ciliated canal, which is about 5.5 µm wide and 20 µm deep. At its bottom, a small olfactory chamber is formed comprising less than 10 primary sensory cells. Other sensory organs are unknown so far. In addition, the animals possess numerous primary sensory cells of different types, which have been described by Purschke (1999). Collar receptors typical in aquatic metazoans, including polychaetes (Purschke 2005, 2016, Schmidt-Rhaesa 2007), are absent in Parergodrilidae, probably also due to their terrestrial or semiterrestrial lifestyle.

**Body cavities.** Although of comparatively small size and unlike most other interstitial annelids (Fransen 1980, 1988, Rieger and Purschke 2005), parergodrilids are coelomate organisms. The peritoneal coelomic lining is made up of a thin endothelium above the muscle fibers of the body wall or covers the epidermis directly in the gaps between these muscle fibers (Fig. 7.1.3.4 A). Usually, the coelothelial cells are only 80–100 nm thick, except for the regions with the nuclei. The mesodermal cells build up a myoepithelium around the intestine (Fig. 7.1.3.4 B). Spaces in the extracellular matrix between the intestinal epithelium and the coelothelium form the blood sinus surrounding the gut. Only one septum is present, which is situated between the first and second chaetigers. It may be regarded as a gular membrane (Karling 1958, Rouse & Pleijel 2001) (Fig. 7.1.3.2 A, B). This septum is absent in *Parergodrilus* (Reisinger 1960).

**Blood vascular system.** The blood vascular system is complete and closed, in contrast to earlier literature (Reisinger 1960). The coelomic cavity and the blood spaces are clearly separated from each other. The main blood vessel is an anterior-posterior ventral vessel. Other important blood spaces are an intestinal sinus surrounding the gut, a sinus enclosing the ovaries (Fig. 7.1.3.6 F), and a contractile ring-shaped blood vessel around the esophagus (Fig. 7.1.3.2 B, E, F), called esophageal bulb by Karling (1958). With respect to contractibility, this structure may better be termed a heart. As typical for annelids, the blood vessels represent spaces in the ECM between adjacent epithelia (Fransen 1988, Westheide 1997) (Fig. 7.1.3.4 B, C). The sinus surrounding the gut is formed by the intestinal epithelium and the overlying coelothelium; the latter is contractile and responsible for the transportation of blood in the sinus, as well as the content of the gut (Fig. 7.1.3.4 B). In the myoepithelium of the gut, the same cells bear bundles of myofilaments oriented perpendicular to each other. Smaller vessels connecting the periphery with the major vessels may be formed by single cells, which may be rolled up oriented with their basal membranes toward the blood space (Fig. 7.1.3.4 C).

The most important vessel is the esophageal bulb (Figs. 7.1.3.2 A, B, E and 7.1.3.4 D, E). Although its wall is contractile, it is formed by podocytes (Fig. 7.1.3.4 D, E). From the cell bodies, pedicels extend toward the extracellular matrix, where the small processes form a dense cover above the extracellular matrix. Certain pedicels contain bundles of myofilaments, which are responsible for the pulsatile contractions of the bulb (Fig. 7.1.3.4 D). All myofilaments run in a circuit around the bulb, and contraction leads to compression of the bulb, whereas the systole is passive by relaxation. Besides a probable heart-like function, the esophageal bulb is the site for ultrafiltration and, thus, the formation site of the coelomic fluid. The bulb contains a thickened epithelium at the esophageal wall, which can be considered to represent a heart body (Fransen 1988, Rouse & Pleijel 2001).

**Excretory system.** Excretory organs are typical metanephridia and well developed (Reisinger 1925, 1960, Karling 1958, Rota 1997). There are two pairs in *P. heideri* opening in chaetigers 2 and 3, and six pairs in *S. subterranea* opening in chaetigers 2, 3, 4, and 7, as well as in the achaetous segment following the 10th chaetiger (Fig. 7.1.3.2 A, C, D, H). There are no nephridia in the genital segments. They are characterized by a long, heavily ciliated funnel and a highly convoluted duct opening to the outside via a small bladder-like extension (Fig. 7.1.3.2 D, H). The comparatively well-developed excretory organs are most likely related to the specific environment of these animals.

**Reproductive organs.** Parergodrilids are gonochoristic (Fig. 7.1.3.5 A–D) (Karling 1958, Reisinger 1960, Rouse & Pleijel 2001, Purschke 2006, Westheide 2008). At first, only female *P. heideri* were found, but they were described as hermaphrodites by Reisinger (1925). However, after a reinvestigation, Karling (1958) interpreted this material as females, and a subsequent reinvestigation confirmed

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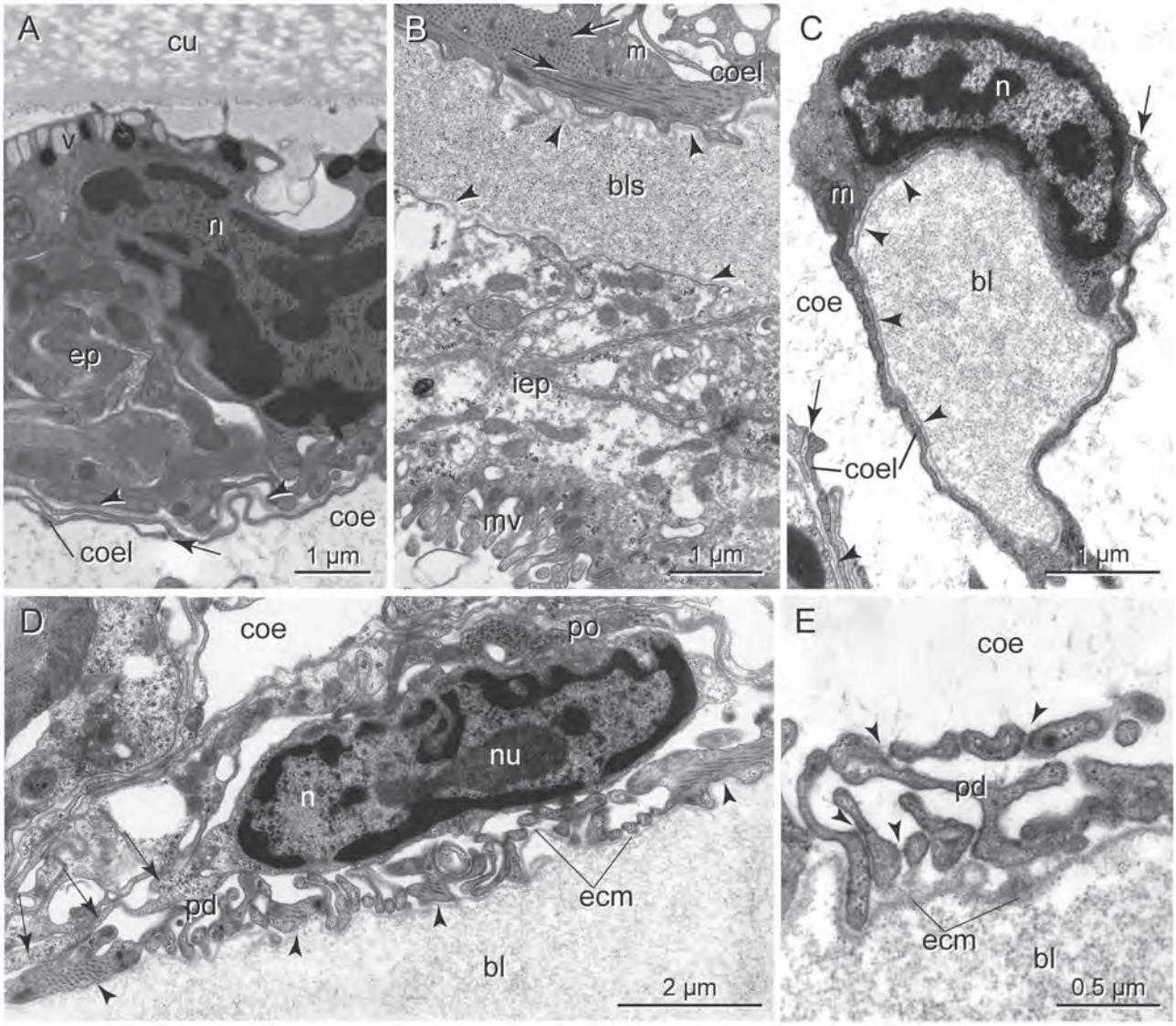


**Fig. 7.1.3.4:** Parergodrilidae. Coelom and blood vascular system. A, B, D, E, *Stygocapitella subterranea*. C, *Parergodrilus heideri*. A, Cuticle (cu), epidermis (ep), and thin coelomic lining (coel); arrowheads point to extracellular matrix (ECM), arrow: zonula adhaerens between coelothel cells. B, Blood sinus (bls) surrounding the intestine; arrowheads: ECM; arrows: myofilaments in coelomic lining with perpendicular oriented myofilaments. C, Small blood vessel formed by a single cell and traversing the coelom (coe); arrowheads: ECM; arrow: zonula adhaerens. D, Podocyte-like epithelium (po) of esophageal bulb; arrowheads point to myofilaments in pedicels; arrows: processes extending from cell body. E, Enlargement of epithelium forming the esophageal bulb; arrowheads point to junctions between pedicels. bl, blood; bls, blood sinus; coe, coelom; coel, coelothelium; cu, cuticle; ecm, extracellular matrix; ep, epidermis; iep, intestinal epithelium; m, mitochondrion; mv, microvillus; n, nucleus; nu, nucleolus; pd, pedicel; po, podocyte.

his hypothesis and males were described for the first time (Reisinger 1960). However, males occur in considerably lower numbers than females, and most individuals found today are female (Reisinger 1960, Purschke 1999). The observed male:female sex ratio is between 1:8 and 1:170. The reasons are unknown but may be related to a different behavior, different longevity, and smaller size of the males (Reisinger 1960). Although some doubts still remain on the gonochoristic situation, Reisinger's interpretation has not yet been disproven. In *Stygocapitella*, the sex ratio is about 1:1.

In *S. subterranea*, the female organs comprise an unpaired ovisac containing a fused pair of ovaries (Fig. 7.1.3.5 E). A pair of female ducts opens to the outside between chaetiger 9 and 10, which are differentiated to a receptaculum seminis close to the opening. In the following segments, ventral cocoon forming glands are present (Fig. 7.1.3.5 C). In *S. subterranea*, bundles of sperm may also

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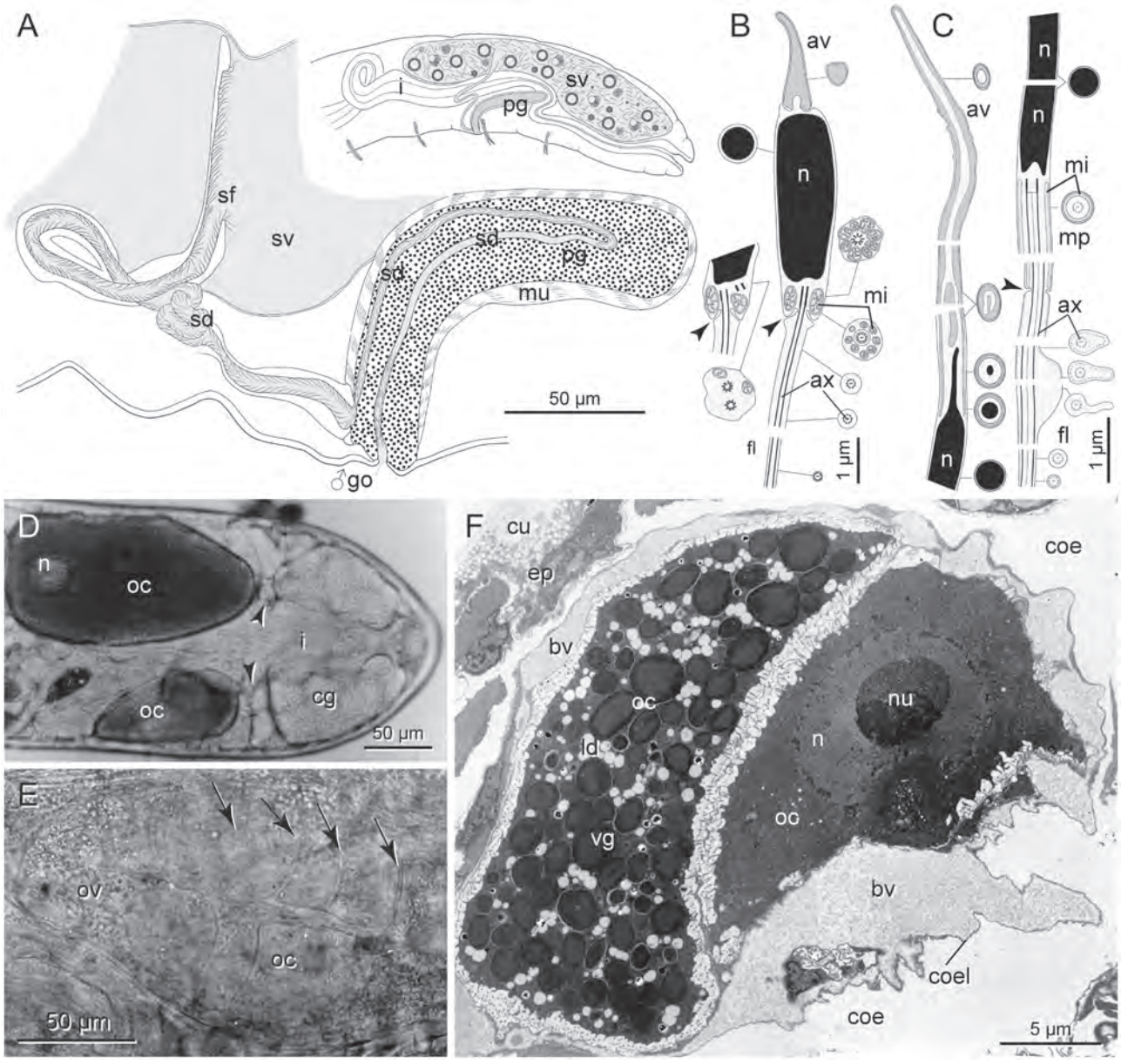


**Fig. 7.1.3.5:** Parergodrilidae. Genital organs and gametes. A, *Stygocapitella subterranea*. Male organs composed of paired ciliated gonoducts forming a loop inside the prostate gland and opening together with the gland cells on chaetiger 9. B, C, Ultrastructure of the sperm, schematic representations in longitudinal and cross-sections. B, Sperm of *Parergodrilus heideri* with distinct head, midpiece, and tail region. C, Filiform sperm of *S. subterranea*. D–F, Female organs. D, *P. heideri*. Ovaries with two vitellogenic oocytes (oc); arrowheads point to receptacles each with a few spermatozoa. E, *S. subterranea.* Fused pair of ovaries with previtellogenic oocytes arranged like a roll of coins; arrows point to cell borders. F, *P. heideri*, transmission electron microscopy micrograph of ovary containing a vitellogenic oocyte and a previtellogenic oocyte, the latter with a large nucleus and nucelouls (n, nu); note blood sinus surrounding the ovary and the close contact of blood and oocytes. ♂go, male opening; av, acrosomal vesicle; ax, axoneme; bv, blood vessel; cg, cocoon gland; coe, colom; coel, coelothelium; cu, cuticle; ep, epidermis; fl, flagellum; i, intestine; ld, lipid droplet; mi, mitochondrium; mp, midpiece; mu, muscle; n, nucleus; nu, nucleolus; oc, oocyte; ov, ovary; pg, prostate gland; sd, sperm duct; sf, seminal funnel; sv, seminal vesicle; vg, vitelline granule. A, Redrawn from Purschke & Jördens (2007); B, from Purschke (2002); C, from Purschke & Fursman (2005).

be found in the body cavity close the female openings. In *P. heideri*, all structures are paired and the female openings are directly associated with the cocoon glands at the posterior end and the receptacles are situated more proximally (Fig. 7.1.3.5 D). It is remarkable that mature sperm are found in the receptacles of every mature female, but their number is comparatively low (Reisinger 1925, 1960, Rota 1997, 1998, Purschke 1999, 2002). The ovaries are separated from the coelom by a thin peritoneal lining and the oocytes are in close contact with the blood in both genera (Fig. 7.1.3.5 F).

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In *S. subterranea*, the male organs comprise a large unpaired seminal vesicle extending over several segments and a pair of long, highly convoluted sperm ducts connected to the seminal vesicle by prominent ciliated funnels. The ducts enter the multicellular prostate glands, form a loop inside the gland, and open to the outside ventrally on chaetiger 9. The male opening is surrounded by a circle of prostate gland cell openings (Purschke & Jördens 2007). Other prostate gland cells open directly into the male duct. In *P. heideri,* the male organs are similar, but the vesicles are paired; there are two pairs of sperm ducts, which are associated with so-called copulatory chaetae and prostate gland cells (Reisinger 1960, Purschke 2002, 2006). The sperm ducts open into a common genital atrium (Purschke 2002). The copulatory chaetae and a pair of additional chaetae have been assigned to two additional segments so that male *P. heideri* have two chaetigers more than females do and the same number of chaetigers as *S. subterranea*. Although direct transfer of sperm is generally assumed, true copulatory organs are absent (Purschke 2006). The vesicles are formed by adjacent coelothelia, but prominent blood spaces between the epithelial layers are absent. The testes are situated ventrally in the vesicles and spermiogenesis takes place in the vesicles.

**Gametes.** The ovaries always comprise a number of previtellogenic oocytes but usually only one mature oocyte at a time (Figs. 7.1.3.1 A, C and 5 D–F). These are comparatively large: 150 µm in diameter in *P. heideri* and up to 300–400 µm by 150 µm in *S. subterranea* (Purschke 1999). Follicle cells are absent and oogenesis is intraovarian.

Spermatogonia are produced by mitotic divisions in the testes and then they are released into the seminal vesicles. In *P. heideri*, these directly undergo meiosis and form small cytophores with only four spermatids (Purschke 2002). In *S. subterranea*, they undergo additional mitotic divisions without separation, and finally, larger cytophores with at least 128 spermatids are formed (Purschke & Fursman 2005). Whereas in *P. heideri* the spermatozoa are distinctly divided into the head, midpiece, and tail, those of *S. subterranea* are filiform (Fig. 7.1.3.5 B, C). In the latter, they are about 320 µm long and thus are among the longest spermatozoa known for annelids. However, there are common traits between the two species: The acrosome is elongated and comprises a single vesicle, the number of mitochondria is eight (although they fuse to a ring-like structure during spermatogenesis in *S. subterranea*), and the border between the midpiece and the tail is marked by a fold of the plasma membrane. Other characters such as presence of an accessory centriole in *P. heideri* might distinguish the two species.

Eggs are laid singly in cocoons, which are deposited on the substrate (Reisinger 1960, Purschke 1999). Parergodrilidae have direct development, but cleavage has been observed only in *P. heideri*. It can be described as an unequal spiral cleavage (Reisinger 1960). The embryonic development is completed after 8–10 days in *P. heideri*. In both species, hatching juveniles possess four chaetigers and segments are continuously added during growth. In *P. heideri*, these juveniles are only 60–80 µm long and possess both pairs of nephridia (Reisinger 1960). In *S. subterranea,* hatchlings are 0.73 mm long and have the first three pairs of nephridia. Although all types of chaetae are present, there is only one bilimbate chaeta with a long whip-like distal extension and one bilimbate and two forked chaetae present in the first chaetiger. Also, in the second chaetiger, there are only two bilambates and two forked chaetae. New segments are formed subsequently until the final numbers are reached (individuals with five chaetigers measure 0.9 mm; those with six chaetigers, 1.1 mm; with seven chaetigers, 1.2 mm; with eight chaetigers, 1.4 mm; and with nine chaetigers, 1.5 mm). Nephridia are formed when respective segments appear so that the final number of nephridia is present after the last achaetous segment has developed. At the five-chaetiger stage, the second bilimbate with extension appears; at the six-chaetiger stage, the second bilimbate in chaetiger 1 is formed; and at the seven-chaetiger stage, the adult chaetal pattern is reached. Immature individuals with 10 chaetigers measure 1.6–1.8 mm.

## Biology and ecology

Data on the ecology and biology of Parergodrilidae are comparatively scarce. Nevertheless, more ecological data are available for *S. subterranea* than for *P. heideri*. Whereas for the latter species mainly faunistic data have been gathered, the former has been studied more extensively in several tidal and nontidal beaches (e.g., Renaud-Debysier 1963, Schmidt 1969, 1970, 1972a,b, Westheide 1972, Rota 1997, 1998, Erséus and Rota 1998, Purschke 1999, Rota *et al*. 2010, Rota and Jong 2015, Struck *et al*. 2017). In *S. subterranea,* the distribution pattern in tidal beaches corresponds to the upper shore throughout the year, with the highest abundance in samples taken close to the high tide level (Fig. 7.1.3.6 A, B). In a broad scale, abundance of individuals is usually low, between 1 and 10 individuals/100 cm³. However, close to high tide level, the number of individuals found in 100 cm³ sediment may be up to about 30–40.

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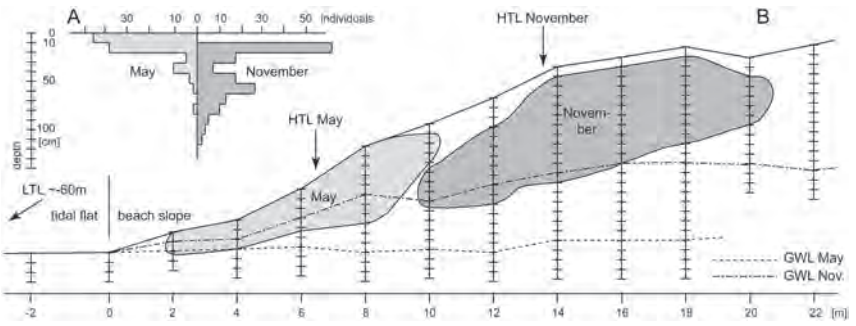


**Fig. 7.1.3.6:** *Stygocapitella subterranea*. Distribution in a tidal beach on the North Sea Island of Sylt, Germany, in two representative months. A, Vertical distribution and abundance in spring and winter. B, Zonation pattern at low tide; shaded areas represent inhabited regions of the beach. Note a clear correlation to the respective high tide level (HTL); each vertical line represents a core of sediment divided into 10-cm sections with a volume of 100 cm³. Redrawn from Purschke (1999).

The highest abundance was observed in a beach in List/Sylt with 70 individuals/100 cm³ (Purschke 1999). Vertically, the uppermost sediment layers were preferred and most individuals were found at depths of 0–20 cm (Schmidt 1970, Purschke 1999). This level was occupied throughout the year and the populations migrated with changes in high water level according to the moon cycle and seasonal variations. The uppermost sediment layers were avoided only during the winter months and if the sand was completely desiccated (Fig. 7.1.3.6 A). Although, occasionally, a few individuals occurred deeper in the sediment down to water saturated parts as well as in the ground water, it was obvious that a zone of damp sand with a water content of 3% of the sediment dry weight was preferred. Individuals were found in sediments with water contents between 2.5% and 21.5% (=water saturation) of the sediment dry weight. The lower values are comparable to the water content in terrestrial soils (Purschke 1999). Generally, these areas are characterized not only by low water content and semiterrestrial conditions but also by a lower and changing salinity, as well as a more harsh temperature regime. The salinity in samples containing *S. subterranea* individuals varied from 14 to 31‰, with most animals found in samples of 22 to 29‰ salinity. Thus, the species inhabits a transition zone between the marine and terrestrial/freshwater realms.

The observation that *S. subterranea* showed the highest tolerance of low temperatures among several interstitial annelids studied corresponds to its distribution pattern (Purschke 1981). In the nontidal beaches investigated, such as in the Baltic or in the Mediterranean (Schmidt 1970, Westheide 1972), and sites of low exposure or low tidal amplitudes, such as several beaches on the North Sea Island of Sylt (Purschke and Struck, unpublished observation), the species occurs in an area far above high water level, which is only occasionally influenced by the sea (Schmidt 1970).

In the investigated *S. subterranea* populations, mature and juvenile individuals were found throughout the year. Due to the lack of additional experimental evidence, no data are available about the longevity of this species. The populations usually comprised females and males in a ratio of 1:1, and between 70 and 90% of all individuals were adult but not fully mature. Among the juveniles, all classes have been observed throughout the year (Purschke, unpublished observation).

As mentioned earlier, *P. heideri* occurs in the leaf litter of humid beech woods mainly inhabiting thick layers of decomposing leaves (Reisinger 1925, 1960, Rota 1997, Purschke 1999). Other records report the species from other forest types as well (Rota *et al*. 2010, Rota and DeJong 2015). It was assumed that the species cannot withstand longer periods of either desiccation or submersion. However, records from various biotopes show that the species is at least well capable of surviving temporary flooding (Rota *et al*. 2010). Only a few data on abundance and life cycle have been obtained so far (Reisinger 1960). According to his observations in Austrian forests males are mostly found during summer. These observations may lead to the conclusion that reproduction takes place mainly during this period. However, unpublished observations in a monthly survey revealed mature females with vitellogenic oocytes and spermatozoa in their receptacles throughout the year in a beech forest near Göttingen, Germany (Purschke unpublished observation).

**Distribution**

All Parergodrildae found so far are either marine or terrestrial. Since the marine species are known from the upper eulittoral or supralittoral of sandy beaches, they may even be regarded as being semiterrestrial (Purschke 1999). Although only two genera are known to date, which have been described from central Europe, parergodrilids have now been recorded from various places

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**Fig. 7.1.3.7:** Distribution of Parergodrilidae. Red squares: *Stygocapitella subterranea*; red circles: *Stygocapitella australis*; red polygon: *Stygocapitella minuta*; green squares: *Parergodrilus heideri*. From various sources.

and appear to have a worldwide distribution (Schmidt 1970, Purschke 1999, Westheide 2008, Rota & Jong 2015, Struck *et al*. 2017). The paucity of records outside Europe is presumably due to the lack of sampling activities rather than to true absence, as proved by recent new findings (Rouse & Pleijel 2001, Rota & Jong 2015, Struck *et al*. 2017).

Records of *P. heideri* are restricted to the Northern hemisphere, whereas *Stygocapitella* occurs on the Southern and Northern hemispheres, except for the tropics (Fig. 7.1.3.7) (Purschke 1999, Westheide 2008, Rota & Jong 2015). *Parergodrilus heideri* inhabits the leaf litter and upper organic soil zones in different types of forests, mainly beech. It has been found in Austria, Croatia, Czech Republic, Denmark, France, Germany, Italy, Spain, Sweden, USA (Minnesota and Wisconsin), and Korea (Chalupský 1992, Rota 1997, 1998, Purschke 1999, Martínez-Ansemil & Parapar 2009, Dózsa-Farkas & Hong 2010, Rota *et al*. 2010, Schlaghamerský & Freilich 2012, Rota & Jong 2015).

*Stygocapitella subterranea* was described from the Baltic (Kiel-Schilksee, Germany) by Knöllner (1934); later, it was found in various other places in the Baltic and North Sea (Brinck *et al*. 1955, Karling 1958, Westheide 1966, 1977, 2008, Schmidt 1969, 1970, 1972a, Purschke 1999), as well as from the European Atlantic Coast (Renaud-Debysier 1963, Schmidt 1970, 1972b) (Fig. 7.1.3.7). These findings were complemented by records from the Mediterranean (Europe and northern Africa) and from the Black Sea (Valkanov 1954, Schmidt 1970, Westheide 1972, Rota *et al*. 2001). Further studies revealed several new localities in Europe, North America (USA and Canada), and also from Australia and New Zealand (Riser 1980, 1984, Purschke 1999, Schmidt & Westheide 2000, Worsfold 2006, Struck *et al*. 2017). So far, *Stygocapitella minuta* is known only from South Africa (Struck *et al*. 2017), and the records of *S. subterranea* from Australia (Hartmann-Schröder 1983) have now been assigned to *Stygocapitella australis* (Struck *et al*. 2017). The record of *S. subterranea* from New Zealand probably also represents *S. australis*, as discussed by Struck *et al*. (2017). The higher number of localities from European waters is certainly due to a higher sampling activity rather than true absences in other parts of the world. Records from the Asian Pacific Coasts as well as from the tropics are still lacking. However, the distribution gap of *Stygocapitella* in the tropics and most of the subtropics is very likely to represent true

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absence since several attempts to find *Stygocapitella* in these regions have failed (personal observations of T.H. Struck, G. Purschke, and W. Westheide, University of Osnabrück). Biological data indicate that this species is well adapted to temperate and colder climate conditions (Schmidt 1970, Purschke 1981). Struck *et al*. (2017) provide a new hypothesis explaining this distribution pattern by plate tectonics, climate change, and evolution over time.

## Phylogeny and taxonomy

### Phylogeny

For a long time, the phylogeny and systematics of *Parergodrilus* and *Stygocapitella* remained unresolved, enigmatic, and controversial. *P. heideri* was first described as an archiannelid by Reisinger (1925) and placed into a new family taxon, Parergodrilidae. On the basis of this description, Meyer (1927) regarded the species to be an oligochaete, which was strongly rejected by Reisinger (1929). Knöllner (1934) described *S. subterranea* and placed it into Capitellidae without noticing any relationship to *P. heideri*. It was Karling (1958), in his detailed anatomical investigation on *S. subterranea*, who was the first to become aware of the similarities between the two species. This was confirmed by Reisinger (1960) and later supported by an ultrastructural analysis of the ventral pharynx by Purschke (1987). Fauchald (1977) grouped Parergodrilidae with Ctenodrilidae as Ctenodrilida but without giving common derived characters. This view was followed by Hartmann-Schröder (1996) and others. A close relationship to *Hrabeiella periglandulata* was suggested by Pizl and Chalupsky (1984) but was not supported by any other investigation (Rota 1998, Purschke 1999, 2006, Rota *et al*. 2001, Struck *et al*. 2002, Jördens *et al*. 2004). Thus, their position remained uncertain, and consequently, Fauchald and Rouse (1997) placed Parergodrilidae as incertae sedis within Polychaeta in their phylogenetic analysis.

Thanks to phylogenetic analyses with the application of molecular data, their position could finally be resolved. Whereas the first studies using molecular data could not present clear evidence for their phylogenetic position (e.g., Rota *et al*. 2001, Rousset *et al*. 2007), in subsequent studies, Parergodrilidae usually grouped together and were sister to Orbiniidae (Struck *et al*. 2002, 2008, 2014, 2015, Bleidorn *et al*. 2003, Jördens *et al*. 2004, Bleidorn 2005, 2007, Zrzavý *et al*. 2009). Moreover, a close relationship to *H. periglandulata* could be rejected with certainty. Struck *et al*. (2017) were able to show that *Stygocapitella* is monophyletic and comprises at least three distinct species. Within these species, *S. minuta* is sister to a clade formed by *S. australis* and *S. subterranea*. The distribution patterns and their morphology and phylogenetic relationship suggest an invasion of terrestrial environments via the damp zone of sandy beaches (Graefe 1977, Purschke 1999).

### Taxonomy

#### Parergodrilidae Reisinger, 1925

**Type species:** *Parergodrilus heideri* Reisinger, 1925
**Synonyms:** Stygocapitellidae Karling, 1958
**Diagnosis:** Small, cylindrical, grub-shaped animals. Prostomium, peristomium, species-specific number of segments, first and varying number of posterior segment without chaetae. Palps, antennae, parapodia, and pygidial cirri absent. Body not differentiated into regions. Chaetae more or less simple, arranged in paired ventrolateral bundles. Epidermis without locomotory cilia, whitish transparent, body surface slightly iridescent, eyes absent, nuchal organs either internalized or absent, gonochoristic, gonoducts present, direct development (Reisinger 1925, 1960, Karling 1958, Purschke 1999, Westheide 2008, Hartmann-Schröder 1996).

#### *Parergodrilus heideri* Reisinger, 1925 (Figs. 7.1.3.1 A, B and 7.1.3.3 G, H)

**Type species:** *Parergodrilus heideri* Reisinger, 1925
Monotypic
**Diagnosis:** Body cylindrical with a slight posterior swelling in males, whitish transparent, prostomium rounded and small, brain with posterior lobes extending into peristomium, first segment chaetigerous, ♀♀ with 8 chaetigers and pygidium, ♂♂ with 10 chaetigers and pygidium, chaetae simple elongated rods with thickened base, in ♂♂ chaetae of chaetiger 10 enlarged (copulatory chaetae), terrestrial.
**Remarks:** So far, only known from Northern Hemisphere, most records from Europe, probably comprising several cryptic species.

#### *Stygocapitella* Knöllner, 1934 (Figs. 7.1.3.1 C, D, 7.1.3.2 A, and 7.1.3.3 A–F)

**Type species:** *Stygocapitella subterranea* Knöllner, 1934
**Three described species:** *Stygocapitella subterranea* Knöllner, 1934; *S. minuta* Struck *et al*., 2017; *S. australis* Struck *et al*., 2017.
**Diagnosis:** Marine Parergodrilidae with rounded prostomium. Body comprising at least 12 segments, simple chaetae of three different types: bilimbate chaetae with

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long whip-like prolongation, up to 300 µm long, simple bilimbate, and forked chaetae.

**Remarks:** Most likely comprising several cryptic species in the Southern and Northern Hemispheres, worldwide distribution, records lacking from tropical regions. *S. subterranea* Knöllner, 1934 is now restricted to the Northern hemisphere; populations from Europe, Atlantic, and Pacific coast of North America are most likely genetically separated from each other but morphologically identical (Schmidt and Westheide 2000, Westheide 2008, Struck *et al.* 2017), *S. minuta* Struck *et al.*, 2017 so far known only from South Africa, *S. australis* Struck *et al.*, 2017 known only from South East Australia; systematic affiliation of specimens from New Zealand uncertain.

## References


Bleidorn, C. (2005): Phylogenetic relationships and evolution of Orbiniidae (Annelida, Polychaeta) based on molecular data. *Zoological Journal of the Linnean Society* 144: 59–73.

Bleidorn, C. (2007): The role of character loss in phylogenetic reconstruction as exemplified for the Annelida. *Journal of zoological Systematics and Evolutionary Research* 45: 299–307.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003): New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 29: 279–288.

Brinck, P., Dahl, E. & Wieser, W. (1955): On the littoral subsoil fauna of the Simrishamn Beach in Eastern Scania. *Kunglia Fysiografiska Sällskapets i Lund Förhandlingar* 25: 109–129.

Chalupský, J. (1992): Terrestrial Enchytraeidae (Oligochaeta) and Parergodrilidae from Sweden, with description of a new enchytraeid species. *Zoologica Scripta* 21: 133–150.

Dózsa-Farkas, K. & Hong, Y. (2010): Three new *Hemienchytraeus* species (Enchytraeidae, Oligochaeta, Annelida) from Korea, with first records of other enchytraeids and terrestrial polychaetes (Annelida). *Zootaxa* 2406: 29–56.

Erséus, C. & Rota, E. (1998): Havsborstmaskar på torra land. *Fauna och Flora Årg*. 93: 97–104.

Fransen, M.E. (1980): Ultrastructure of coelomic organization in annelids. I. Archiannelids and other small polychaetes. *Zoomorphology* 95: 235–249.

Fransen, M.E. (1988): Coelomic and vascular systems. *Mikrofauna Marina* 4: 199–213.

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

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

Graefe, U. (1977): *Adenodrilus* Graefe (in press) and *Parergodrilus* Reisinger two aberrant Annelida in forest soils. *Publicaciones del Centro pirenaico de Biología Experimental* 9: 25.

Hartmann-Schröder, G. (1983): Teil 9 Die Polychaeten der antiborealen Südwestküste Australiens (zwischen Dunsborough im Norden und Denmark im Süden). *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 80: 123–167.

Hartmann-Schröder, G. (1996): Annelida, Borstenwürmer, Polychaeta. In: Schumann, H. (ed.) *Die Tierwelt Deutschlands 58.Teil*. 2nd ed. Gustav Fischer, Jena: 1–648.

Jördens, J., Struck, T. & Purschke, G. (2004): Phylogenetic interference regarding Parergodrilidae and *Hrabeiella periglandulata* ("Polychaeta", Annelida) based on 18S rDNA and COI sequences. *Journal of zoological Systematics and Evolutionary Research* 42: 270–280.

Karling, T. (1958): Zur Kenntnis von *Stygocapitella subterranea* Knöllner und *Parergodrilus heideri* Reisinger (Annelida). *Arkiv för Zoologi* 11: 307–341.

Knöllner, F. (1934): *Stypocapitella* [sic] *subterranea* n. gen.; n. spec. *Schriften des naturwissenschaftlichen Vereins für Schleswig-Holstein* 20: 468–472.

Martínez-Ansemil, E. & Parapar, J. (2009): Primera cita en la península Ibérica del poliqueto terrestre *Parergodrilus heideri* Reisinger, 1925 (Polychaeta, Parergodrilidae). *Graellsia* 65: 235–240.

Meyer, A. (1927): Ist *Parergodrilus heideri* (Reisinger) ein Archiannelide? *Zoologischer Anzeiger* 72: 19–35.

Michel, C. (1988): Intestine and digestive glands. *Mikrofauna Marina* 4: 157–175.

Pizl, V. & Chalupsky, J. (1984): *Hrabeiella periglandulata* gen. et sp. n. (Annelida) – a curious worm from Czechoslovakia. *Vest. cs. Spolec. Zool.* 48: 291–295.

Purschke, G. (1981): Tolerance to freezing and supercooling of interstitial Turbellaria and Polychaeta from a sandy tidal beach of the Island of Sylt (North Sea). *Marine Biology* 63: 257–267.

Purschke, G. (1986): Ultrastructure of the nuchal organ in the interstitial polychaete *Stygocapitella subterranea* (Parergodrilidae). *Zoologica Scripta* 16: 13–20.

Purschke, G. (1987): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). III. The pharynx of the Parergodrilidae. *Zoologische Jahrbücher Anatomie* 115: 331–362.

Purschke, G. (1999): Terrestrial polychaetes – models for the evolution of the Clitellata (Annelida)? *Hydrobiologia* 406: 87–99.

Purschke, G. (2002): Male genital organs, spermatogenesis and spermatozoa in the enigmatic terrestrial polychaete *Parergodrilus heideri* (Annelida, Parergodrilidae) *Zoomorphology* 121: 125–138.

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

Purschke, G. (2006): Problematic annelid groups. In: Rouse, G. & Pleijel, F. (eds.) *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield: 639–667.

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

Purschke, G. & Fursman, M.C. (2005): Spermatogenesis and spermatozoa in *Stygocapitella subterranea* (Annelida: Parergodrilidae), an enigmatic supralittoral polychaete. *Zoomorphology* 124: 137–148.

Purschke, G. & Jördens, J. (2007): Male genital organs in the eulittoral meiofaunal polychaete *Stygocapitella subterranea* (Annelida, Parergodrilidae): Ultrastructure,


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functional and phylogenetic significance. *Zoomorphology* 126: 283–297.
Tzetlin, A. & Purschke, G. (2005): Pharynx and intestine. *Hydrobiologia* 535/536: 199–225.
Reisinger, E. (1925): Ein landbewohnender Archiannelide (Zugleich ein Beitrag zur Systematik der Archianneliden). *Zeitschrift für Morphologie und Ökologie der Tiere* 3: 197–254.
Reisinger, E. (1929): Die systematische Stellung von *Parergodrilus heideri* Reisinger. *Zoologischer Anzeiger* 80: 12–20.
Reisinger, E. (1960): Die Lösung des *Parergodrilus*-Problems. *Zeitschrift für Morphologie und Ökologie der Tiere* 48: 517–544.
Renaud-Debysier, J. (1963): Recherches écologiques sur la faune interstitielle des sables. Bassin d'Arcachon, île de Bimini, Bahamas. *Vie Milieu Supplement* 15: 1–157.
Rieger, R.M. & Purschke, G. (2005): The coelom and the origin of the annelid body plan. *Hydrobiologia* 535/536: 127–137.
Riser, N.W. (1980): The aberrant polychaete *Stygocapitella suberranea* from some American beaches. *The Wasman Journal of Biology* 38: 10–17.
Riser, N.W. (1984): General observations on the intertidal interstitial fauna of New Zealand. *Tane* 30: 239–250.
Rota, E. (1997): First Italian record of the terrestrial polychaete *Parergodrilus* Reisinger, with anatomical and ecological notes. *Italian Journal of Zoology* 64: 91–96.
Rota, E. (1998): Morphology and adaptations of *Parergodrilus* Reisinger and *Hrabeiella* Pizl & Chalupsky, two enigmatic soil-dwelling animals. *Italian Journal of Zoology* 65: 75–84.
Rota, E. & Jong, Y. de (2015): Fauna Europaea: Annelida – Terrestrial Oligochaeta (Enchytraeidae and Megadrili), Aphanoneura and Polychaeta. *Biodiversity Data Journal* 3: 1–47.
Rota, E., Martin, P. & Erseus, C. (2001): Soil-dwelling polychaetes: enigmatic as ever? Some hints on their phylogenetic relationships as suggested by maximum parsimony analysis of 18S rDNA sequences. *Contributions to Zoology* 70: 127–138.
Rota, E., Nicola, F. de & Bargagli, R. (2010): *Parergodrilus heideri* Reisinger, 1925 (Annelida: Polychaeta) from a holm oak wood in an extinct volcano of southern Italy. *Zootaxa* 2687: 65–68.
Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, New York.
Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.
Schlaghamerský, J. & Freilich, L.E. (2012): First records of *Parergodrilus heideri* (Annelida: "Polychaeta") from North America. *Zootaxa* 3498: 81–86.
Schmidt, P. (1969): Die quantitative Verteilung und Populationsdynamik des Mesopsammons am Gezeiten-Sandstrand der Nordseeinsel Sylt. II: quantitative Verteilung und Populationsdynamik einzelner Arten. *Internationale Revue der gesamten Hydrobiologie* 54: 723–779.
Schmidt, P. (1970): Zonation of the interstitial polychaete *Stygocapitella subterranea* (Stygocapitellidae) in European sandy beaches. *Marine Biology* 7: 319–323.
Schmidt, P. (1972a): Zonierung und jahreszeitliche Fluktuationen des Mesopsammons im Sandstrand von Schilksee (Kieler Bucht). *Mikrofauna des Meeresbodens* 10: 1–60.
Schmidt, P. (1972b): Zonierung und jahreszeitliche Fluktuationen der interstitiellen Fauna in Sandstränden des Gebietes von Tromsø (Norwegen). *Mikrofauna des Meeresbodens* 12: 1–86.
Schmidt, H. & Westheide, W. (2000): Are the meiofaunal polychaetes *Hesionides arenaria* and *Stygocapitella subterranea* true cosmopolitan species? – Results of RAPD-PCR investigations. *Zoologica Scripta* 29: 17–27.
Schmidt-Rhaesa, A. (2007): *The Evolution of Organ Systems*. Oxford University Press, Oxford.
Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C., Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.
Struck, T.H., Hessling, R. & Purschke, G. (2002): The phylogenetic position of Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of "Polychaeta". *Journal of Zoological Systematics and Evolutionary Research* 40: 155–163.
Struck, T.H., Koczula, J., Stateczny, D., Meyer, C., Purschke, G. (2017): Two new species in the annelid genus *Stygocapitella* (Orbiniida, Parergodilidae) with comments on their biogeography. *Zootaxa* 4286: 301–332.
Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.
Struck, T.H., Purschke, G., Dordel, J., Hösel, C., Nesnidal, M.P., Diering, F., Bleidorn, C., Paul, C., Hill, N., Tiedemann, R., Selbig, J. Hartmann, S. (2014): Phylogeny and evolution of Annelida based on molecular data. In: Wägele, W. & Bartolomaeus, T. (eds.) *Deep Metazoan Phylogeny: The Backbone of the Tree of Life*. De Gruyter, Berlin: 143–160.
Valkanov, A. (1954): Zwei neue Polychaeten für das Schwarze Meer. *Arbeiten aus der Biologischen Station Varna* 18: 49–53 [In Bulgarian with German Summary].
Westheide, W. (1966): Zur Polychaetenfauna des Eulitorals der Nordseeinsel Sylt. *Helgoländer wissenschaftliche Meeresuntersuchungen* 13: 203–209.
Westheide, W. (1972): La faune des polychètes et des archiannélides dans les plages sableuses à ressac de la côte méditerranéenne de la Tunisie. *Bulletin de l'Institut d'Océanographique et de Pêche de Salammbô* 2: 449–468.
Westheide, W. (1977): The geographical distribution of interstitial polychaetes. *Mikrofauna des Meeresbodens* 61: 287–302.
Westheide, W. (1990): *Polychaetes: Interstitial families. Synopses of the British Fauna (New Series)*. Universal Book Services/ Dr. W. Backhuys, Oegstgeest.
Westheide, W. (1997): The direction of evolution within the Polychaeta. *Journal of Natural HIstory* 31: 1–15.
Westheide, W. (2008): *Polychaetes: Interstitial Families. Synopses of the British Fauna (New Series)*. No. 44, 2nd. ed. The Linnean Society of London, London.
Worsfold, T.M. (2006): British records of the interstitial polychaete *Stygocapitella subterranea* (Annelida: Parergodrilidae). *Journal of the Marine Biological Association of the United Kingdom. Marine Biodiversity Records* 5429: 1–3.
Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189: 1–14.

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Christoph Bleidorn and Conrad Helm

## 7.1.4 Orbiniidae Hartman, 1942

### Introduction

Orbiniidae are a taxon of sedentary annelids that vary in size from a few millimeters up to 50 cm. A total of 204 species are described, and most species can be found burrowing in sediment. Orbiniids are known from all marine habitats, including intertidal forms from sandy and rocky shores, as well as deep-sea forms. The deepest recorded orbiniid is *Berkeleyia hadala*, which has been found in abyssal depths in the Peru-Chile Trench in 6143 m (Blake 2017). The body is usually homonomously segmented and can bear up to some hundred chaetigers. Many of the large species are fragile and are only incompletely known. The by far best investigated species are members of the *Scoloplos armiger* species complex, which often are reported as highly abundant in ecological studies. The interstitial Questidae, questids have recently been transferred to Orbiniidae (Bleidorn *et al.* 2009). Since they superficially resemble clitellates in their reproductive biology and certain structures, they formerly have been discussed as being probably closely related to them (Almeida *et al.* 2003).

### Morphology

#### External morphology

Orbiniidae are homonomously segmented, slender worms that usually bear a rounded (Fig. 7.1.4.1 B) or pointed (Fig. 7.1.4.1 A) prostomium without appendages. The peristomium forms one or two rings (Fig. 7.1.4.1 A, D), but this distinction can be blurred, and the number may vary between juveniles and adults. The peristomium of *Orbiniella branchiata* seems to form three rings (Hartman 1967). The pygidium is small and collar like, and up to two pairs of cirri might be present (Fig. 7.1.4.2 D). The body of several orbiniid genera can be separated into a muscular and dorsally flattened thorax region and a more cylindrically appearing abdomen (Fig. 7.1.4.1 D). The parapodia of the abdominal region are shifted dorsally. Especially many small (e.g., *Orbiniella* spp.), but also some large species (e.g., *Methanoaricia dendrobranchiata*) do not show such a separation of different body regions. The parapodia are biramous and might be more (Fig. 7.1.4.1 B) or less (Fig. 7.1.4.1 E) prominently developed. Many genera bear notopodial and/or neuropodial postchaetal lobes and interramal cirri can be found in some species, e.g., *Orbinia latreillii* (Hartman 1957).

An autapomorphic character for Orbiinidae is the presence of camerated capillary chaetae, which show characteristic crenulations (Figs. 7.1.4.2 E and 7.1.4.3 B, D). Hausam and Bartolomaeus (2001) investigated the formation of these chaetae in two species of *Orbinia* and found that during chaetal development, an incomplete ring of microvilli is regularly formed. These microvilli lie peripheral to an outer layer of microvilli, performing the chaetal shaft. Fusion of both layers of microvilli results in the camerated appearance of the capillary chaetae. Additionally, especially the neuropodia often bear strong acicular spines. Notopodia and abdominal neuropodia often include supportive chaetae; however, it is doubted if these can be homologized with the supportive chaetae of other errant annelids (Hoffmann and Hausen 2007). Furcate chaetae occur in several orbiniid species, and lines of this type of chaetae ventrally surrounding bundles of capillary chaetae may be present (Hausam and Bartolomaeus 2001). Several types of chaetae are restricted to one or a few genera. *Pettibonella multiuncinata* and *Proscoloplos cygnochaetus* bear swan-shaped chaetae in some posterior neuropodia (Solis-Weiss and Fauchald 1989), which are remarkably similar, but most likely based on a parsimonious reasoning given their nested derived position within Orbiniidae convergently evolved, to uncini (Hoffmann and Hausen 2007). The genus *Califia* is characterized in bearing brush-topped chaetae (Hartman 1957) and the camerated capillaries of *Orbiniella plumisetosa* show hairs originating from the crenulation (Buzhinskaja 1992). The presence of modified spines ("Wehrstachel") is diagnostic for the genus *Phylo*. Three types of chaetae can be found in the genus *Questa*, which include, besides camerated capillaries (Fig. 7.1.4.2 E) and furcate chaetae (Fig. 7.1.4.2 F), bi- or trifid crotches (Fig. 7.1.4.2 C) representing a different type of chaetae not present in any other orbiniid (Giere *et al.* 2008).

#### Anatomy

**Digestive system.** Whereas an axial pharynx can be found in most adult orbiniids (Fig. 7.1.4.4 E) (e.g., *S. armiger* and *Phylo ornata*), juveniles and small species (e.g., *Protoaricia oerstedii* and *Questa paucibranchiata*) bear a ventral pharynx (Fig. 7.1.4.4 F) (Purschke 1988, Tzetlin and Zhadan 2009, Beermann *et al.* 2011). The axial pharynx includes epithelial, glandular, and sensory cells and an only weakly developed musculature. Comparable pharynges are known from other annelids with a similar style of life, e.g., Opheliidae or Paraonidae (Tzetlin and Zhadan 2009). Ventral pharyngeal organs have been studied in detail, and according to their fine structure, these organs have been classified into six types (Tzetlin and Filipova

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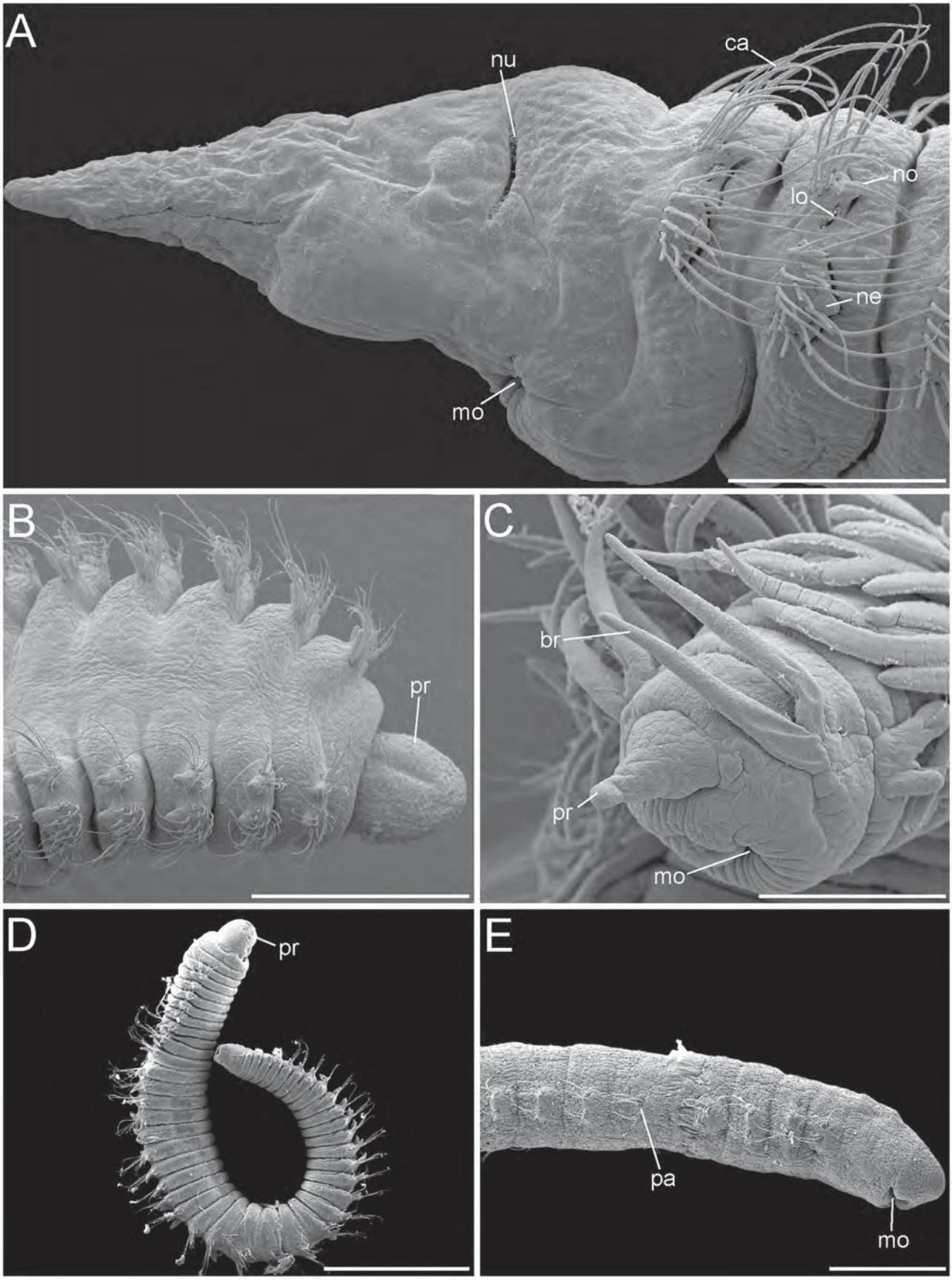


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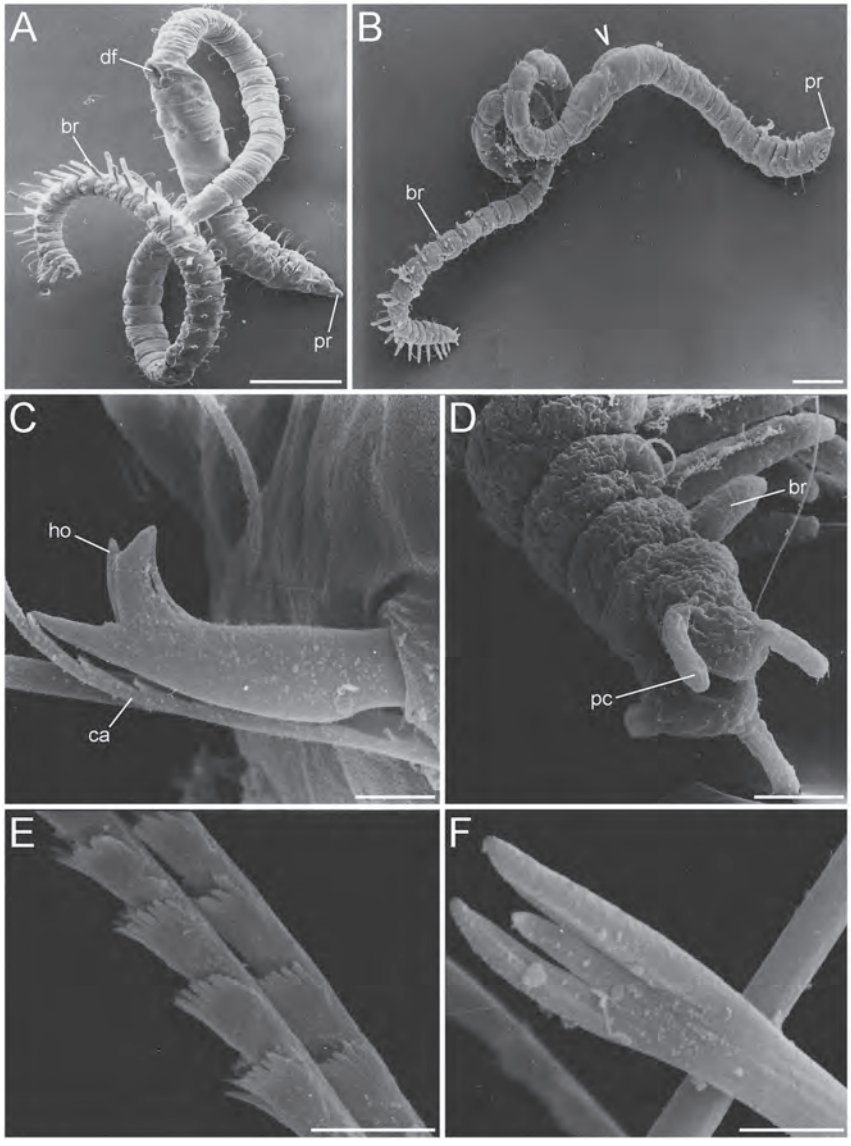


**Fig. 7.1.4.2:** Scanning electron microscopy (SEM) micrographs of different questid Orbiniidae. A, *Questa bicirrata*. Male worm. Note the dorsal fold on the segments 13–14. B, *Questa paucibranchiata*. Female worm with swollen ovigerous segments (v). C, *Questa trifurcata*. Hooked and capillary chaetae. D, *Questa mediterranea*. Pygidium with a ventral and dorsal pair of pygidial cirri (pc). E, *Q. mediterranea*. Capillary chaeta. F, *Questa trifurcata*. Trifurcate chaeta in the dorsal bundle of the fifth segment. br, branchiae; ca, camerated capillary chaeta; df, dorsal fold; ho, hooked chaeta; pc, pygidial cirrus; pr, prostomium. Reproduced with permission from the publisher. Anterior is right in A and B. Scale bar in A and B = 300 µm, in C = 3 µm, in D = 30 µm, in E and F = 3 µm. Micrographs are modified from Giere and Erseus (1998).

2005). The ventral pharynx of orbiniids belongs to type I, the most common type found among annelids. In the muscular bulb, transverse muscle fibers are separated by rows of interstitial cells. The muscular bulbus is followed by a tongue-like organ. Epithelial cells in these tongue-like organs often show a high secretory activity. The cuticles of the bulbus epithelium, as well as of the epithelium of the tongue-like organ of *S. armiger*, exhibit tooth-like structures (Purschke 1988). Interestingly, as already shown by Eisig (1914), juveniles of many larger orbiniid species possess a ventral pharynx, which is later replaced by the axial pharynx in adults. This suggests a progenetic origin of many small orbiniid genera (e.g., *Protoaricia*, *Proscoloplos*, and *Questa*), as those usually also possess a ventral pharynx (Helm *et al.* 2015). The orbiniid pharynx (proboscis) is often lobed or branched and can be everted due to changes in hydrostatic pressure.

◂ **Fig. 7.1.4.1:** Scanning electron microscopy (SEM) micrographs of different Orbiniidae. Anterior is left in A and C, anterior is right in B and E, and up in D. Scale bar in A = 300 µm, in B and E = 500 µm, and in C and D = 1 mm. A, *Scoloplos acmeceps*, anterior end. Note the prominent nuchal organ (nu). B, *Naineris robusta*, anterior end. The prostomium (pr) is marked out vigorously. C, *Methanoaricia dendrobranchiata*, anterior end. Note the distinct branchiae (br). D, *Protoaricia oerstedii*, whole animal. E, *Orbiniella nuda*, anterior end. br, branchia; ca, camerated capillary chaetae; lo, lateral organ; mo, mouth opening; no, notopodium; ne, neuropodium; nu, nuchal organ; pa, parapodium; pr, prostomium.

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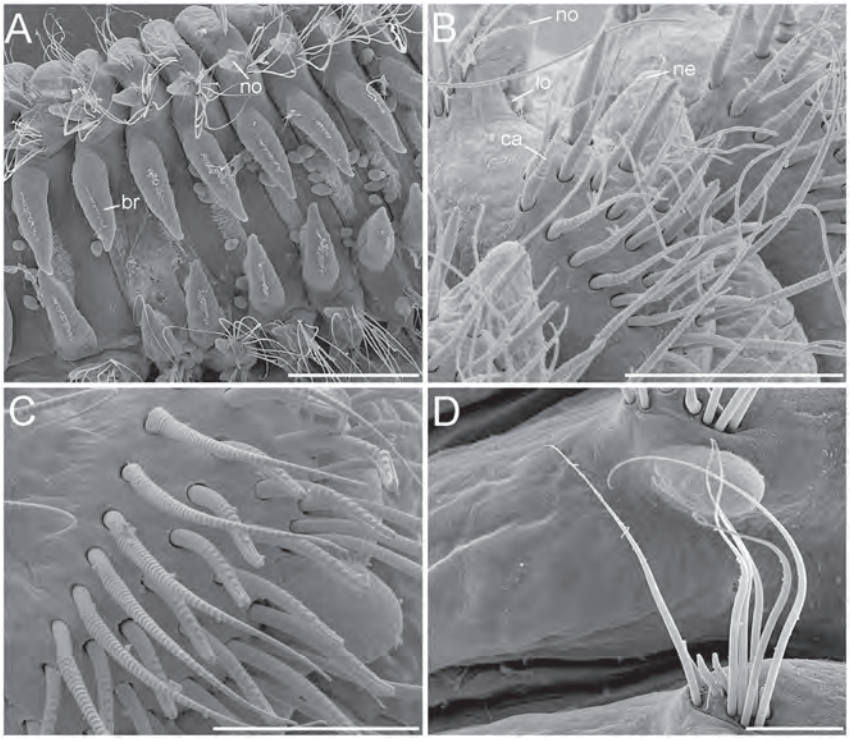


**Fig. 7.1.4.3:** Scanning electron microscopy (SEM) micrographs of prominent orbiniid structures. A, *Protoaricia oerstedii*, dorsal view showing the distinct branchiae (br). B, *Naineris robusta*. Note the distinct lateral organ (lo). C, *Scoloplos acmeceps*. Detailed micrograph showing the camerated capillary chaetae. D, *Protoaricia oerstedii*. Detailed micrograph showing the camerated capillary chaetae. ca, camerated capillary chaeta; br, branchiae; lo, lateral organ; ne, neuropodium; no, notopodium. Scale bar in A = 300 µm, in B = 100 µm, in C = 50 µm and in D = 30 µm.

**Musculature.** The musculature is characterized by the presence of an outer, complete circular muscle ring and a well-developed inner longitudinal musculature, which forms two ventral and two dorsal bundles (Fig. 7.1.4.4 C, D). Moreover, inner transversal muscles can be found in thoracal segments (Fig. 7.1.4.4 C). A cup-shaped assemblage of muscle fibers around its brain is reported for *P. cygnochaetus*, a feature that has not been found in other annelids so far (Helm *et al*. 2015).

**Blood vascular system.** Orbiniids possess a closed circulatory system including dorsal and ventral longitudinal vessels (Eisig 1914). The circulatory system of *Questa* shows some peculiarities with a prominent antecerebral loop, which was recorded for *Questa trifurcata* and *Q. paucibranchiata*, as well as a series of circumintestinal blood vessels in restricted anterior segments (Giere and Riser 1981, Giere and Erseus 1998). Metanephridia are used as excretory organs in adults and are usually distributed along the body (Eisig 1914, Bartolomaeus and Quast 2005). Larvae of *S. armiger* bear a pair of protonephridia, the so-called head kidneys, which are composed of three multiciliary cells: terminal cell, duct cell, and nephroporus cell (Bartolomaeus 1998). Most orbiniids possess pairs of dorsally located branchiae along the body. The starting point is variable and is often used as a diagnostic character to distinguish species. With the exception of branched branchiae in *Methanoaricia* (Fig. 7.1.4.1 C), orbiniid (and questid) branchiae usually form a single branch and are often ciliated (Fig. 7.1.4.3 A). They contain two blood vessels, a central one that is delimited through epithelia and an intraepidermal vessel; both are connected through thin capillaries (Eisig 1914). Some smaller species, as for example *Orbiniella nuda*, are reported to lack branchiae completely (Hobson 1974).

**Nervous system and sense organs.** The orbiniid brain consists of a large neuropile, which is connected to the ventral nerve cord due to the circumesophageal connectives (Orrhage 1966, Wilkens and Purschke 2009, Helm *et al*. 2015). These form a wide arc around the mouth. In the prostomium, each connective splits up into two roots, and each root is subdivided into two commissures (Fig. 7.1.4.4 A, B). Interestingly, palp nerve roots are visible even though no palps are present, indicating the loss of these structures. The ventral nerve cord consists of two main nerves, a pair of paramedian nerves, and a single median nerve in larvae of *S. armiger* (Orrhage and Müller 2005). These nerves are fused in adults and a pair of ganglia can be found in each segment. The position of the ventral nervous system changes during development in *S. armiger*. It is located intraepidermally in early stages. Older stages show a basiepidermal but still intraepithelial position, whereas a subepidermal location is found in adults (Anderson 1959,

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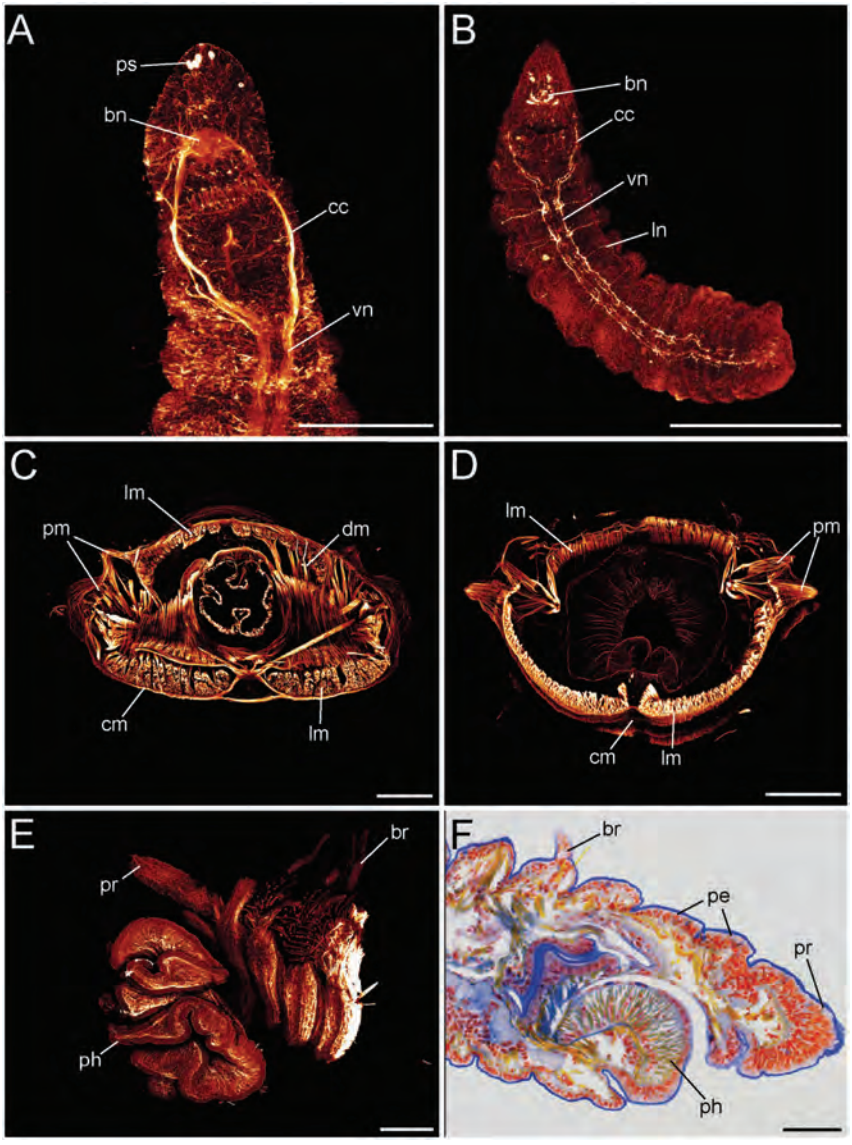


**Fig. 7.1.4.4:** Neuronal and muscular organization in Orbiniidae. Labeling with antityrosinated tubulin (A), antidopamine (B), phalloidin-rhodamine (C–E), and azan-staining (F): confocal maximum projections (A–E) and light microscopic image (F). Anterior is up in A and B, left in E, and right in F. Dorsal is up in C, D, and F. A and B are in lateral view, C and D are cross-sections. E is in lateral view. F is a sagittal section. A, 20-day-old juvenile of *Scoloplos armiger*. Note the phaosomes (ps) at the anterior end. B, 20-day-old juvenile of *S. armiger*. C, Anterior cross-section of an adult *Naineris* cf. *bicornis*. Note the prominent dorsoventral muscle fibers (dm). D, Posterior cross-section of an adult *N.* cf. *bicornis*. No prominent dorsoventral muscle fibers (dm) are visible. E, Anterior end of *N.* cf. *bicornis*. The pharynx (ph) is everted. F, Anterior end of *Proscoloplos cygnochaetus*. Note the ventral orientation of the pharynx (ph). bn, brain; br, branchia; cc, circumesophageal connective; cm, circular muscle fiber; dm, dorsoventral muscle fiber; lm, longitudinal muscle fiber; ln, lateral nerve; pe, peristomium; ph, pharynx; ps, phaosome; pm, parapodial musculature; pr, prostomium; vn, ventral nerve. Scale bar in A = 100 µm, in B–F = 200 µm.

Helm *et al.* 2015). Consistent with the hypothesis of heterochronic evolution, the location of the ventral nerve cord in adult *P. cygnochaetus* individuals is comparable with its position in juvenile *S. armiger* (Helm *et al.* 2015). A pair of pigmented eyes is located on the prostomium, in front of the nuchal organs in many orbiniid species. The ultrastructure of the eyes of *S. armiger* has been investigated, and each eye consists of a pigmented cell, a supportive cell, and three everse rhabdomeric sensory cells (Wilkens and Purschke 2009). Pigmented eyes are often only hardly visible in adults, as maybe the pigmentation or the whole structure is greatly reduced. Additionally, several ciliary phaosomes (Fig. 7.1.4.4 A) consisting of a single sensory cell enclosing a cavity are present in juvenile stages (Wilkens and Purschke 2009). Moreover, unpigmented rhabdomeric photoreceptor-like sense organs have been found in subadults *of S. armiger*. These organs are composed of a rhabdomeric receptor cell and an unpigmented supportive cell, which are interconnected via junctional complexes (Wilkens and Purschke 2009). Such organs, as well as true phaosomes, have been found in several other annelid taxa as well (Purschke *et al.* 2006). Orbiniids bear a pair of slit-like nuchal organs on both sides of the prostomium (Fig. 7.1.4.1 A). These organs lie in deep pits and are retractable. The nuchal organs are innervated by three nerves originating from different parts of the brain (Wilkens and Purschke 2009). As typical for polychaete annelids, the nuchal organs are composed of ciliated supporting cells, bipolar primary cells, and a retractor muscle (Rullier 1951). A space between the supporting cells is described

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as olfactory chamber, where processes of the sensory cells end. The cuticle covering the supporting cells is modified in orbiniids. The cuticle itself is strongly reduced and the presence of swollen microvilli tips gives this modified cuticle a paving-stone-like appearance (Koch 2005). Such a modified cuticle covering the nuchal organs is also known for other polychaetes, e.g., Protodrilida, Spionida, Paraonidae, and Capitellidae (Purschke 1997, Hausen 2001). Due to the structural similarity, a homology of this cuticle covers seems reasonable and might refer back to an origin in the last common ancestor of sedentary annelids. Additionally, most orbiniids bear dorsal organs, which are organized as paired fields of cilia. Interestingly, the ultrastructure of these organs is identical to that of the nuchal organs (Koch 2005), and consequently, a similar function as for the nuchal organs can be assumed. A serial homology of both types of organs has been already suggested by Rullier (1951) and is also known for Spionidae (Jelsing 2002). Lateral organs have been described for several Orbiniidae. These organs are composed of a brush of cilia and are located between neuro- and notopodium at the base of the notopodial lobe (Fig. 7.1.4.3 B) (Rullier 1951, Giere and Erseus 1998, Purschke and Hausen 2007). The ultrastructure of these organs has been investigated for *S. armiger*, where they consist of sensory cells, supportive cells, and muscle cells. Two types of receptor cells were found, a situation that is also found in lateral organs of many other annelids, and consequently, a homology is assumed (Purschke and Hausen 2007). In some orbiniids (e.g., *Orbinia* spp. and *Phylo* spp.), an interramal cirrus occurs instead of a ciliary brush, but a homology of both these structures is hypothesized (Eisig 1914). Some orbiniid species bear dorsally located statocysts, which are usually present in thoracal segments only and can be found at the base of branchiae, if a segment is bearing those (Eisig 1914), as for example in the genera *Naineris* and *Protoaricia*. Other species bear subpodial papillae (e.g., *Orbina* spp.). Eisig (1914) speculated about a possible function as a sensory organ for these papillae, as species that bear several of them usually lack statocysts and lateral organs. However, there are no ultrastructural investigations for these structures in Orbiniidae available yet.

**Reproduction and development**

Most orbiniids are gonochoristic, and external fertilization seems to be present in most species (Chapman 1965). Eisig (1914) speculates that *Naineris laevigata* might represent a protandric hermaphroditic species, as he found large size differences between ripe males and females, but this could not be confirmed in subsequent studies on the same species (Giangrande and Petraroli 1991). However, at least for *P. cygnochaetus*, asexual fissiparous reproduction has been demonstrated (Meyer *et al.* 2008), and the presence of many regenerating individuals has been reported, without finding any bearing eggs or sperms (Kelaher and Rouse 2003). Orbiniids have large yolky eggs, which usually range between 150 and 280 µm in diameter (Eckelbarger and Young 2002).

Most investigated orbiniids have, according to the classification of Jamieson and Rouse (1989), ect-aquasperms. However, the sperms of the deep-sea species *M. dendrobranchiata* show a highly derived morphology with their elongated nucleus and a greatly elongated and curved acrosome and are classified as ent-aquasperms (Eckelbarger and Young 2002). Jamieson (1983) described the ultrastructure of sperms of a questid species, which, according to their reproductive biology, should be regarded as introsperms, and found nine triads of accessory flagellar microtubules in the axoneme. Such an arrangement is found in no other annelid. Developing sperms are released into the coelom, where usually fully developed sperms as well as spermatids can be detected in ripe males (Giangrande and Petraroli 1991).

Both extraovarian and intraovarian oogenesis is reported for orbiniids, whereas the latter type seems to be commonly found in this taxon (Giangrande and Petraroli 1991, Eckelbarger and Young 2002). Reproduction might be restricted seasonally, even though continuous brooding is reported for some species (Blake 1993). Hardy (1977) studied the life cycle of the direct developing Antarctic species *Leodamas marginatus* and found that up to 3 years are required for development and reproduction, with mature females living at least 5 years.

Larval development has been described for several orbiniid species. The most detailed studies were conducted

▸ **Fig. 7.1.4.5:** Organization of ciliary bands in different larval stages of *Scoloplos armiger*. Labeling with antiacetylated tubulin; confocal maximum projections. Anterior is up, A and B are in lateral view, C–F are in ventral view. A, Early lecitotrophic trochophore at 1 dpf (days past fertilization). No distinct ciliary bands are formed. B, 3 dpf. Note the presence of ciliation at the prototroch (pt), the akrotroch (at), and the telotroch (tt). C, 4 dpf. The larval body starts to elongate and the ciliation increases. D, 5 dpf. First cilia (ci) anterior of the mouth opening and in the region of the neurotroch (nt) are visible. E, 6 dpf. Notably, the metatroch (mt) and the gastrotrochs (gt) start to develop. F, 7 dpf. The larvae are shortly before hatching and all ciliary bands are developed. The ciliary bands are named according to Anderson (1959). at, akrotroch; ci, cilia; gt 1–3, gastrotroch 1–3; mt, metatroch; nt, neurotroch; pt, prototroch; tt, telotroch. Scale bar in A and B = 100 µm, in C–F = 150 µm.

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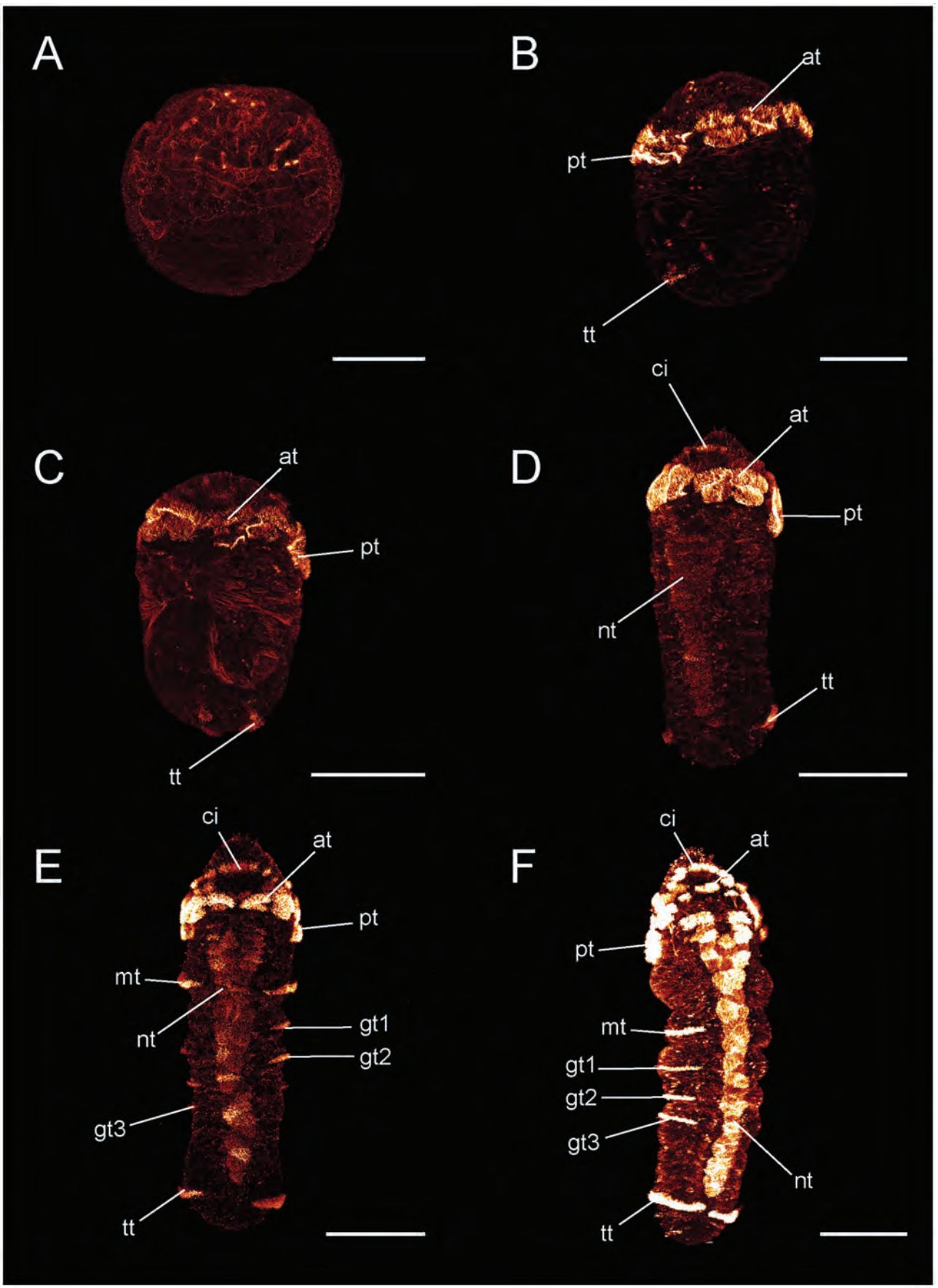


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for members of the *S. armiger* species complex. With the occurrence of lecitotrophic and planktotrophic larvae, two different types of development thought to be widespread in Orbiniidae can be found in closely related members of this species complex (Plate and Husemann 1991). Gelatinous egg cocoons, released from the glandular nephridopores of the females, are known to be present in several species, e.g., *Leitoscoplos pugettensis* and *S.* cf. *armiger* (Blake 1980). The presence of several protist species inside the cocoon is reported, and some authors suggest that they affect its viscosity (Gibbs 1968). Mature eggs undergo unequal spiral cleavage (Delsman 1916), and gastrulation results in a trochophore, bearing a prototroch, metratroch, and telotroch, as well as a neurotroch (Fig. 7.1.4.5 A–F).

In *S. armiger*, 12 embryonic trunk segments are developed before hatching, each bearing a mesodermal somite descended from the 4d cell, which will give rise to the coelomic cavities (Anderson 1959). Hatching occurs after between 1 and 22 days and results in the loss of cilia. The duration of the pelagic phase is up to 20 days. During the pelagic phase, 3–12 trunk segments are developed before settlement (Blake 1980). According to Anderson (1961), larvae do not feed during their planktonic phase. All species where the larval development was investigated are orbiniids, which show a single peristomal ring as adults. Interestingly, whereas this condition is already present in the juveniles of *Scoloplos* and *Leitoscoloplos*, juveniles of *Naineris* possess two peristomal rings, which seem to fuse later to a single one in adults (Giangrande and Petraroli 1991).

The reproductive biology of the interstitial genus *Questa* is remarkably similar to clitellates. Both sexes in this genus have gonads limited to few anterior segments and also show external genitalia (Giere and Riser 1981). Females bear a glandular epidermis in restricted anterior segments (Fig. 7.1.4.2 B), which was homologized with the clitellum of the Clitellata by some authors (Almeida *et al.* 2003). The males bear sperm sacs in segments 10–12, which are connected to gonopores, which open out into the so-called dorsal fold (Fig. 7.1.4.2 A), a cup-like dorsally located structure unknown for any other annelid. Reproductive behavior has not been observed so far; however, Giere and Riser (1981) speculate that it might be similar to those of oligochaetes. As such, it is hypothesized that males attach their cup-like dorsal fold (Fig. 7.1.4.2 A) to the spermathecal segments of females, which may produce a mucous slime to tighten the connection. Animals separate after filling of the spermathecae and the female secretes a gelatinous, lemon-shaped cocoon containing the mature eggs. A cocoon of *Q. trifurcata* inspected by Giere and Riser (1981) contained a single embryo that hatched after roughly a month, showing seven chaetigers. Interestingly, gland-like structures that might be related to a reproductive biology connected to copulation are also reported for male *Microrbinia linea* individuals (Blake 1993).

## Biology and ecology

Orbiniid species are globally distributed and can be found in all types of marine habitats, including brackish, intertidal, subtidal, mangrove, and deep-sea habitats. Many species inhabit sandy sediments in shallow waters, where they live as deposit feeders, some of which may be feeding selectively (Fauchald and Jumars 1979, Rice *et al.* 1986, Jumars *et al.* 2015). The interstitially living questids are regarded as epistrate feeders, and their guts have been often found filled with diatom shells, sand grains, and debris (Giere and Erseus 1998). The preferred habitat of orbiniids often correlates with the form of the prostomium, as those with a pointed prostomium (e.g., *Orbinia* spp.) are usually found in muddy sediments, whereas species with a rounded prostomium are often recorded between sandy sediments in algal holdfasts (e.g., *Naineris* spp.).

All orbiniids that have been investigated burrow by retrograde peristalsis, in which the wave of contraction travels opposite the direction of motion (Francoeur and Dorgan 2014). Parkinson (1978) investigated the burrowing behavior of *L. pugettensis* (named *Haploscoloplos elongatus* in his publication). Interestingly, it was shown that mainly the prostomium is used for burrowing, whereas the proboscis is everted only for deposit feeding. Francoeur and Dorgan (2014) found some differences in burrowing behavior between species with a rounded protostomium (*Naineris dendritica*) and a pointed prostomium (*Leitoscoloplos puggetensis* and *Orbinia johnsoni*).

Some species have been shown to play an important role as bioturbators (Giangrande *et al.* 2002). Temporal and spatial population dynamics were mainly studied for *S.* cf. *armiger* and *N. laevigata* (Gibbs 1968, Reise 1979, Giangrande and Fraschetti 1995, van der Meer *et al.* 2000). These species are reported to occur in densities of 100–500 individuals per $m^2$, with a peak in the summer. Juveniles of *S.* cf. *armiger* occur in small aggregates, which can conglomerate to larger ones and overlap with clusters of adult worms (Reise 1979). In the presence of lugworms (*Arenicola marina*), juvenile *Scoloplos* tend to aggregate near lugworm tail shafts. These are usually places with lower sulphide concentrations and an inflow of oxygen-rich water (Volkenborn and Reise 2006). Surprisingly, *S.* cf. *armiger* is quite intolerant to hypoxic conditions for an intertidal species, and individuals actively move

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into oxidized upper sediment layers during low tides (Schöttler and Grieshaber 1988).

The presence of some orbiniid species like *Phylo foetida* can be easily recognized by a strong garlic-like smell. First speculations that this odor is secreted by glands ("Wehrdrüsen") that are connected with the modified spines of this species ("Wehrstachel") were rejected by Eisig (1914). Instead, he was able to demonstrate that worms where segments containing these glands were amputated also spread the above described smell. It remains unclear if this smell is produced by the epidermis or if it is connected to the ingested sediment. No orbiniids are described from the fossil record (Rouse and Pleijel 2001). However, trace fossils of the *Chondrites* type have been shown to closely resemble burrows of *S. armiger* (Hertweck *et al.* 2007).

An interesting lifestyle is recorded for the deep-sea species *M. dendrobranchiata*. This species was discovered in the early 1990s to be widely distributed and associated with mussels (*Bathymodiolus childressi*) at deep-sea hydrocarbon seeps in the Gulf of Mexico (Blake 2000, Hourdez *et al.* 2001). The habitat is known to be strongly hypoxic, as well as sulfidic, and several adaptations to this unfriendly environment are described for *Methanoaricia*. As such, it has been observed that these worms extend their anterior body region above the mussels, in overlying, more oxygen-rich water (Hourdez *et al.* 2001). Especially the anterior body region is equipped with numerous branched and ciliated gills (Fig. 7.1.4.1 C). Fittingly, the anterior gills provide 90% of the total gill surface area in this species. Moreover, *Methanoaricia* shows a high hemoglobin-oxygen affinity and is able to withstand extended periods of anoxia (Hourdez *et al.* 2002). The brine pools also exhibit high salinity. *Methanoaricia* can tolerate short stays in this extreme environment but usually avoids them by aggregating on top of the mussel beds (Van Gaest *et al.* 2007).

Only few population genetic studies are available for orbiniids, mostly addressing the *S. armiger* species complex. *Scoloplos armiger*, originally described from Kristiansand (Norway), is a dominant macrofauna species reported in many ecological studies, showing a worldwide distribution with records as widely separated as American Pacific Coast, Central Europe, Russian White Sea, and Japan (Bleidorn *et al.* 2006). Moreover, as mentioned earlier, different reproductive modes have been reported for this species. First studies based on randomly amplified polymorphic DNA (RAPDs) have already shown genetic differences between intertidal and subtidal populations in the North Sea (Kruse *et al.* 2003). Subsequent studies using mitochondrial genes suggested an even greater number of so far unrecognized species, giving evidence for at least three species in the North Sea alone (Bleidorn *et al.* 2006, Luttikhuizen *et al.* 2011). These results are corroborated by analyses of a nuclear gene fragment (Bleidorn unpublished data), and species descriptions are partially in preparation (Kruse personal communication). In contrast to this, genetic and morphological analyses revealed that three *Proscoloplos* species from Australia, Chile, and France indeed seem to represent widespread members of a single species, namely, *P. cygnochaetus* (Meyer *et al.* 2008). It is highly likely that this distribution pattern stems from human transport by ships. Another report of an alien orbiniid species comes from Italy, where *Naineris setosa*, a species with a putative subtropical origin, was collected in high abundance from an aquaculture (Blake and Giangrande 2011). Interestingly, it seems that this species disappeared in this aquaculture, but new records were reported from the Western Mediterranean (Khedhri *et al.* 2014). A DNA barcoding study focusing on Canadian polychaetes revealed several molecular operational taxonomic units for *L. pugettensis*, indicating that this might be also a complex of several species (Carr *et al.* 2011). Sequence-based analyses (unpublished, GenBank Accession number KC460270) revealed that individuals usually referred to as *Orbinia bioreti*, which has been originally described from Madagascar and was repeatedly reported from the French Atlantic coast (Fauvel 1927, Dauvin *et al.* 2003), most likely are *Orbinia cornidei* (Rioja 1923), which has the Spanish Atlantic coast as type locality. This is of importance as the "French" *O. bioreti* has been included in some molecular systematic and morphological studies (Hausam and Bartolomaeus 2001, Bleidorn 2005, Bleidorn *et al.* 2009).

## Phylogeny and taxonomy

### Taxonomic history and phylogeny

The family Orbiniidae was formerly known as Ariciidae, a name given by Malmgren (1867) but reaching back to Audouin and Milne Edwards (1833), who introduced Ariciens. These names refer to the oldest generic name, *Aricia* Savigny, 1822, given to the species *Aricia sertulata* Savigny, 1822. Later, in his classification of annelids, Quatrefages (1865) transferred this species to the new genus *Orbinia*. Hartman (1936) recognized that the name *Aricia* was already preoccupied for a genus of lycanaeid butterflies, replaced *Aricia* with *Orbinia*, and later changed the family name to Orbiniidae (Hartman 1942). The first described orbiniid species is *S. armiger* (Müller, 1776). The Latin word *armiger* means "carrying weapons or armor," and Müller chose this name as he mistakenly misinterpreted the branchiae as kind of weapons.

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Several attempts to classify orbiinids have been proposed, and a detailed discussion of these can be found in Hartman (1957). Ørsted (1842) erected four groups, including species now referred to as Spionidae, Sphaerodoridae, Cirratulidae, and Opheliidae. Quatrefages (1865) was the first to include *Anthostoma* (now synonymized with *Naineris*) within Orbiniidae. Kinberg (1866a) included several newly described genera within this family (e.g., *Leodamas* and *Phylo*) but erected a new family Anthostomea for the genus *Anthostoma* (=*Naineris*). Czerniavsky (1881) divided the family into five genera and several new subgenera, of which presently *Protoaricia* is in use as a genus name. Mesnil and Caullery (1898) divided orbiniids into three groups, *Aricia*, *Scoloplos* s.str., and *Scoloplos* (*Nainereis*), using the shape of the prostomium for the distinction of the latter two. Further important works and additional species descriptions are given in an extensive revision mainly focusing on Mediterranean orbiniids by Eisig (1914), as well as in publications by Chamberlin (1919) and Fauvel (1927).

A comprehensive revision and classification of Orbiniidae can be found in Hartman (1957). She divided Orbiniidae into the two subfamilies: Orbiniinae (comprising those orbiniids with a single peristomial ring in adults) and Protoariciinae (comprising those with two peristomal rings in adults). Most of the included genera are still in use. Hartman (1957) already noticed that species of Protoariciinae are usually much smaller and slenderer than those of Orbiniinae. One of the genera included in Orbiniinae was *Haploscoloplos* Monro, 1933, which was part of some taxonomic confusion as the designated type species *Scoloplos cylindrifer* Ehlers, 1905 lacked the main diagnostic feature of this genus, namely, the absence of acicular spines in the thoracical neuropodia. Consequently, Day (1977) erected the new genus *Leitoscoplos* for the remaining species, and Mackie (1987) revised this genus, transferred some species to the genus *Scoloplos*, and acknowledged a putative polyphyly of *Leitoscoloplos*.

Solis-Weiss and Fauchald (1989) were the first to provide a cladistic analysis of orbiniids. They described two new genera of Protoariciinae (*Pararicia* and *Pettibonella*) and analyzed the phylogenetic relationships of this subfamily in general. However, the resolution was quite weak and the consensus tree shows several polytomies. Moreover, they based their analyses on the a priori assumption all the included genera as well as the subfamily are monophyletic. This view has been challenged in subsequent phylogenetic analyses of Orbiniidae. Describing the new and aberrant appearing orbiniid genus *Methanoaricia* discovered from deep-sea methane seeps, Blake (2000) conducted a cladistic analysis of all orbiniid genera. Based on a data matrix of 23 morphological characters, he found *Methanoaricia* to be the sister taxon of all other Orbiniidae, with the latter dividing into Microrbiniinae and Orbiniinae. The genus *Proscoloplos* has not been included in one of these subfamilies and branches off as part of a polytomy. The main distinction of these two subfamilies is the presence of different body regions (called thorax and abdomen) in Orbiniinae, which is lacking in Microrbiniinae. Nevertheless, as Blake (2000) assumed the monophyly of all included genera, which has been already seriously doubted by Mackie (1987), this classification was far from being stable.

Bleidorn *et al.* (2003) conducted the first molecular phylogenetic analyses including some Orbiniidae taxa and surprisingly found strong support for a close relationship of Orbiniidae and the enigmatic Questidae. Focusing on orbiniid relationships, Bleidorn (2005) found no support for the proposed classifications by Blake (2000) or Hartman (1957) when analyzing a dataset based on the 18S rRNA gene. Instead, a protoariciin and/or microrbiniin taxa cluster between members of the Orbiniinae and also a nested position of *Methanoaricia* could be shown. In a more comprehensive subsequent analysis, including more taxa and more genes, Bleidorn *et al.* (2009) found that *Questa* can be regarded as an orbiniid ingroup (Fig. 7.1.4.6). Moreover, nearly all orbiniid genera that are represented by more than one species appeared to be paraphyletic (*Leitoscoloplos*, *Leodamas*, *Orbinia*, *Phylo*, and *Scoloplos*). Moreover, an individual determined as *Protoariciella uncinata*, a genus of the former Protoariciinae, was found to be genetically identical with individuals from the orbiniin species *Leodamas tribulosus*. This is congruent with ideas from Blake (1996) that many species/genera of the Protoariciinae might be misidentified juvenile stages of Orbiniinae. However, for many other taxa of the former Protoariciinae, there is good evidence that they represent valid species, due to the presence of eggs/sperms or unique morphological features as, e.g., specialized chaetae in *Proscoloplos* and *Pettibonella*. As a progenetic origin is assumed for several of these species, a polyphyletic origin of protoariciin taxa is no surprise (Bleidorn 2005, Bleidorn *et al.* 2009).

Additionally, species which that been included with various representatives often showed distinct branch length differences (a proxy of genetic distance), pointing to so far unrecognized species complexes (e.g., *S. armiger*, *P. foetida*, and *L. pugettensis*). Previous studies have already shown in detail that the common and widely distributed species *S. armiger* represents a complex of many species (Kruse and Reise 2003, Kruse *et al.* 2003, Bleidorn *et al.* 2006, Luttikhuizen *et al.* 2011). In the phylogenetic system proposed by Bleidorn *et al.* (2009), six different major clades have been distinguished, with two *Leodamas* species representing the

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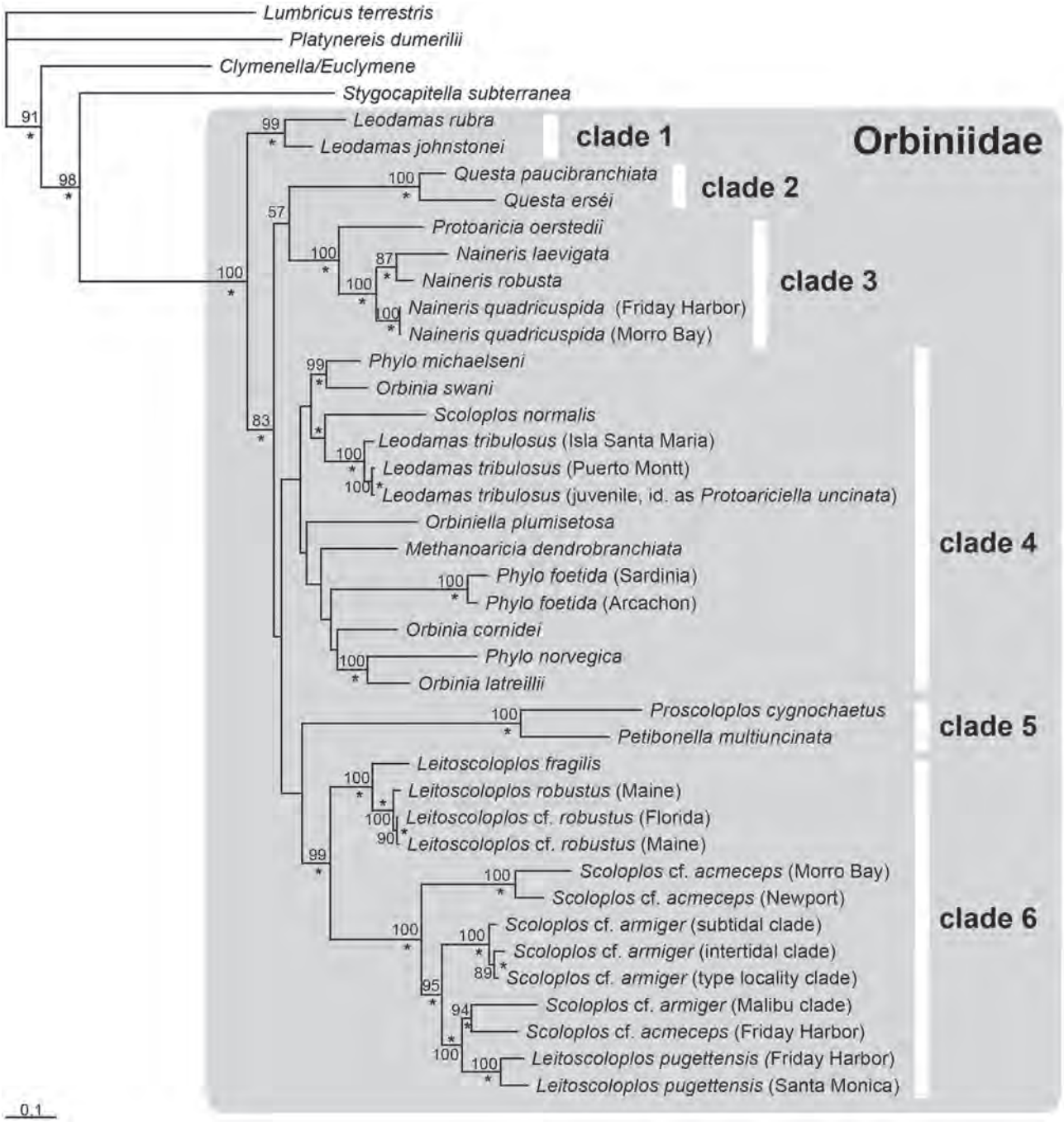


**Fig. 7.1.4.6:** Phylogenetic hypothesis of orbiniid relationships as in Bleidorn *et al.* (2009). Maximum likelihood analyses based on six concatenated gene fragments (*18S*, *16S*, *cox1*, *cox3*, *nad1*, and *nad4*) distinguish six orbiniid clades, without support for the monophyly of most genera, including more than one species in the analysis. Numbers at the nodes represent bootstrap values from 1,000 replicates; asterisks (*) indicate nodes that were supported by a posterior probability of >0.95 in the Bayesian analysis. Reproduced with permission from publisher.

sister taxon of all other orbiniids. However, the statistical support for many nodes is weak and additional data are urgently needed to gain a robust phylogeny.

Questidae featured a prominent role in the discussion about the origin of clitellates, as these polychaetes resemble them in features of their reproductive biology. Some authors used this superficial resemblance as a support for a sister-group relationship of questids and clitellates (Almeida *et al.* 2003, Christoffersen 2012). However, the homology of the clitellum-like structure

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in questids and the clitellum of the Clitellata has been seriously doubted in previous studies (Giere and Riser 1981, Giere and Erseus 1998). Analyzing mitochondrial gene order and analyzing a multigene dataset, Bleidorn *et al.* (2009) convincingly showed that questids are close relatives of orbiniids, and their phylogeny even supported a nested position within these. Recently, 10 valid questid species are accepted, all part of the genus *Questa*. *Periquesta canariensis* (Brito and Nunez 2002) is now regarded to be a member of the paraonid genus *Levinsenia* (Giere *et al.* 2008) and the monotypic genus *Novaquesta* (Hobson 1970) has been synonymized with *Questa* (Giere and Erseus 1998). The phylogenetic relationships of the genus *Questa* have been analyzed using morphological data matrices by Giere and Erseus (1998) and Giere *et al.* (2008). Unfortunately, the lack of useful parsimony-informative morphological characters results in a weak resolution.

Phylogenomic analyses recover Orbiniidae as part of the Sedentaria (Weigert *et al.* 2014). Interestingly, there is strong support for a grouping of Orbiniidae with several interstitial annelid taxa that have been formerly classified as Archiannelida (Struck *et al.* 2015). This taxon is called Orbiniida and comprises Orbiniidae, Parergodrilidae, Diurodrilidae, *Apharyngtus*, Nerillidae, and Dinophilidae. All these groups show a strong tendency of progenetic evolution, which might have started from an orbiniid-like ancestor. The sister taxon of Orbiniidae are Parergodrilidae (Struck *et al.* 2015).

**Taxonomy**

Currently, 204 orbiniid species belonging to 20 genera are described (see Fig. 7.1.4.7 for an overview showing most of the genera). However, given the caveats of unrecognized species diversity and the paraphyly of most genera, as shown by phylogenetic analyses, these numbers have to be taken with a grain of salt. Many originally locally described species have been later synonymized, suggesting a transoceanic distribution pattern for many species (e.g., Hartman 1948). However, molecular studies usually suggest a much more restricted occurrence of species (Bleidorn *et al.* 2006). For example, we do not follow synonymizing *Naineris robusta* Moore, 1909 with *Naineris denritica* (Kinberg, 1866b) (see also Andrade *et al.* 2015). Moreover, the obviously recurrent pattern of independent progenetic evolution within Orbiniidae complicates systematic and taxonomic studies.

The monotypic genus *Falklandiella* was originally described as part of an unnamed family "near Orbiniidae" (Hartman 1967) and later rendered as *incertae sedis* (Fauchald 1977). Nevertheless, the presence of camerated capillaries clearly supports an inclusion within Orbiniidae, and subsequently this genus was synonymized with *Orbiniella* (Buzhinskaja 1992, Gillet 1999). The genus *Orbiniella* shows a heterogeneous appearance and might be polyphyletic. Some authors exclude *O. branchiata* Hartman, 1967, which differs from all other species of this genus by having a peristomium forming three rings and bearing branchiae, from this genus without giving an alternative classification (Gillet 1999, Parapar *et al.* 2015). *Orbiniella drakei* Hartman, 1967 differs from all other member of this genus by having a body separated into different body regions and has been transferred to *Leitoscloplos* (see Blake 2017). However, we included *Scoloplosia minima* (Rullier, 1972) as part of *Orbiniella*, as it fits the genus diagnosis. This genus clearly needs revision, but for practical purposes, both species (*drakei* and *minima*) are included in this genus here. The monotypic genus *Scoloplella* (Day, 1963) is regarded here as undistinguishable from juveniles of the genus *Leitoscoloplos* and consequently synonymized. Diagnoses for all accepted genera are given in the following.

**Orbiniidae Hartman, 1942: 57**

**Diagnosis:** Long and cylindrical body, often separated into thorax and abdomen; prostomium without appendages, either pointed or rounded; peristomium forms up to three rings; eyes absent or present; parapodia generally biramous or vestigial, abdominal parapodia can be shifted dorsally; pairs of branchiae may be present dorsal to parapodia; chaetae usually simple, may include camerated capillary chaetae, furcate chaetae, bifid crotchets, or acicular spines. Pygidium small and collar-like, with up to several pairs of cirri or cirri absent.

▸ **Fig. 7.1.4.7:** Illustrations of orbiniid genera. A, *Berkeleyia profunda*, anterior end and chaetae of abdominal parapodia (redrawn after Hartman 1971). B, *Leodamas minutus,* anterior end (redrawn after Lopez *et al.* 2003). C, *Orbinia oligopapillata,* anterior end (redrawn after Lopez *et al.* 2006). D, *Scoloplos normalis,* anterior end (redrawn after Glasby 2000). E, *Leitoscoloplos kerguelensis,* anterior end (redrawn after Hartman 1957). F, *Phylo felix,* anterior end and modified spine (redrawn after Hartman 1957). G, *Califia schmitti,* anterior end and brush-topped chaeta (redrawn after Pettibone 1957). H, *Methanoaricia dendrobranchiata,* anterior end (redrawn after Blake 2000). I, *Naineris robusta,* anterior end (redrawn after Blake 1996). J, *Protoariciella oligobranchia,* anterior end (redrawn after Hobson 1976). K, *Orbiniella andeepia,* anterior end (redrawn after Narayanaswamy and Blake 2005). L, *Protoaricia pigmentata,* anterior end (redrawn after Solis-Weiss and Blake 1989). M, *Pettibonella multiuncinata,* anterior end and swan-shaped hooks (redrawn after Solis-Weiss and Blake 1989).

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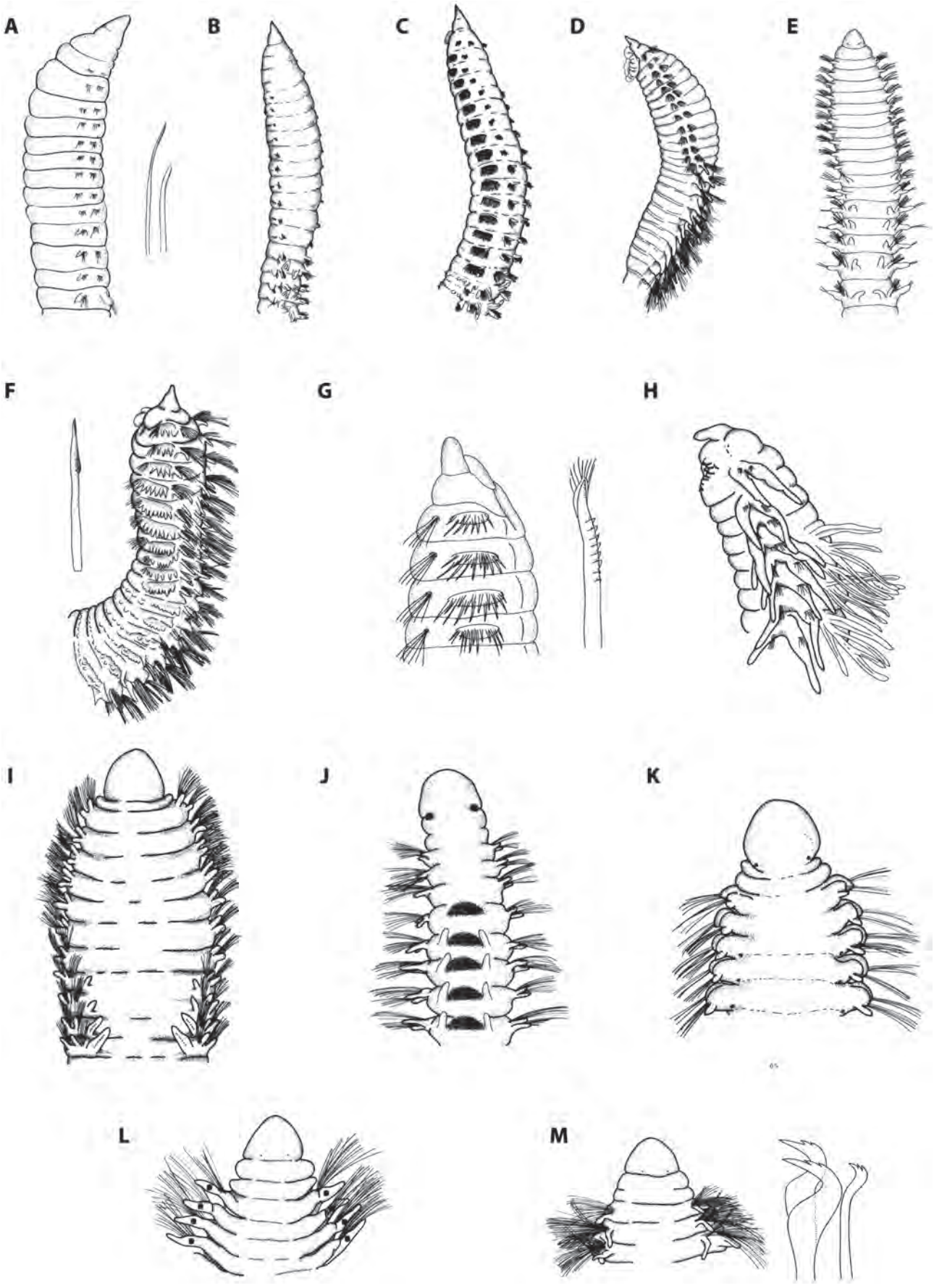


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***Berkeleyia* Hartman, 1971: 1409**
**Type species:** *Berkeleyia profunda* Hartman, 1971
Five species
**Diagnosis:** Prostomium pointed, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; thoracic parapodia with camerated capillaries only; abdominal parapodia with camerated capillaries, furcate chaetae present or absent, and acicular spines.

***Califia* Hartman, 1957: 305**
**Type species:** *Califia calida* Hartman, 1957
Four species
**Diagnosis:** Prostomium triangular, peristomium forming one ring; body separated into thorax and abdomen; branchiae present, not before segment 8; chaetae as camerated capillaries, brush-topped chaetae and acicular spines.

***Leitoscoloplos* Day, 1977: 218**
**Type species:** *Haploscoloplos bifurcatus* Hartman, 1957
30 species
**Diagnosis:** Prostomium pointed, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; thoracic parapodia with camerated capillaries only, abdominal parapodia with camerated capillaries, furcate chaetae might be present.

***Leodamas* Kinberg, 1866: 252**
**Type species:** *Leodamas verax* Kinberg, 1866
26 species
**Diagnosis:** Prostomium pointed, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; abdominal parapodia with large and numerous acicular spines accompanied by few or no camerated capillaries and sometimes with furcate chaetae.

***Methanoaricia* Blake, 2000: 439–440**
**Type species:** *Methanoaricia dendrobranchiata* Blake, 2000
Monotypic
**Diagnosis:** Prostomium narrow, elongated, rounded anteriorly; peristomium forming one ring; no body regions separated; branchiae branched, with numerous dichotomies, reduced to single unbranched branchiae posteriorly; parapodia bearing camerated capillaries and narrow pointed spines; pygidium with several long cirri.

***Microrbinia* Hartman, 1965: 129**
**Type species:** *Microrbinia linea* Hartman, 1965
Monotypic
**Diagnosis:** Prostomium conical; peristomium forming one ring; no body regions separated; branchiae absent; parapodia bearing camerated capillaries and acicular spines.

***Naineris* Blainville, 1928: 490–491**
**Type species:** *Nais quadricuspida* Fabricius, 1780
23 species
**Diagnosis:** Prostomium rounded or truncate, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; parapodia bear camerated capillaries and acicular spines, furcate chaetae may be present in abdominal parapodia.

***Orbinia* Quatrefages, 1865: 288**
**Type species:** *Aricia cuvierii* Audouin and Milne Edwards, 1833
22 species
**Diagnosis:** Prostomium pointed, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; posterior thoracic parapodia with several accessory papillae and numerous ventral papillae; parapodia bear camerated capillaries and acicular spines, furcate chaetae may be present in abdominal parapodia.

***Orbiniella* Day, 1954: 22–23**
**Type species:** *Orbiniella minuta* Day, 1954
15 species
**Diagnosis:** Prostomium rounded or conical, peristomium forming two or three rings; no body regions separated or body separated into thorax and abdomen; branchiae absent or present; parapodia bearing camerated capillaries and sometimes acicular spines; pygidium has few or no anal cirri.

***Paraorbiniella* Rullier, 1974: 58.**
**Type species:** *Paraorbiniella paucibranchiata* Rullier, 1974
Monotypic
**Diagnosis:** Prostomium rounded, peristomium forming two rings; no body regions separated; branchiae present, starting on chaetiger 6 and restricted to three to five segments; parapodia with camerated capillaries, some with curved acicular spines; five achaetous segments, pygidium with four anal lobes.

***Pararicia* Solis-Weiss and Fauchald, 1989: 789**
**Type species:** *Pararicia beliziensis* Solis-Weiss and Fauchald, 1989
Monotypic
**Diagnosis:** Prostomium rounded, peristomium forming two rings; no body regions separated; branchiae present;

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parapodia with camerated capillaries and furcate chaetae, some abdominal parapodia with acicular spines; pygidium with four anal cirri.

***Pettibonella* Solis-Weiss and Fauchald, 1989: 785**
**Type species:** *Pettibonella multiuncinata* Solis-Weiss and Fauchald, 1989
Two species
**Diagnosis:** Prostomium rounded, peristomium forming two rings; body regions separated into thorax and abdomen; branchiae present; parapodia with camerated capillaries and acicular spines, some posterior parapodia bear additional swan-shaped chaetae; pygidium with four anal cirri.

***Phylo* Kinberg, 1866: 251**
**Type species:** *Phylo felix* Kinberg, 1866
13 species
**Diagnosis:** Prostomium pointed, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; posterior thoracic parapodia with several accessory papillae and numerous ventral papillae; parapodia bear camerated capillaries and acicular spines, furcate chaetae may be present in abdominal parapodia; some thoracic parapodia bear modified spines.

***Proscoloplos* Day, 1954: 21**
**Type species:** *Proscoloplos cygnochaetus* Day, 1954
Monotypic
**Diagnosis:** Prostomium rounded, peristomium forming two rings; no body regions separated; branchiae present; parapodia with camerated capillaries, some posterior parapodia bear additional swan-shaped chaetae; pygidium with four anal cirri.

***Protoaricia* Czerniavsky, 1881: 372**
**Type species:** *Aricia oerstedii* Claparède, 1864
Three species
**Diagnosis:** Prostomium rounded, peristomium forming two rings; body regions separated into thorax and abdomen; branchiae present, only on abdominal segments; parapodia with camerated capillaries and acicular spines; pygidium with four anal papillae or anal cirri absent.

***Protoariciella* Hartmann-Schröder, 1962: 133–134**
**Type species:** *Protoariciella uncinata* Hartmann-Schröder, 1962
Six species
**Diagnosis:** Prostomium rounded, peristomium forming two rings; no body regions separated; branchiae present; parapodia with camerated capillaries and acicular spines; anal cirri absent.

***Questa* Hartman, 1966: 197**
**Type species:** *Questa caudicirra* Hartman, 1966
10 species
**Diagnosis:** Prostomium triangular, peristomium forming one ring; no body regions separated; branchiae absent or present; parapodia vestigial, with camerated capillaries and bifid crotchets; external genital region visible, dorsal fold in segments 13–14(15) in mature males, egg region (segments 12–13) swollen in mature females; pygidium bilobed, with or without pairs of cirri.

***Schroederella* Laubier, 1962: 232**
**Type species:** *Schroederella pauliana* Laubier, 1962
Three species
**Diagnosis:** Prostomium pointed, peristomium forming two rings; body regions separated into thorax and abdomen; branchiae present, only on abdominal segments; parapodia with camerated capillaries and acicular spines; pygidium with dorsal anus, four anal lobes present.

***Scoloplos* Blainville, 1828: 493**
**Type species:** *Lumbricus armiger* Müller, 1776
36 species
**Diagnosis:** Prostomium pointed, peristomium forming one ring; body separated into thorax and abdomen; branchiae present; abdominal parapodia with large and numerous acicular spines accompanied by several capillaries and sometimes with furcate chaetae.

***Uncorbinia* Hartmann-Schröder, 1979: 132**
**Type species:** *Uncorbinia brevibranchiata* Hartmann-Schröder, 1979
Monotypic
**Diagnosis:** Prostomium rounded, peristomium forming one ring; body separated into thorax and abdomen; branchiae present, in abdominal segments only; first four chaetigers with notopodia only, bearing acicular spines; remaining parapodia with camerated capillaries and acicular spines.

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## References

Almeida, W.O., Christoffersen, M.L., Amorim, D.S., Garrafoni, A.R.S. & Silva, G.S. (2003): Polychaeta, Annelida, and Articulata are not monophyletic: articulating the Metameria (Metazoa, Coelomata). *Revista Brasileira de Zoologia* 20: 23–57.

Anderson, D.T. (1959): The embryology of the polychaete *Scoloplos armiger*. *Quarterly Journal of Microscopical Science* 100: 89–166.

Anderson, D.T. (1961): The development of the polychaete *Haploscoloplos fragilis*. *Quarterly Journal of Microscopical Science* 102: 257–272.

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Audouin, J.V. & Milne Edwards, H. (1833): Classification des Annélides et description de celles qui habitent les côtes de la France. *Annales des sciences naturelles, Paris ser.* 1, 29: 388–412.

Bartolomaeus, T. (1998): Head kidneys in hatchlings of *Scoloplos armiger* (Annelida: Orbiniida): implications for the occurrence of protonephridia in lecithotrophic larvae. *Journal of the Marine Biological Association of the United Kingdom* 78: 183–192.

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

Beermann, A., Giere, O. & Purschke, G. (2011): Ultrastructure of the ventral pharynx in the interstitial annelid *Questa paucibranchiata* (Orbiniidae) and its phylogenetic significance. *Zoomorphology* 130: 167–180.

de Blainville, H.M.D. (1828): *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement a l'utilité qu'en peuvent retirer la médicine, l'agriculture, le commerce et les arts. Suivi d'une biographie des plus célèbres naturalistes*. F.G. Levrault, Strasbourg & Paris.

Blake, J.A. (1980): The larval development of Polychaeta from the Northern California coast. IV. *Leitoscoloplos pugettensis* and *Scoloplos acmeceps* (Family Orbiniidae). *Ophelia* 19: 1–18.

Blake, J.A. (1993): Life history analysis of five dominant in faunal polychaete species from the Continental slope off North Carolina. *Journal of the Marine Biological Association of the United Kingdom* 73: 123–141.

Blake, J.A. (1996): Family Orbiniidae Hartman, 1942. In: Blake, J.A., Hilbig, B. & Scott, P.H. (eds.) *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel, Vol. 6: The Annelida, Part 3: Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara, CA: 1–26.

Blake, J.A. (2000): A new genus and species of polychaete worm (Family Orbiniidae) from methane seeps in the Gulf of Mexico, with a review of the systematics and phylogenetic interrelationships of the genera of Orbiniidae. *Cahiers De Biologie Marine* 41: 435–449.

Blake, J.A. (2017): Polychaeta Orbiniidae from Antarctica, the Southern Ocean, the Abyssal Pacific Ocean, and off South America. *Zootaxa* 4218: 1–145.

Blake, J.A. & Giangrande, A. (2011): *Naineris setosa* (Verrill) (Polychaeta, Orbiniidae), an American subtropical-tropical polychaete collected from an aquaculture facility in Brindisi (Adriatic Sea, Italy): a possible alien species. *Italian Journal of Zoology* 78: 20–26.

Bleidorn, C. (2005): Phylogenetic relationships and evolution of Orbiniidae (Annelida, Polychaeta) based on molecular data. *Zoological Journal of the Linnean Society* 144: 59–73.

Bleidorn, C., Hill, N., Erseus, C. & Tiedemann, R. (2009): On the role of character loss in orbiniid phylogeny (Annelida): molecules vs. morphology. *Molecular Phylogenetics and Evolution* 52: 57–69.

Bleidorn, C., Kruse, I., Albrecht, S. & Bartolomaeus, T. (2006): Mitochondrial sequence data expose the putative cosmopolitan polychaete *Scoloplos armiger* (Annelida, Orbiniidae) as a species complex. *BMC Evolutionary Biology* 6: 47.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003): A contribution to sedentary polychaete phylogeny using 18S rRNA sequence data. *Journal of Zoological Systematics and Evolutionary Research* 41: 186–195.

Brito, M.D. & Nunez, J. (2002): A new genus and species of Questidae (Annelida: Polychaeta) from the central Macaronesian region and a cladistic analysis of the family. *Sarsia* 87: 281–289.

Buzhinskaja, G.N. (1992): *Orbiniella plumisetosa* sp. n. - first find of a polychaete of the subfamily Protoariciinae in the northwestern Pacific and characteristics of the genus Orbiniella (Polychaeta: Orbiniidae). In: Buzhinskaja, G.N. (ed.) *Polychaeta and Their Ecological Significance. Explorations of the Fauna of the Seas 43 (51)*. Zoological Institute, Russian Academy of Sciences, St. Petersburg: 76–81.

Carr, C.M., Hardy, S.M., Brown, T.M., Macdonald, T.A. & Hebert, P.D.N. (2011): A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLoS ONE* 6: e22232.

Chamberlin, R.V. (1919): New polychaetous annelids from Laguna Beach, California. *Pomona College Journal of Entomology and Zoology* 11: 1–23.

Chapman, G. (1965): Egg cocoons of *Scoloplos armiger* O.F. Müller. *Biological Bulletin* 128: 189–197.

Christoffersen, M.L. (2012): Phylogeny of basal descendants of cocoon-forming annelids (Clitellata). *Turkish Journal of Zoology* 36: 95–119.

Czerniavsky, V. (1881): Material ad zoographiam Ponticam comparatam. Fasc. III Vermes. *Bulletin de la Société Impériale des naturalistes de Moscou* 56: 338–420.

Dauvin, J.C., Dewarumez, J.M. & Gentil, F. (2003): Liste actuelisée de espéces d'Annelides Polychétes présentes en Manche. *Cahiers De Biologie Marine* 44: 67–95.

Day, J.H. (1954): The Polychaeta of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938*. 29: 1–35.

Day, J.H. (1963): The Polychaete fauna of South Africa. Part 8: new species and records from grab samples and dredgings. *Bulletin*

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

*of the British Museum (Natural History), Ser. Zoology* 10: 384–445.
Day, J.H. (1977): A review of the Australian and New Zealand Orbiniidae (Annelida: Polychaeta). In: Reish, D.J. & Fauchald, K. (eds.) *Essays on Polychaetous annelids in memory of Dr. Olga Hartman*. The Allan Hancock Foundation, University of Southern California: 217–246.
Delsman, H.C. (1916): Eifurchung und Keimblattbildung bei *Scoloplos armiger* O.F. Müller. *Tijdschrift van de Nederlandsche Dierkundige Vereeniging, Leiden* 2/14: 383–498.
Eckelbarger, K.J. & Young, C.M. (2002): Spermiogenesis and modified sperm morphology in the "seepworm" *Methanoaricia dendrobranchiata* (Polychaeta: Orbiniidae) from a methane seep environment in the Gulf of Mexico: implications for fertilization biology. *Biological Bulletin* 203: 134–143.
Eisig, H. (1914): Zur Systematik, Anatomie und Morphologie der Ariciden nebst Beiträgen zur generellen Systematik. *Mitteilungen aus der zoologischen Station zu Neapel* 21: 153–500.
Fauchald, K. (1977): The polychaete worms, definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County: Los Angeles, CA (USA) Science Series* 28: 1–188.
Fauchald, K. & Jumars, P.A. (1979): The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17, 193–284.
Fauvel, P. (1927): Polychétes sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. *Faune de France* 16: 1–494.
Francoeur, A.A. & Dorgan, K.M. (2014): Burrowing behavior in mud and sand of morphologically divergent polychaete species (Annelida: Orbiniidae). *Biological Bulletin* 226: 131–145.
Giangrande, A. & Fraschetti, S. (1995): A population study of *Naineris laevigata* (Polychaeta, Orbiniidae) in a fluctuating environment (Mediterranean Sea). *Scientia Marina* 59: 39–48.
Giangrande, A., Montresor, M., Cavallo, A. & Licciano, M. (2002): Influence of *Naineris laevigata* (Polychaeta: Orbiniidae) on vertical grain size distribution, and dinoflagellate resting stages in the sediment. *Journal of Sea Research* 47: 97–108.
Giangrande, A. & Petraroli, A. (1991): Reproduction, larval development and postlarval growth of *Naineris laevigata* (Polychaeta, Orbiniidae) in the Mediterranean Sea. *Marine Biology* 111: 129–137.
Gibbs, P.E. (1968): Observations on the populations of *Scoloplos armiger* at Whitstable. *Journal of the Marine Biological Association of the United Kingdom* 48: 225–254.
Giere, A., Ebbe, B. & Erseus, C. (2008): *Questa* (Annelida, Polychaeta, Orbiniidae) from Pacific regions – new species and reassessment of the genus *Periquesta*. *Organisms Diversity and Evolution* 7: 304–319.
Giere, O. & Erseus, C. (1998): A systematic account of the Questidae (Annelida, Polychaeta), with description of new taxa. *Zoologica Scripta* 27: 345–360.
Giere, O.W. & Riser, N.W. (1981): Questidae – polychaetes with oligochaetoid morphology and development. *Zoologica Scripta* 10: 95–103.
Gillet, P. (1999): A new species of *Orbiniella* (Orbiniidae: Polychaeta) from Marion Island, Indian Ocean. *Proceedings of the Biological Society of Washington* 112: 592–597.
Glasby, C.J. (2000): Family Orbiniidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.) *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia, Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 79–82.
Hardy, P. (1977) *Scoloplos marginatus mcleani*: life cycle and adaptations to the Antarctic benthic environment. In: Llano, G.A. (ed.) *Adaptations within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology*. Smithsonian Institution, Washington, DC: 209–226.
Hartman, O. (1936): Nomenclatural changes involving California polychaete worms. *Journal of the Washington Academy of Sciences* 26: 31–32.
Hartman, O. (1942): A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin of the Bingham Oceanographic Collection, Yale University* 8: 1–98.
Hartman, O. (1948): The marine annelids erected by Kinberg. With some notes on some other types in the Swedish State Museum. *Arkiv för Zoologi* 42A: 1–137.
Hartman, O. (1957): Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pacific Expeditions* 15: 211–393.
Hartman, O. (1965): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occasional Papers of the Allan Hancock Foundation* 28: 1–378.
Hartman, O. (1966): Quantitative survey of the benthos of San Pedro Basin, southern California. Part II. Final results and conclusions. *Allan Hancock Pacific Expeditions* 19: 187–455.
Hartman, O. (1967): Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas. *Allan Hancock Monographs in Marine Biology* 2: 1–387.
Hartman, O. (1971): Abyssal polychaetous annelids from the Mozambique Basin off southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. *Journal of the Fisheries Research Board of Canada* 28: 1407–1428.
Hartmann-Schröder, G. (1962): Zweiter Beitrag zur Polychaetenfauna von Peru. *Kieler Meeresforschungen* 18: 109–147.
Hartmann-Schröder, G. (1979): Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). Teil 2. IN: Hartmann-Schröder, G. and Gerd Hartmann. Zur Kenntnis des Eulitorals der australischen Küsten unter besonder Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 76: 77–218.
Hausam, B. & Bartolomaeus, T. (2001): Ultrastructure and development of forked and capillary setae in the polychaetes *Orbinia bioreti* and *Orbinia latreillii* (Annelida: Orbiniidae). *Invertebrate Biology* 120: 13–28.
Hausen, H. (2001): *Untersuchungen zur Phylogenie "spiomorpher" Polychaeten (Annelida)*. Logos, Berlin.
Helm, C., Krause, A. & Bleidorn, C. (2015): Immunohistochemical investigations of the development of *Scoloplos armiger* ("intertidalis clade") indicate a paedomorphic origin of *Proscoloplos cygnochaetus* (Annelida, Orbiniidae). *Invertebrate Biology* 134: 214–230.
Hertweck, G., Wehrmann, A. & Liebezeit, G. (2007): Bioturbation structures of polychaetes in modern shallow marine environments and their analogues to *Chondrites* group traces. *Palaeogeography Palaeoclimatology Palaeoecology* 245: 382–389.
Hobson, K.D. (1970): *Novaquesta trifurcata*, a new genus and species of the family Questidae (Annelida, Polychaeta) from

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Cape Cod Bay, Massachusetts. *Proceedings of the Biological Society of Washington* 83: 191–194.
Hobson, K.D. (1974): *Orbiniella nuda* new species (Orbiniidae) and 9 new records of other sedentariate polychaetous annelids from Washington and British Columbia. *Canadian Journal of Zoology* 52: 69–75.
Hobson, K.D. (1976): *Protoariciella oligobranchia* new species (Orbiniidae) and six new records of Orbiniidae, Questidae, and Paraonidae (Annelida, Polychaeta) from British Columbia. *Canadian Journal of Zoology* 54: 591–596.
Hoffmann, S. & Hausen, H. (2007): Chaetal arrangement in Orbiniidae (Annelida, Polychaeta) and its significance for systematics. *Zoomorphology* 126: 215–227.
Hourdez, S., Frederick, L.A., Schernecke, A. & Fisher, C.R. (2001): Functional respiratory anatomy of a deep-sea orbiniid polychaete from the Brine Pool NR-1 in the Gulf of Mexico. *Invertebrate Biology* 120: 29–40.
Hourdez, S., Weber, R.E., Green, B.N., Kenney, J.M. & Fisher, C.R. (2002): Respiratory adaptations in a deep-sea orbiniid polychaete from Gulf of Mexico brine pool NR-1: metabolic rates and hemoglobin structure/function relationships. *Journal of Experimental Biology* 205: 1669–1681.
Jamieson, B.G.M. (1983): The ultrastructure of the spermatozoon of the oligochaetoid polychaete *Questa* sp. (Questidae, Annelida) and its phjylogenetic significance. *Journal of Ultrastructure Research* 84: 238–251.
Jamieson, B.G.M. & Rouse, G.W. (1989): The spermatozoa of the Polychaeta (Annelida) – an ultrastructural review. *Biological Reviews of the Cambridge Philosophical Society* 64: 93–157.
Jelsing, J. (2002): Ultrastructural investigations on the cephalic and metameric nuchal organs of *Spio* cf. *filicornis* (Polychaeta, Spionidae). *Zoomorphology* 121: 213–220.
Jumars, P.A., Dogan, K.M. & Lindsay, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520.
Kelaher, B.P. & Rouse, G.W. (2003): The role of colonization in determining spatial patterns of *Proscoloplos bondi* sp nov (Orbiniidae: Annelida) in coralline algal turf. *Marine Biology* 143: 909–917.
Khedhri, I., Lavesque, N., Bonifacio, P., Djabou, H. & Afli, A. (2014): First record of *Naineris setosa* (Verrill, 1900) (Annelida: Polychaeta: Orbiniidae) in the Western Mediterranean Sea. *BioInvasions Records* 3: 83–88.
Kinberg, J.G.H. (1866a): Annulata nova. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* 22: 239–258.
Kinberg, J.G.H. (1866b): Annulata nova. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm* 23: 337–357.
Koch, C. (2005): *Ultrastruktur der Nuchal- und Dorsalorgane bei Scoloplos armiger (Annelida: Orbiniidae) und deren phylogenetische Bedeutung. Institut für Zoologie*. FU Berlin, Berlin: 45.
Kruse, I. & Reise, K. (2003): Reproductive isolation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae) indicates sibling species in the North Sea. *Marine Biology* 143: 511–517.
Kruse, I., Reusch, T.B.H. & Schneider, M.V. (2003): Sibling species or poecilogony in the polychaete *Scoloplos armiger*? *Marine Biology* 142: 937–947.
Laubier, L. (1962): *Schroederella pauliani* gen.nov., sp.nov., un nouvel orbiniide (polychètes sédentaires) de la faune interstitielle d'Afrique. *Annals of the Transvaal Museum* 2: 231–238.
Lopez, E., Cladera, P. & San Martin, G. (2003): Two new species of the genus *Leodamas* (Orbiniidae: Scolecida: Polychaeta) from the Pacific coast of Panama. *Journal of the Marine Biological Association of the United Kingdom* 83: 367–374.
Lopez, E., Cladera, P. & San Martin, G. (2013): Orbiniidae polychaetes (Polychaeta: Scolecida) from Coiba Island, eastern Pacific of Panama, with description of a new species. *Revista de Biologia Tropical* 54: 1307–1318.
Luttikhuizen, P.C., Bol, A., Cardoso, J. & Dekker, R. (2011): Overlapping distributions of cryptic *Scoloplos* cf. *armiger* species in the western Wadden Sea. *Journal of Sea Research* 66: 231–237.
Mackie, A.S.Y. (1987): A review of species currently assigned to the genus *Leitoscoloplos* Day, 1977 (Polychaeta, Orbiniidae), with descriptions of species newly referred to *Scoloplos* Blainville, 1828. *Sarsia* 72: 1–28.
Malmgren, A.J. (1867): Annulata Polychaeta Spitsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita. *Öfversigt af Koniglich Vetenskapsakademiens Forhandlingar* 24: 127–235.
Mesnil, F. & Caullery, M. (1898): Études de morphologie externe chez les Annélides. IV. La famille nouvelle des Leviséniens. Révisions des Ariciens – affinités des deux familles. Les Apistobranchiens. *Bulletin scientifique de la France et de la Belgique* 31: 126–151.
Meyer, A., Bleidorn, C., Rouse, G.W. & Hausen, H. (2008): Morphological and molecular data suggest a cosmopolitan distribution of the polychaete *Proscoloplos cygnochaetus* Day, 1954 (Annelida, Orbiniidae). *Marine Biology* 153: 879–889.
Müller, O.F. (1776): Zoologica Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characters, nomine, et synonyma imprimis popularium. Havniae.
Narayanaswamy, B.E. & Blake, J.A. (2005): A new species of *Orbiniella* (Polychaeta: Orbiniidae) from deep basins of Antarctica. *Journal of the Marine Biological Association of the United Kingdom* 85: 843–846.
Ørsted, A.S. (1842): Udtog af en Beskrivelse af Grönlands Annulata dorsibranchiata. *Naturhistorisk Tidsskrift* 4: 109–127.
Orrhage, L. (1966): Über die Anatomie des zentralen Nervensystems der sedentären Polychaeten – ein Beitrag zur Diskussion über die Architektur des Polychaeten-Gehirns und über den Begriff Palpen bei den Borstenwürmern. *Arkiv för Zoologi* 19: 99–133.
Orrhage, L. & Muller, M.C.M. (2005): Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536: 79–111.
Parapar, J., Moreira, J. & Helgason, G.V. (2015): First record of genus *Orbiniella* Day, 1954 (Polychaeta: Orbiniidae) in North Atlantic Ocean with the description of a new species. *Zootaxa* 4006: 330–346.
Parkinson, G.T. (1978): Aspects of feeding, burrowing, and distribution of *Haploscoloplos elongatus* (Polychaeta: Orbiniidae) at Bodega Harbor, California. *Pacific Science* 32: 149–155.
Pettibone, M.H. (1957): North American genera of the family Orbiniidae (Annelida: Polychaeta), with descriptions of new

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species. *Journal of the Washington Academy of Sciences* 47: 159–167.
Plate, S. & Husemann, E. (1991): An alternative mode of larval development in *Scoloplos armiger* (O.F. Müller, 1776) (Polychaeta, Orbiniidae). *Helgoländer Meeresuntersuchungen* 45: 487–492.
Purschke, G. (1988): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). V. The pharynges of the Ctenodrilidae and Orbiniidae. *Zoomorphology* 108: 119–135.
Purschke, G. (1997): Ultrastructure of nuchal organs in polychaetes (Annelida) – new results and review. *Acta Zoologica* 78: 123–143.
Purschke, G., Arendt, D., Hausen, H. & Müller, M.C.M. (2006): Photoreceptor cells and eyes in Annelida. *Arthropod Structure and Development* 35: 211–230.
Purschke, G. & Hausen, H. (2007): Lateral organs in sedentary polychaetes (Annelida) – ultrastructure and phylogenetic significance of an insufficiently known sense organ. *Acta Zoologica* 88: 23–39.
de Quatrefages, A. (1865): Note sur la Classification des Annelides. *Annales des sciences naturelles, Paris ser.* 5, t. 3: 253–296.
Reise, K. (1979): Spatial configurations generated by motile benthic polychaetes. *Helgoländer wissenschaftliche Meeresuntersuchungen* 32: 55–72.
Rice, D.L., Bianchi, T.S. & Roper, E.H. (1986): Experimental studies of sediment reworking and growth of *Scoloplos* spp. (Orbiniidae, Polychaeta). *Marine Ecology-Progress Series* 30: 9–19.
Rioja, E. (1923): Algunas especies de anelidos poliquetos de las costas de Galicia. *Boletín de la Real Sociedad Española de Historia Natural* 23: 333–345.
Rouse, G.W. & Pleijel, F. (2001): *Polychaetes*. Oxford University Press, New York.
Rullier, F. (1951): Étude morphologique, histologique et physiologique de l'organe nucal chez les annélides polychétes sédentaires. *Annales de l'insitut Océanographique de Monaco* 25: 207–341.
Rullier, F. (1974): Quelques annelides polychetes de Cuba recueillies dans des eponges. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa"* 14: 9–77.
Savigny, J.C. (1822): Système des annelides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les caractères tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Espèces. Description de l'Egypte. *Histoire Naturelle, Paris* 1: 1–128.
Schöttler, U. & Grieshaber, M. (1988): Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions. *Marine Biology* 99: 215–222.
Solis-Weiss, V. & Fauchald, K. (1989): Orbiniidae (Annelida, Polychaeta) from mangrove root-mats in Belize, with a revision of protoariciin genera. *Proceedings of the Biological Society of Washington* 102: 772–792.
Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015). The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.
Tzetlin, A.B. & Filipova, A.V. (2005): Muscular system in polychaetes (Annelida). *Hydrobiologia* 535/536: 113–126.
Tzetlin, A.B. & Zhadan, A. (2009): Morphological variation of axial non-muscular proboscis types in the Polychaeta. *Zoosymposia* 2: 415–427.
van der Meer, J., Beukema, J.J. & Dekker, R. (2000): Population dynamics of two marine polychaetes: the relative role of density dependence, predation, and winter conditions. *Ices Journal of Marine Science* 57: 1488–1494.
Van Gaest, A.L., Young, C.M., Young, J.J., Helms, A.R. & Arellano, S.M. (2007): Physiological and behavioral responses of *Bathynerita naticoidea* (Gastropoda: Neritidae) and *Methanoaricia dendrobranchiata* (Polychaeta: Orbiniidae) to hypersaline conditions at a brine pool cold seep. Marine Ecology 28: 199–207.
Volkenborn, N. & Reise, K. (2006): Lugworm exclusion experiment: responses by deposit feeding worms to biogenic habitat transformations. *Journal of Experimental Marine Biology and Ecology* 330: 169–179.
Weigert, A., Helm, M., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.
Wilkens, V. & Purschke, G. (2009): Pigmented eyes, photoreceptor-like sense organs and central nervous system in the polychaete *Scoloplos armiger* (Orbiniidae, Annelida) and their phylogenetic importance. *Journal of Morphology* 270: 1296–1310.

# 7.2 Sedentaria incertae sedis

Andrew S.Y. Mackie

## 7.2.1 Aberrantidae Wolf, 1987

### Introduction

Aberrantidae Wolf, 1987 is a family of small, free-living polychaete annelids found on muddy or sandy sediments from shallow shelf to several thousand meter depths (Hartman 1965, Wolf 1984, 1987, Mackie and Pleijel 1996, Mackie *et al*. 2005, Hilbig and Blake 2006, Santos and Rizzo 2013).

*Aberranta* was erected by Hartman (1965) for the aptly named *Aberranta enigmatica* found off New England, USA (300 m depth). The affinities of the species were unclear and she referred it to "Family unknown, near Spionidae" due to the presence of two large palps. Hobson (1971), examining shallower (68 m) material from the same region, augmented the description with additional information on the presence of a smooth median antenna, neuropodial lyriform chaetae, and lanceolate anal cirri, which possessed the same spindle-like inclusions as the postchaetal lobes (or dorsal and ventral cirri) figured by

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Hartman. Fauchald (1977) treated the genus as nonaffiliated pending new information.

Wolf (1984) discovered a second species from shallow (35–46 m) sands in the Gulf of Mexico and suggested that the genus may be intermediate to Paraonidae and Spionidae, noting also that the lyriform chaetae were similar to those found in paraonids. He pointed out that (contrary to Hartman's 1965 description) the grooved palps were ventral and not dorsal, as in spionids. This species was subsequently formally described (Wolf 1987) as *Aberranta palpata*, and Aberrantidae established on the basis of the palp position (now interpreted as lateral) and the presence of two achaetous peristomial segments; however, the relationships of the new family with other polychaetes were not discussed.

Mackie *et al*. (2005) described two further species, *Aberranta banyulensis* from shallow (32–80 m) detritus-laden muds off Banyuls-sur-Mer, Mediterranean France, and *Aberranta sulcata* from very shallow (4–9 m) silty sands northeast of Hong Kong, China. In addition, they reexamined both previously known species and emended the generic diagnosis to include annulated antennae (all except *A. palpata*?; see morphology), three achaetous "peristomial annuli" (all species), and a midventral pygidial papilla (all species). The elongate anterior achaetous region, ventrolateral grooved palps, one or three prostomial annulated antennae, and a pair of dorsolateral anal cirri of similar shape and structure (with large light-reflecting internal glands) to the dorsal and ventral parapodial cirri were distinctly nonspionid characteristics. Instead, the overall morphology, ciliation patterns, and ability to move by ventral ciliary motion suggested closer relationships with Nerillidae and/or some Eunicida. Combined morphological and molecular studies provided some support, albeit weak, for this (Worsaae *et al*. 2005).

## Morphology

Members of *Aberranta* are small delicate animals with subcylindrical bodies and up to about 40 similar biramous chaetigers, attaining a maximum length of almost 7 mm. The length and number of branchial pairs are highly correlated with the number of chaetigers. Antennae, parapodial cirri, and anal cirri are easily lost in preserved material. The anterior region is distinctive, with a small rounded prostomium, a pair of ventrolateral grooved palps, and an elongated achaetous "peristomium" comprising three annulations (Figs. 7.2.1.1 A and 7.2.1.2 A, B), the first reduced, visible dorsally as small subtriangular or subrectangular cushion-like shape. The prostomium dorsally bears one (*A. enigmatica* and *A. sulcata*) or three long annulated or pseudoannulated antennae (confirmed for all but *A. palpata*, where these were originally described as smooth); often these are lost in preserved material, their location revealed only by small contiguous stumps or scars (Fig. 7.2.1.2 A). They have one pair of lateral red-brown to black prostomial eyes (*A. palpata* and *A. banyulensis*), or eyes are absent. Nuchal organs are small, inconspicuous, and situated dorsolaterally at the junction between the prostomium and first peristomial annulus. Ventrally, the palp grooves converge medially and enter the upper region of the mouth, continuing inside as dorsolateral ciliated folds; the lower margin of the mouth is U shaped (Fig. 7.2.1.2 B). The buccal region has a ventral muscularized organ; jaws are absent. The pharynx is straight and muscular, reaching from the mouth to chaetiger 4; thereafter, the gut is a delicate straight tube, briefly widened at each intersegmental junction. Prostomium, palps, and palp grooves are highly ciliated. Living animals are transparent yellowish-brown with darker alimentary canal (Pleijel 2001). Preserved animals are white or yellowish white.

Chaetigerous segments have dorsal transverse ciliated bands (Fig. 7.2.1.2 A), anterior chaetigers have two bands, and median chaetigers have three bands. A single longitudinal midventral ciliated band is present (Fig. 7.2.1.2 B). Small lateral biramous parapodial lobes each bear single dorsal and ventral fusiform cirri positioned behind the chaetae (Fig. 7.2.1.1 C). Parapodial cirri are subequal in three species: the dorsal cirri in *A. palpata* are markedly larger than the ventrals. Each parapodial cirrus contains several large, longitudinally striated glands (Fig. 7.2.1.1 D); the fibers (?) therein are very light-reflective. The glands open on the cirri surfaces via small pores and show some similarity with the bacilliary glands found in certain members of other polychaete families (e.g., Syllidae, Nerillidae, Sabellidae, and Spionidae). Strap-like subcylindrical branchiae arise just superior to the notochaetae from chaetiger 3 or 4 for a variable number of segments; absent from the posterior region. The lateral and distal margins of the branchiae are conspicuously adorned with long cilia. The pygidium is small with a terminal anus and short midventral papilla (Fig. 7.2.1.1 F). A single pair of anal cirri, of similar shape and structure to parapodial cirri, arise dorsolaterally (Fig. 7.2.1.1 E, F), but are easily lost in preserved material.

Small conical or rounded noto- and neuropodia are each supported by two to four robust capillaries that originate more deeply in parapodia and are up to 1.5–2 times the thickness of other chaetae. Their emergent tips are short and finely tapered, with minute, barely visible (×1000 magnification) distal spinules (Fig. 7.2.1.1 G, *A. enigmatica*; *A. sulcata*) or with long conspicuous spinules (Fig. 7.2.1.1 I, *A. banyulensis*; *A. palpata*). All chaetae are

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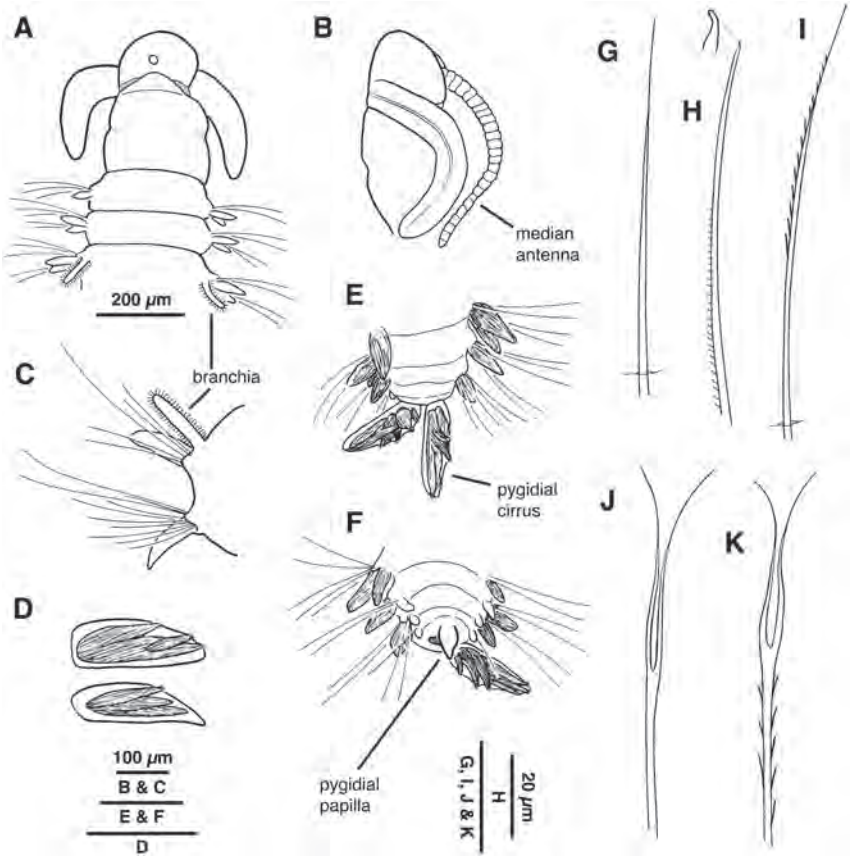


**Fig. 7.2.1.1:** *Aberranta* morphology. *Aberranta enigmatica*, nontype (A, C, D, USNM 158356; B, USNM 158369; E, F, USNM 158399; G, H, J, USNM 158329); *Aberranta banyulensis* (I, K, NMW.Z.1992.003.0027): A, Anterior region, dorsal, prostomial antenna missing. B, Anterior region, lateral. C, Chaetiger 11, anterior view. D, Parapodial cirri, chaetiger 11. E, Posterior region, dorsal. F, Posterior region, ventral (right pygidial cirrus missing). G, Support neurochaeta, chaetiger 12. H, Hooked neurochaeta, distal region, chaetiger 12. I, Neuropodial support capillary, chaetiger 12. J, Lyriform chaeta, distal region, chaetiger 12. K, Lyriform chaeta, distal region.

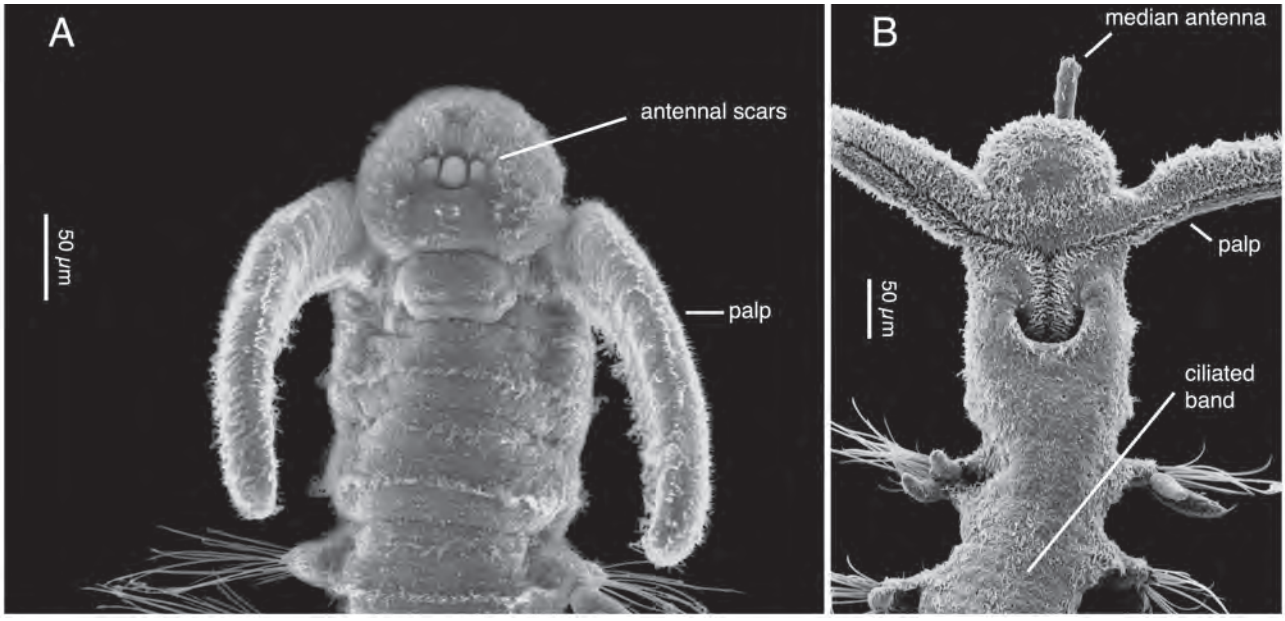


**Fig. 7.2.1.2:** Scanning electron micrographs of *Aberranta banyulensis*. A, Anterior dorsal view, antennae missing (photo courtesy Fredrik Pleijel). B, Anterior ventral view, lateral antennae missing, only basal part of median antenna present (photos courtesy Fredrik Pleijel).

simple; compound chaetae are absent. Notopodial capillaries are long and finely tapered. Neuropodia have long curved hook-tipped chaetae (Fig. 7.2.1.1 H) inferiorly and long lyriform chaetae superiorly. The internal margins of the latter have at least one tine with four to six barely visible spinulations. The convex margins of the long notochaetal capillaries and hooked neurochaetae have small (*A. enigmatica*, *A. sulcata*) or more conspicuous

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spinulations. Lyriform chaetae have smooth (Fig. 7.2.1.1 J, *A. enigmatica; A. sulcata*) or spinose (Fig. 7.2.1.1 K, *A. banyulensis*; *A. palpata*) shafts below the tines.

Segmental organs (*A. banyulensis*) appear to be typical metanephridial-based systems, with a funnel opening into the coelom. The sperm has a spherical head comprising a cap-like acrosome on spherical nucleus abutted by four rounded mitochondria; a pair of centrioles anchoring 9 + 2 axoneme. Mature males are whitish. Ovigerous females have rounded cuboid pink eggs, up to 125 µm in diameter.

## Biology and ecology

Live *A. banyulensis* in a Petri dish were observed to move by ciliary gliding. Nothing is known about their feeding, although it is likely that they graze the sediment surface. Jumars *et al*. (2015) postulated that aberrantids were "motile epibenthic and interstitial feeders using ciliated, grooved palps, the lower lip and the eversible pharynx to encounter and feed selectively on microbial films, microphytobenthos and rich organic detritus." No other biological or ecological data are available.

## Phylogeny and taxonomy

### Phylogeny

From the morphology of the four formally described species, there would seem to be grounds for separating *A. palpata* and *A. banyulensis* from *A. enigmatica* (type species) and *A. sulcata* based on the presence of three antenna (rather than one), lyriform chaetal shafts spinose (not smooth), and more spinose support chaetae. However, this could be premature since the morphological details of an additional four or five undescribed species are not yet fully known. These species are from the Irish Sea/Clyde Sea area (Rob Hensley and Myles O'Reilly personal communication, see Mackie and Erséus 1997; Tim Mackie personal communication), from off Southern California, USA (Richard Rowe personal communication 2003–2005), from 950–2750 m off the Gulf of the Farallones, California, USA (Hilbig and Blake 2006), a mussel bed on the Blake Ridge cold seep off South Carolina, USA (Jennifer Dreyer personal communication 2004), and 25–3250 m off Brazil (Santos and Rizzo 2013). Knowledge of many of these undescribed species has been hampered by the sparseness and/or fragmentary condition of the specimens available. Indeed, their fragility may well be a factor in the lack of aberrantid records from other Ocean regions.

Mackie and Pleijel (1996), Pleijel (2001), Rouse and Pleijel (2003), and Mackie *et al*. (2005) discussed the morphology of *Aberranta* and noted some similarities with Nerillidae and/or Eunicida. Rouse and Fauchald (1997) and Rouse and Pleijel (2001) categorized both *Aberranta* and Nerillidae as *incertae sedis* in Aciculata. One of the problems of morphological analyses concerns the interpretation of characters, for example, concerning the parapodial cirri of Aberrantidae (postchaetal structures or displaced dorsal and ventral cirri?) and single or double interramal cirri of Nerillidae (Worsaae 2005).

Worsaae *et al*. (2005) carried out analyses to examine the phylogenetic positions of Aberrantidae (*A. banyulensis*) and Nerillidae. Morphological and molecular analyses alone were each poorly resolved and provided no insight into the relationships of *Aberranta*. However, the combined morphological and molecular (18S rRNA) analysis indicated weak support for a Nerillidae-*Aberranta* clade, sister to Amphinomidae, with the Nerillidae-*Aberranta*-Amphinomidae clade sister to a predominantly Eunicid group. In a wider study, Zrzavý *et al*. (2009) examined the phylogeny of the Annelida using morphology and six genes, although no additional molecular data to that of Worsaae *et al*. (2005) were available. *Aberranta* was found to belong to one of the most basal clades, and sister to Amphinomida (Amphinomidae and *Euphrosine*), but the relationship and position remained "problematic."

### Taxonomy

#### Family Aberrantidae Wolf, 1987

#### Genus *Aberranta* Hartman, 1965

**Diagnosis:** (Modified from Mackie *et al*. 2005). Prostomium with dorsal median antenna. A pair of lateral antennae arises close to median, or absent. Antennae annulated or smooth. Prostomial eyes present laterally, or absent. Nuchal organs a pair of dorsolateral ciliated grooves. Palps ventrolateral, ventrally grooved, and heavily ciliated. Buccal region with dorsolateral ciliated folds confluent externally with palp grooves, and ventral muscularized organ. Three achaetous "peristomial annuli." Parapodia biramous, small, with fusiform parapodial cirri furnished internally with large light-reflective striated glands. Branchiae simple, strap-like, arising dorsally on notopodia from chaetiger 3 or 4 for variable number of segments. Midventral ciliated band present. Parapodia with several deeply originating, and distally emergent, capillary chaetae; embedded aciculae absent. Notochaetae capillary. Neurochaetae lyriform and distally hooked chaetae. Pygidium with mid-ventral papilla, and pair of dorsolateral cirri of similar shape and structure to parapodial lobes.

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The genus consists of four species: *A. enigmatica*, *A. palpata*, *A. sulcata*, and *A. banyulensis*.
**Type species:** *Aberranta enigmatica*

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**References**

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

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

Hilbig, B. & Blake, J.A. (2006): Deep-sea polychaete communities in the Northeast Pacific Ocean, off the Gulf of the Farallones, California. *Bulletin of Marine Science* 78(2): 243–269.

Hobson, K. (1971): Polychaeta new to New England, with additions to the description of *Aberranta enigmatica* Hartman. *Proceedings of the Biological Society of Washington* 84: 245–252.

Jumars, P.A., Dorgan, K.M. & Lindsay, S.M. (2015): Diet of Worms emended: an update of polychaete feeding guilds. Appendix A. Family-by-family updates. *Annual Review of Marine Science* 7: A1–A350.

Mackie, A.S.Y. & Erséus, C. (1997): Annelida. In: Howson, C.M. & Picton, B.E. (eds.) *The Species Directory of the Marine Fauna and Flora of the British Isles and Surrounding Seas*. 2nd ed. Ulster Museum and The Marine Conservation Society, Belfast and Ross-on-Wye: 103–136.

Mackie, A.S.Y. & Pleijel, F. (1996): The Aberrantidae (Polychaeta, Annelida): morphology, taxonomy and systematics, with the description of a new species from the Mediterranean. In: Mackie, A.S.Y. (ed.) *Taxonomy and Phylogeny of Spioniform Polychaetes (Annelida)*. PhD Thesis, Göteborgs Universitet, Göteborg: 1–18.

Mackie, A.S.Y., Pleijel, F. & Rouse, G.W. (2005): Revision of *Aberranta* Hartman, 1965 (Aberrantidae: Annelida), with descriptions of new species from the Mediterranean and Hong Kong. *Advances in Polychaete Research. A Tribute to Kristian Fauchald. Marine Ecology* 26: 197–208.

Pleijel, F. (2001): *Aberranta* Hartman 1965. In: Rouse, G.W. & Pleijel, F. (ed.) *Polychaetes*. Oxford University Press, Oxford: 175–176.

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

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

Rouse, G.W. & Pleijel, F. (2003): Problems in polychaete systematics. *Advances in Polychaete Research. Proceedings of the 7th International Polychaete Conference, Reykjavik, Iceland 2001. Hydrobiologia* 496: 175–189.

Santos, C. & Rizzo, A. (2013): A new species of *Aberranta* from Brazil and first occurrence of this genus from the Southern Hemisphere. p. 112 in *11th International Polychaete Conference, Australian Museum, 4–9 August 2013: Program and Abstract Book* (Poster Abstract).

Wolf, P.S. (1984): Family A. In: Uebelacker, J.M. & Johnson, P.G. (eds.) *Taxonomic guide to the polychaetes of the northern Gulf of Mexico VII. Final report to the Minerals Management Service, contract 14-12-001-29091*. Barry A. Vittor & Associates, Mobile, AL: 59.1–59.4.

Wolf, P.S. (1987): Aberrantidae: a new family of Polychaeta (Annelida). *Bulletin of the Biological Society of Washington* 7: 50–52.

Worsaae, K. (2005): Phylogeny of Nerillidae (Polychaeta, Annelida) as inferred from combined 18S rDNA and morphological data. *Cladistics* 21: 143–162.

Worsaae, K., Nygren, A., Rouse, G.W., Giribet, G., Persson, J., Sundberg, P. & Pleijel, F. (2005): Phylogenetic position of Nerillidae and *Aberranta* (Polychaeta, Annelida), analysed by direct optimization of combined molecular and morphological data. *Zoologica Scripta* 34: 313–328.

Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9–189: 1–14.

Markus Böggemann

## 7.2.2 Spintheridae Augener, 1913

### Introduction

Spintheridae Augener, 1913 is a small group of easily recognized ovate marine annelids. They are characterized by having notopodia forming long transverse ridges (Fig. 7.2.2.2 A) and a minute prostomium located well behind the frontal margin (Fauchald 1977, Fauchald and Rouse 1997).

Most of the spintherids are parasites or commensals on sponges (Glasby 2000), which they tend to match in coloration (Fig. 7.2.2.1 A; Jumars *et al*. 2015), and occur from cold shallow to bathyal waters but are also present in temperate and tropical waters. The family is known for a single genus, *Spinther* Johnston, 1845, in which just 13 species presently are described. However, the phylogenetic position of this group is still unresolved (Rouse and Fauchald 1997, Pleijel 2001, Andrade *et al*. 2015).

### Morphology

#### External morphology

**Color.** Living Spintheridae resemble their hosts and are therefore highly and variously colorful (Fig. 7.2.2.1 A), with

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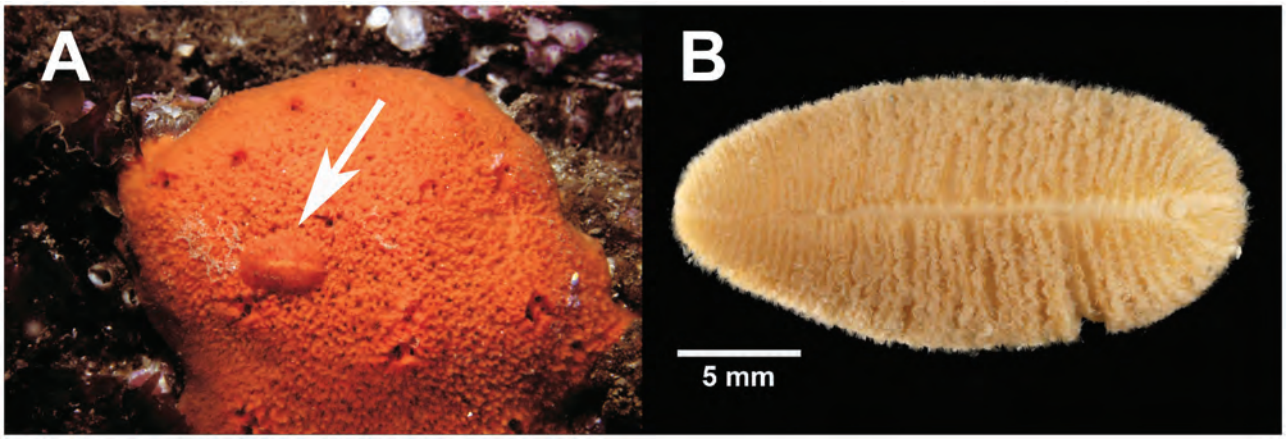


**Fig. 7.2.2.1**: A, *Spinther oniscoides* Johnston, 1845, living specimen (arrow) on sponge from Ria de Vigo, Galicia, Spain (©www.alamy.com). B, *Spinther citrinus* (Stimpson, 1854), preserved specimen from Eastport, ME, USA (YPM IZ 000845.AN), dorsal view (©E. Lazo-Wasem).

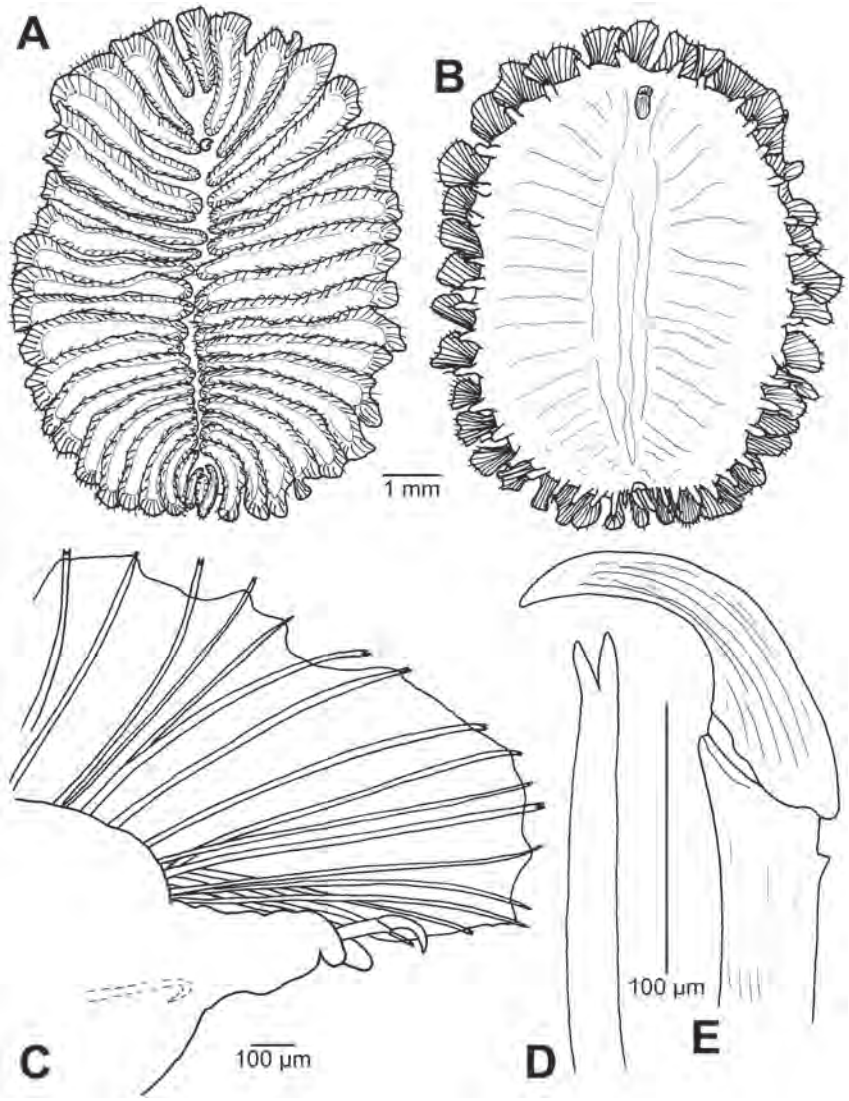


**Fig. 7.2.2.2:** *Spinther* cf. *oniscoides* Johnston, 1845 from Tromsø, Norway. A, Whole animal, dorsal view. B, Whole animal, ventral view. C, Parapodium of midbody, posterior view. D, Notopodial chaeta with bifid tip. E, Neuropodial compound hook.

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different shades of yellow, red, or brown (Grube 1860, von Graff 1887, 1888), and sometimes special pigmentation on the prostomium and notopodial lamellae (Stimpson 1854, Drasche 1885, Augener 1913, Fauvel 1923, Hartmann-Schröder 1996, Andrade *et al.* 2015), but pale when preserved (Fig. 7.2.2.1 B; Johnston 1845, Grube 1860, Sars 1862, Wirén 1883, Yamamoto and Imajima 1985, Imajima 2003). Species-specific color patterns seem to be absent (von Graff 1887, 1888).

**Size.** Spintherids are segmented annelids that can reach small to medium sizes (up to 50 mm long with 52 segments at most; Wirén 1883). The body is discodial as adults (Figs. 7.2.2.1 A, B and 7.2.2.2 A, B) and only slightly longer than wide (Jumars *et al.* 2015).

**Prostomium.** The prostomium is tiny and inconspicuous, carries a single median antenna (Figs. 7.2.2.1 B and 7.2.2.2 A) and is enveloped by a few anterior notopodia (Figs. 7.2.2.1 B and 7.2.2.2 A). The median antenna is contractible and varies in size and shape from conical to globular (von Drasche 1885). Four reddish-brown subepidermal eyes are usually present in quadrate arrangement around the basis of the antenna (von Graff 1887, 1888). These cup-shaped simple eyes consist of pigmented retinula cells without a lens but possible a vitreous body in the middle (von Drasche 1885, Graff 1887, 1888) and an outer cornea (von Graff 1887, 1888). However, Kornfeld (1915) found no refracting organs but great similarities to the direction and light intensity eyes of *Siphonostoma diplochaetos* (=*Flabelligera diplochaitos*) described by Hesse (1899). Nuchal organs are not present (Racovitza 1896, Rouse and Fauchald 1997), but ciliated pits on the anterior portion of the cephalic region are probably sensory (Racovitza 1896).

**Pharynx.** An unarmed, weakly muscular pharynx opens to a ventral mouth in adults (Fig. 7.2.2.2 B; Manton 1967, Jumars *et al.* 2015). It is withdrawn into a cavity and can protrude completely, without turning inside out (von Drasche 1885, Manton 1967, Dales 1977). This so-called proboscis is voluminous and soft but has a richly folded surface, often described as rosette or tongue like or funnel shaped (Fig. 7.2.2.2 B). Drasche (1885) mentioned cilia on the inner groove of the proboscis. According to Manton (1967), the probosis of *Spinther* is unique among annelids, although it resembles a planarian pharynx, but everted probably by fluid pressure as in most polychaetes.

**Peristomium.** Peristomium is interpreted as limited to lips (Fauchald and Rouse 1997, Rouse and Fauchald 1997, Pleijel 2001).

**Parapodia and chaetae.** The parapodia are all biramous (Fig. 7.2.2.2 C), with a few anterior and posterior ones directed forward and backward, respectively, whereas the others are laterally arranged in adult specimens (Figs. 7.2.2.1 B and 7.2.2.2 A) – a pattern that is similar to some amphinomids and euphrosinids. The notopodia form elongated transverse ridges (Figs. 7.2.2.1 B and 7.2.2.2 A–C) and are sometimes arranged in different long double rows (von Drasche 1885, Imajima and Hartman 1964), protecting the dorsum and flanks (Manton 1967). According to Drasche (1885), the rows are movable by muscles and numerous cilia are present at their basis. Graff (1887, 1888) investigated three taxa and pointed out species-specific differences in the arrangement of these dorsal lamellae, but he also found an intraspecific variation within *Spinther miniaceus* Grube, 1860. Furthermore, he observed a contractible sensory papilla ("Tastpapille") on the outer margins of the lamellae (von Graff 1887, 1888). A small gap remains free between the ridges of each side (Figs. 7.2.2.1 A, B and 7.2.2.2 A), creating a central longitudinal stripe that becomes narrower in larger animals (von Graff 1887, 1888). The lamellae are supported by numerous spine-like notochaetae (Fig. 7.2.2.2 C), which are arranged like waves, except at the later margin, where the chaetae are straight (Hartman 1948, Yamamoto and Imajima 1985). The notochaetae are sometimes different in length or diameter and they have uni- and/or bifid tips (Fig. 7.2.2.2 D). The neuropodia are cylindrical, might be annulated (von Graff 1887, 1888), and some of the taxa have a short, cirriform extension distally (Fig. 7.2.2.2 C). One to several neurochaetae (up to eight, Yamamoto and Imajima 1985) are present in each neuropodium, but usually only one or seldom two of these are externally visible, whereas the rest are embedded in the neuropodial lobe and in various stages of development (Fig. 7.2.2.2 C). The yellowish to golden neurochaetae are much thicker than the notochaetae and compound (Fig. 7.2.2.2 E). However, Manton (1967) described that the youngest of the reserve chaetae have no demarcation between blade and shaft. The blades are strongly hooked, and only *Spinther australiensis* Augener, 1913 has an additional large lateral tooth beneath the tip (Augener 1913). The shafts are terminally smooth, crenulated, triloped, or entire at tip (Hartman 1948). Up to 13 slender, tapering, and more transparent aciculae lie around the developing neurochaetae (von Drasche 1885, von Graff 1887, 1888). Branchiae are absent, but Graff (1887, 1888) postulated that the dorsal lamellae might function as respiratory organs.

## Anatomy

**Body wall.** The body is dorsally convex and ventrally flattened in the transverse section and the ventral surface is

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smooth (Fig. 7.2.2.2 B) or papillated. The papillae, if present, are minute warts, slender digitate or spherical in shape and randomly arranged or in more or less distinct patterns (von Graff 1887, 1888, McIntosh 1890, Riddell 1909, Hartman 1948, Imajima 2003). Underneath the thin cuticle and the partly more thickened epidermis (mouth, anus, antenna) lies a continuous musculature, which is usually weakly developed and composed of an outer circular and an inner longitudinal layer (von Drasche 1885, von Graff 1887, 1888). Only the longitudinal muscles of the underside are more well developed and might be responsible for the ventral curling of uncoupled living specimens (von Drasche 1885). Graff (1887, 1888) mentioned an additional third layer of inclined and crossed fibers in this region. Furthermore, muscle fibers are present, e.g., in the interfused segmental septa and as retractors for the parapodia, the chaetae, and the proboscis (von Drasche 1885, Manton 1967). Intersegmental septa are reduced, as in many other polychaete groups (Clark 1962, Manton 1967). The body cavity appears to be full of glandular and other tissue or cells (Manton 1967).

**Nervous system.** The nervous system, mentioned by Grube (1860) for the first time, consists of a brain that is positioned under the median antenna, two circumesophageal connectives, and a ventral nerve cord (von Drasche 1885, von Graff 1887, 1888). The latter structure is composed of two longitudinal nerves with segmentally arranged transverse commissures and weakly developed ganglia, connected with the parapodial ganglia via lateral nerves (von Drasche 1885, von Graff 1887, 1888). Additional nerves from the brain innervate antenna, eyes, esophagus, and proboscis (von Drasche 1885, von Graff 1887, 1888). Furthermore, scattered ciliated sensory cells are present on the whole surface of the animals (von Drasche 1885, von Graff 1887, 1888). According to Racovitza (1896), the cerebral ganglion is reduced due to the parasitic way of life.

**Blood vascular system.** The circulatory system comprises a strong dorsal vessel, which reaches from posterior to the brain, a weaker ventral trunk, and connecting segmental transverse vessels (von Drasche 1885, von Graff 1887, 1888). An excretory system is absent (von Drasche 1885, von Graff 1887, 1888).

**Digestive System.** The digestive tract of adult specimens started with a ventral mouth opening, located well behind the front margin (Fig. 7.2.2.2 B), and ends with a terminal anus on the pygidium (von Drasche 1885, von Graff 1887, 1888). It is separated into proboscis, esophagus, expansive midgut with numerous segmentally arranged diverticula, and short straight hindgut with a specific dorsal blind gut, which joins the intestine in front of the rectum (Grube 1860, von Drasche 1885, von Graff 1887, 1888, Riddell 1909). The pinnate arrangement of the midgut resembles the structures of Aphroditidae (Grube 1860, Fauvel 1923, Mackie *et al*. 2015).

**Pygidium.** The pygidium ends with a single pair of anal cirri (Fig. 7.2.2.2 B). These cirri vary in size and shape from minute warts, club-shaped, digitiform to globular and might be mobile (von Graff 1887, 1888).

### Reproduction and development

The sexes of Spintheridae are separated and the gametes of sexually mature worms fill the body cavity, the neuropodia, and the dorsal lamellae and are visible through the body wall (Grube 1860, von Drasche 1885, von Graff 1887, 1888, Núñez *et al*. 2011). Gametogenesis occurs in the body cavity, and especially in the males, the region of the dorsal blood vessel seems to be connected with the development of the sperms (von Drasche 1885, von Graff 1887, 1888). The largest brick-red eggs in the body of *S. miniaceus* are 80 µm in diameter and the sperms have a conical head with an acute tip of 3.7 µm length, two granules at the base, and a long tail of 57 µm (von Drasche 1885, von Graff 1887, 1888). Grube (1860) suggested that the gametes could be excreted from the body through neuropodial pores, whereas Graff (1887, 1888) mentioned a functional genital opening situated slightly above the anus. Ripe eggs released in seawater have short protoplasmic processes in the body, which elongate subsequently into structures like pseudopodia, somewhat symmetrically arranged as in a radiolarian (von Drasche 1885, von Graff 1887, 1888). These structures disappear shortly after release and therefore postulated by Graff (1887, 1888) to be organs that mediate the attachment of the eggs at the surface of the sponges.

Nothing is known about the larval development of spintherids, but Manton (1967) investigated a few juvenile stages of *Spinther arcticus* (Sars, 1851). She found that the proportions and shape of the body change with age and size, which also was mentioned by Graff (1887, 1888). The mouth is terminal in young specimens and becomes ventrally displaced during ontogeny (Manton 1967). Furthermore, in juveniles, only three pairs of notopodial ridges have swung forward laterally to lie anterior to the prostomium, and the anus is yet posteroventral although the anal lobes are dorsal in position (Manton 1967). With the increase in segment number, the rectum comes to occupy a more posterior position, the intestine becomes longer, more diverticula grow out, and the invaginated hook pouches are carried out to an extremely lateral position, far away from the median intestine and clear of its lateral diverticula (Manton 1967). The great width and flattened form of the adults with the semblance of radial symmetry is therefore a secondary condition

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developed during the life of each worm from an initial "normal" bilateral annelid morphology (Manton 1967).

## Biology and ecology

Most of the Spintheridae are described from cold waters of the Northern Hemisphere (George and Hartmann-Schröder 1985, Hartmann-Schröder 1996), whereas only *Spinther australiensis* from Australia and *Spinther usarpia* Hartman, 1967 from the Antarctic Peninsula are recorded from the Southern Hemisphere (Augener 1913, Hartman 1967), although this may in part reflect collecting effort (Glasby 2000). Generally, the species are stenohaline, but some species occasionally invade polyhaline waters (Hartmann-Schröder 1996). Usually the spintherids live on the surface or in the oscula of sponges (Fig. 7.2.2.1 A), such as *Axinella damicornis*, *Desmacella arenifibrosa*, *Desmacidon* sp., *Esperella* (=*Mycale*) sp., *Halichondria panicea*, *Stylostichon* (=*Phorbas*) *plumosum*, and *Tedania anhelans* (von Drasche 1885, Hornell 1891, Racovitza 1896, Augener 1913, Campoy 1982, George and Hartmann-Schröder 1985, Hartmann-Schröder 1996, Núñez *et al*. 2011), some in association with hydroids (*Antennularia* (=*Nemertesia*) *ramosa*) (Hornell 1891, George and Hartmann-Schröder 1985, Martin and Britayev 1998, Molodtsova *et al*. 2016), whereas individuals of *Spinther wireni* Hartman, 1948 were also found in sand or on stones covered with algae (George and Hartmann-Schröder 1985). The majority of spintherids are known from the continental shelf but have also been reported from tubeworm colonies in hydrocarbon seeps on the central upper Louisiana slope of the Gulf of Mexico (Cordes *et al*. 2006) and from bathyal regions of the North Atlantic (Wesenberg-Lund 1950). Furthermore, specimens of *S. arcticus* were collected in warm waters of the Gulf of Suez (Fauvel 1933) and inside a submarine cave on the Canary Islands (Núñez *et al*. 2011). Additionally, a possible new taxon was collected from French Polynesia (Andrade *et al*. 2015).

Spintheridae are not often mentioned in the literature. They are either very rare or been overlooked because of having the same color as their host (Fig. 7.2.2.1 A; von Graff 1887, 1888, Hornell 1891, Dales 1963, Pettibone 1963, George and Hartmann-Schröder 1985, Hartmann-Schröder 1996, Jumars *et al*. 2015). Examination of the alimentary tract contents suggested that the spintherids feed on soft tissue of sponges (von Drasche 1885, von Graff 1887, 1888, Manton 1967). Only in one case, spicules of the sea cucumber *Holothuria tubulosa* were found (von Graff 1887, 1888). Predominantly, they are considered as carnivores or parasites (von Graff 1887, 1888, McIntosh 1894, Racovitza 1896, Augener 1913, Dales 1963, 1977, Pettibone 1963, Fauchald 1977, George and Hartmann-Schröder 1985, Hartmann-Schröder 1996, Fauchald and Rouse 1997, Pleijel 2001). However, it is also possible that they are kleptoparasites (Dunton and Schell 1987, Jumars *et al*. 2015) or live as commensals (Martin and Britayev 1998, Pleijel 2001) by scavenging dead parts of their host sponges (Fauchald and Jumars 1979) or feeding on the epibionts associated with the host (Glasby 2000). Curiously, spintherids themselves were found in diet samples of bowhead whales from the Bering Sea, together with copepods, euphausiids, fishes, and shrimps (Sheffield *et al*. 2008), but without any indication that sponges were eaten (Jumars *et al*. 2015).

Little is known about the specific behavior of the Spintheridae. Nevertheless, they are regarded as having a sedentary or weakly motile lifestyle, attached to the surface of their host by using clinging hooks (von Graff 1887, 1888, Augener 1913, Pettibone 1963, Manton 1967, George and Hartmann-Schröder 1985, Martin and Britayev 1998, Glasby 2000, Pleijel 2001, Jumars *et al*. 2015). The great battery of replacement hooks in each pouch (Manton 1967) indicates the importance of these organs. Augener (1913) described that spintherids making cavities in the issues of the sponges precisely match the contours of the animals. The ventral side of the spintherids also has a thicker musculature and more gland cells (von Drasche 1885, von Graff 1887, 1888), and the living animals can be removed from the substrate only by using a scalpel (von Drasche 1885). The very mobile proboscis will enable plenty of food matter to be reached without the need for much locomotory movement (Manton 1967).

## Phylogeny and taxonomy

Johnston (1845) established the genus *Spinther*, and he placed his supposedly exannulate and acephalous *Spinther oniscoides* Johnston, 1845 from Belfast Bay (Ireland) within Aphroditidaceæ. This was contested by Grube (1850), who supposed a closer relationship with Siphonostomae (=Flabelligeridae) or some Amphinomea. Sars (1851) and Stimpson (1854) preferred the latter group because they considered their new taxa *Oniscosoma arcticum* Sars, 1851 from the Komagfjord (Norway) and *Cryptonota citrina* Stimpson, 1854 from the Bay of Fundy (Canada) to be close to *Euphrosine*. This was followed by Johnston (1865) with a question mark. The two new genera were considered junior synonyms of *Spinther* by Grube (1860, 1861), Sars (1862), and most later authors, so that the family is accepted as monotypic until now. Racovitza (1894, 1895, 1896) pointed out, that *Spinther* cannot be the direct descendant of *Euphrosine* and that both genera form distinct branches from the stem of the Amphinomidae. Augener (1913), however, found sufficient differences to the *Euphrosine*-like taxa and

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erected the family Spintheridae, which in some points resembles Myzostomida as also noted by Graff (1887, 1888). Nevertheless, afterward, the spintherids often have been classified under Amphinomidae (Fauvel 1923, Treadwell 1937, Uschakov 1950, Wesenberg-Lund 1950) and Amphinomorpha (Clark 1969), or assigned to their own order (Fauchald 1977, George and Hartmann-Schröder 1985, Sardá 1985, Jussien *et al*. 1994, Hartmann-Schröder 1996, Imajima 2003). According to Sharov (1966), *Spinther* is an ancient and basal animal group, but the investigations of Manton (1967) provided no evidence to support Sharov's claims on the origin and evolution of Arthropoda. Graff (1887, 1888) already mentioned that the specific body plan is certainly a secondary adaptation to their special mode of life and not a primitive state. The probably convergent evolution of such highly specialized symbiotic annelids makes the determination of their systematic position complicated. Therefore, it was unsurprising that in the morphological phylogenetic analyses of Rouse and Fauchald (1997), the spintherids form a clade with Myzostomida or have a sister-group relationship with the amphinomids and euphrosinids. In their complete analysis, Aberrantidae, Nerillidae, and Spintheridae were placed as incertae sedis within the clade Aciculata (Rouse and Fauchald 1997), but further study is required to resolve this (Pleijel 2001). Recently, Andrade *et al*. (2015) found in molecular phylogenetic analyses that the spintherids mostly joined a clade including *Dinophilus*, Myzostomida, and *Osedax*, possibly owing to confounding long-branch effects. However, *Spinther* also appears to be related to the orbiniid *Naineris* and sometimes form a grade at the base of the Sedentaria (Andrade *et al*. 2015). This completely differs from the previous hypotheses, but aciculae and a ventral buccal organ are present in both groups; therefore, further morphological comparisons are needed (Andrade *et al*. 2015). In summary, more than 125 years after Graeff's (1887, 1888) conclusion ("Doch lässt sich heute noch nicht angeben, wo diese Ahnen der Gattung *Spinther* zu suchen sind"), the Spintheridae are still an enigmatic group of annelids with no obvious close relatives among extant families (Glasby 2000, Andrade *et al*. 2015).

Additional fossil taxa are unknown. Wade (1972) suggested that the Ediacaran *Dickinsonia* had an ancestral relationship to the spintherids. However, the resemblance is probably a product of parallel evolution (Conway Morris 1979) because *Dickinsonia* showed indeterminate growth and reached lengths of 1.4 m (Jenkins 1992, Retallack 2007).

**Family Spintheridae Augener, 1913**

**Genus *Spinther* Johnston, 1845**

**Type species:** *Spinther oniscoides* Johnston, 1845: 9

**Synonyms:** *Oniscosoma* Sars, 1851: 210

*Cryptonota* Stimpson, 1854: 35

**Diagnosis:** Body oval, convex dorsally, flattened ventrally, with ventral surface papillose or smooth (Figs. 7.2.2.1 A, B and 7.2.2.2 A, B). Prostomium tiny, inconspicuous, constricted by anterior segments, between the notopodial ridges and immediately over the ventral mouth; with a conical to globular median antenna (Figs. 7.2.2.1 B and 7.2.2.2 A), usually with two pairs of eyes at the base of the antenna. Proboscis voluminous, eversible, unarmed, rosette like, or funnel shaped (Fig. 7.2.2.2 B). Parapodia biramous (Fig. 7.2.2.2 C). Notopodia forming elongated transverse ridges covering the dorsum, except central longitudinal stripe, with delicate lamellae supported by numerous spine-like notochaetae in transverse rows (Figs. 7.2.2.1 B and 7.2.2.2 A–C). Notochaetae with uni- and/or bifid tips (Fig. 7.2.2.2 D). Neuropodia cylindrical, sometimes distally with a short, cirriform extension (Fig. 7.2.2.2 C). Each neuropodia with one to several, thick, compound neurochaetae, blades strongly hooked and shafts terminally smooth or serrated (Fig. 7.2.2.2 E). Neuroaciculae present. Single pair of pygidial cirri (Fig. 7.2.2.2 B).

The genus consists of 14 nominal species, in part confused due to potential synonymies (see McIntosh 1900, Hartman 1948, Uschakov 1955): *Spinther alaskensis* Hartman, 1948; *S. arcticus* (Sars, 1851); *S. australiensis* Augener, 1913; *S. citrinus* (Stimpson, 1854); *Spinther ericinus* Yamamoto & Imajima, 1985; *Spinther hystrix* Uschakov, 1950; *Spinther japonicus* Imajima & Hartman, 1964; *Spinther major* Levinsen, 1883; *S. miniaceus* Grube, 1860; *S. oniscoides* Johnson, 1845; *Spinther sagamiensis* Imajima, 2003; *S. usarpia* Hartman, 1967; *Spinther vegae* Augener, 1928; *S. wireni* Hartman, 1948; of which only 11 are recognized as valid.

Hansen (1880) gave a description of *S. arcticus* M. Sars, which was erected by Levinsen (1883) to the new species *S. major*. Graff (1887, 1888) examined Hansen's specimen and a specimen of *S. citrinus* from near the type locality (Bay of Fundy) and showed that both were identical, but unfortunately, he placed them under the name *S. oniscoides*. Riddell (1909) redescribed *S. oniscoides* and pointed out that Graff had misidentified *S. oniscoides* and that his specimens (including *S. major*) in fact belonged to *S. citrinus*.

*Spinther miniaceus* Grube, 1860 and *Spinther arcticus* Sars, 1851 were considered synonymous by Graff (1887, 1888), but he applied the junior name, which is against the rules of zoological nomenclature (Hartman 1948).

Wirén (1883) mentioned specimens of *S. arcticus* from the Vega expedition, but which, as he himself noted, differed in many respects from Sars' species. Nevertheless, the taxon was in use as a valid species name (von Graff 1887, 1888) until Augener (1928) proposed changing the name to *S. vegae*. This was ignored by Hartman (1948), who replaced

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the name with *S. wireni*. The description of *S. hystrix* by Uschakov (1950) shows great similarities to *S. vegae*/*wireni*, and this name may represent a junior synonym. However, an investigation of the type material is needed.

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## References

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Giribet, G. & Rouse, G.W. (2015): Articulating "Archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32(11): 2860–2875.

Augener, H. (1913): Polychaeta I, Errantia. In: Michaelsen, W. & Hartmeyer, R. (eds.) *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905*. Gustav Fischer Verlag, Jena 4(5): 65–304; pls. 2–3.

Augener, H. (1928): Die Polychäten von Spitzbergen. *Fauna Arctica* 5 (3): 647–834.

Campoy, A. (1982): Fauna de España. Fauna de Anélidos Poliquetos de la Península Ibérica. *Publicaciones de la Universidad de Navarra, Serie Zoológica* 7: 1–400.

Clark, R.B. (1962): On the structure and functions of polychaete septa. *Proceedings of the Zoological Society of London* 138(4): 543–578.

Clark, R.B. (1969): Chapter 1. Systematics and phylogeny: Annelida, Echiura, Sipuncula. In: Florkin, M. & Scheer, B.T. (eds.) *Chemical zoology. 4. Annelida, Echiura, Sipuncula*. Academic Press, New York: 1–68.

Conway Morris, S. (1979): Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Philosophical Transactions of the Royal Society of London, Series B* 285(1007): 227–274.

Cordes, E.E., Bergquist, D.C., Predmore, B.L., Jones, C., Deines, P., Telesnicki, G. & Fisher, C.R. (2006): Alternate unstable states: convergent paths of succession in hydrocarbon-seep tubeworm-associated communities. *Journal of Experimental Marine Biology and Ecology* 339: 159–176.

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

Dales, R.P. (1977): The polychaete stomatodeum and phylogeny. In: Reish, D.J. & Fauchald, K. (eds.) *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. The Allan Hancock Foundation, University of Southern California, Los Angeles: 525–546.

von Drasche, R. (1885): *Beiträge zur feineren Anatomie der Polychaeten. 1. Anatomie von Spinther miniaceus Grube*. Verlag von Carl Gerold's Sohn, Wien.

Dunton, K.H. & Schell, D.M. (1987): Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: $\delta^{13}C$ evidence. *Marine Biology* 93: 615–625.

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

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

Fauchald, K. & Rouse, G. (1997): Polychaete systematics: past and present. *Zoologica Scripta* 26(2): 71–138.

Fauvel, P. (1923): Polychètes Errantes. *Faune de France* 5: 1–488.

Fauvel, P. (1933): Résumé analytique du mémoire sur les Polychètes. *Bulletin de l'Institut d'Égypte* 15: 131–144.

George, J.D. & Hartmann-Schröder, G. (1985): Polychaetes: British *Amphinomida, Spintherida & Eunicida*. Keys and notes for the identification of the species. *Synopses of the British Fauna, New Series* 32: 1–221.

Glasby, C.J. (2000): Family Spintheridae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. Vol. 4. CSIRO Publishing, Melbourne: 171–172.

von Graff, L. (1887): Die Annelidengattung *Spinther*. *Arbeiten aus dem Zoologischen Institut zu Graz* 2(3): 75–140, pls. 1–9.

von Graff, L. (1888): Die Annelidengattung *Spinther*. *Zeitschrift für Wissenschaftliche Zoologie* 46(1): 1–66, pls. 1–9.

Grube, E. (1850): Die Familien der Anneliden. *Archiv für Naturgeschichte* 16(1): 249–364.

Grube, E. (1860): Beschreibung neuer oder wenig bekannter Anneliden. *Archiv für Naturgeschichte* 26(1): 71–118, pls. 3–5.

Grube, A.E. (1861): *Ein Ausflug nach Triest und dem Quarnero. Beiträge zur Kenntniss der Thierwelt dieses Gebietes*. Nicolaische Verlagsbuchhandlung, Berlin.

Hansen, G.A. (1880): Annelider fra den norske Nordhavsexpedition i 1878. *Nyt Magazin for Naturvidenskaberne* 25(3): 224–234, pls. 1–5.

Hartman, O. (1948): The polychaetous annelids of Alaska. *Pacific Science*, 2(1): 3–58.

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

Hartmann-Schröder, G. (1996): *Annelida, Borstenwürmer, Polychaeta. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise*, Gustav Fischer Verlag, Jena 2. Auflage, 58: 1–648.

Hesse, R. (1899): Untersuchungen über die Organe der Lichtempfindung bei niederen Tieren. V. Die Augen der polychäten Anneliden. *Zeitschrift für Wissenschaftliche Zoologie* 65(3):446–516, pls. 22–26.

Hornell, J. (1891): Report on the polychætous annelids of the L.M.B.C. district. *Proceedings and Transactions of the Liverpool Biological Society* 5: 223–268, pls. 13–15.

Imajima, M. (2003): Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo (II). Orders included within Phyllodocida, Amphinomida, Spintherida and Eunicida. *National Science Museum Monographs* 23: 1–221.

Imajima, M. & Hartman, O. (1964): The polychaetous annelids of Japan. Part I. *Allan Hancock Foundation Publications, Occasional Paper* 26: 1–237.

Jenkins, R.J.F. (1992): Chapter 5. Functional and ecological aspects of Ediacaran assemblages. In: Lipps, J.H. & Signor, P.W. (eds.) *Origin and Early Evolution of the Metazoa*. Plenum Press, New York and London: 131–176.

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Johnston, G. (1845): II. Miscellanea Zoologica. *The Annals and Magazine of Natural History Including Zoology, Botany, and Geology* 16(102): 4–10, pl. 2.

Johnston, G. (1865): *A Catalogue of the British Non-Parasitical Worms in the Collection of the British Museum*. Taylor and Francis, London.

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

Jussien N., Verger, V., L'Hospitalier, Y., Augereau, B. & Gillet, P. (1994): Le système expert «*Nereis*» des annélides polychètes de France (ordre des Phyllodocida, Amphinomida, Spintherida et Eunicida). *Canadian Journal of Zoology*, 72(12): 2255–2260.

Kornfeld, W. (1915): Über die Augen von *Spinther miniaceus*. *Zoologischer Anzeiger* 45(11): 516–523.

Levinsen, G.M.R. (1883): Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. Anden Halvdel. *Videnskabelige Meddelelser fra den naturhistorisk Forening i Kjøbenhavn* 1883: 92–350, pls. 2–3.

Mackie, A.S.Y., Oliver, P.G. & Nygren, A. (2015): *Antonbruunia sociabilis* sp. nov. (Annelida: Antonbruunidae) associated with the chemosynthetic deep-sea bivalve *Thyasira scotiae* Oliver & Drewery, 2014, and a re-examination of the systematic affinities of Antonbruunidae. *Zootaxa* 3995(1): 20–36.

Manton, S. M. (1967): The polychaete Spinther and the origin of the Arthropoda. *Journal of Natural History* 1: 1–22.

Martin, D. & Britayev, T.A. (1998): Symbiotic polychaetes: review of known species. *Oceanography and Marine Biology, An Annual Review* 36: 217–340.

McIntosh, W.C. (1890): XXII. Notes from the St. Andrews Marine Laboratory (under the Fishery Board for Scotland). No. XII. 1. Preliminary note on the occurrence of pelagic annelids and chætognaths in St. Andrews Bay throughout the year. 2. On the British species of *Spinther*. 3. On the young stages of the Gunnel (*Centronotus gunnellus*). *The Annals and Magazine of Natural History including Zoology, Botany, and Geology* 6(32): 174–185.

McIntosh, W.C. (1894): A contribution to our knowledge of the Annelida. On some points in the structure of Euphrosyne. On certain young stages of *Magelona*, and on Claparède's unknown larval *Spio*. *Quarterly Journal of Microscopical Science, New Series* 36(141): 53–76, pls. 6–8.

McIntosh, W.C. (1900): *A Monograph of the British Annelids. Part II. Polychæta. Amphinomidæ to Sigalionidæ*. The Ray Society, London, 1: 215–442, pls. 24–26, $26_A$, 27–42.

Molodtsova, T.N., Britayev, T.A. & Martin, D. (2016): Chapter 25. Cnidarians and their polychaete symbionts. In: Goffredo, S. & Dubinsky, Z. (eds.) *The Cnidaria, Past, Present and Future*. Springer International Publishing, Switzerland: 387–413.

Núñez, J., Maggio, Y., Moro, L. & Herrera, R. (2011): Primer registro de la familia Spintheridae (Annelida: Polychaeta) en las Islas Canarias. *Revista de la Academia Canaria de Ciencias, Sección Biología* 22(3): 155–160.

Pettibone, M.H. (1963): Marine polychaete worms of the New England region. 1. Families Aphroditidae through Trochochaetidae. *United States National Museum, Smithsonian Institution, Bulletin* 227(1): 1–356.

Pleijel, F. (2001): *Spinther* Johnston, 1845. In: Rouse, G.W. & Pleijel, F. (eds.) *Polychaetes*. Oxford University Press, Hong Kong: 180–181.

Racovitza, É.-G. (1894): Sur le lobe céphalique des *Euphrosines*. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences* 119: 1226–1228.

Racovitza, É.-G. (1895): On the cephalic lobe of *Euphrosine*. *The Annals and Magazine of Natural History including Zoology, Botany, and Geology* 15(87): 279–281.

Racovitza, É.-G. (1896): Le lobe céphalique et l'encéphale des annélides polychètes (anatomie, morphologie, histologie). *Archives de Zoologie Expérimentale et Générale* 4: 133–343, pls. 1–5.

Retallack, G.J. (2007): Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa: An Australasian Journal of Palaeontology* 31(3): 215–240.

Riddell, W. (1909): *Spinther oniscoides*, Johnston. *The Irish Naturalist* 18: 101–108, pl. 1.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26(2): 139–204.

Sardá, R. (1985): Anélidos poliquetos del estrecho de Gibraltar. I. Amphinomida, Spintherida y Phillodocida. *Miscellània Zoològica* 9: 65–78.

Sars, M. (1851): Beretning om en i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken. *Nyt Magazin for Naturvidenskaberne* 6(2): 121–211.

Sars, M. (1862): Uddrag af en Afhandling, ledsaget af detaillerede Afbildninger, over folgende norske Annelider. *Forhandlinger i Videnskabs-Selskabet i Christiania aar 1861*: 50–67.

Sharov, A.G. (1966): *Basic Arthropodan Stock, with Special Reference to Insects*. Pergamon Press, Oxford.

Sheffield, G., George, J.C. & Hanns, C. (2008): *Bowhead whale diet investigation: St. Lawrence Island, Alaska, Bering Sea. Final Project Report*. Cooperative Agreement 06-017. Alaska Dept. of Fish & Game, North Slope Borough: 1–29.

Stimpson, W. (1854): Synopsis of the marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge* 6(5): 1–67, pls. 1–3.

Treadwell, A.L. (1937): Polychaetous annelids collected by Captain Robert A. Bartlett in Greenland, Fox Basin, and Labrador. *Journal of the Washington Academy of Sciences* 27(1): 23–36.

Uschakov, P.V. (1950): Polychaeta of the Sea of Okhotsk. *Issledovaniya Dal'nevostochnykh Morei SSSR* 2: 140–234, pls. 1–2.

Uschakov, P.V. (1955): Polychaeta of the Far Eastern Seas of the U.S.S.R. [in Russian] *Izdatel'stvo Akademii Nauk SSSR* 56: 1–445. [Translated by the Israel Program for Scientific Translations 1965: 1–419.]

Wade, M. (1972): *Dickinsonia*: polychaete worms from the late Precambrian Ediacara fauna, South Australia. *Memoirs of the Queensland Museum* 16(2): 171–190, pls. 5–7.

Wesenberg-Lund, E. (1950): Polychæta. *The Danish Ingolf-Expedition* 4(14): 1–92, pls. 1–10.

Wirén, A. (1883): Chætopoder från Sibiriska Ishafvet och Berings Haf insamlade under Vega-Expeditionen 1878–1879. *Vega-Expeditiones Vetenskapliga Iakttagelser* 2: 381–428, pls. 27–32.

Yamamoto, R. & Imajima, M. (1985): A new species of the genus *Spinther* (Polychaeta, Spintheridae) from Japan. *Bulletin of the National Science Museum, Tokyo, Series A, Zoology* 11(3): 129–135.

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# 7.3 Sedentaria: Cirratulida

## 7.3.1 Cirratuliformia

James A. Blake

### 7.3.1.1 Paraonidae Cerruti, 1909

#### Introduction

The paraonids are small, elongate burrowing worms that rarely exceed 20 mm in length. Their bodies are somewhat expanded and flattened anteriorly, narrowing to numerous posterior segments. The bodies of some species are tightly spiraled after preservation, resembling a corkscrew, suggesting that they maintain this position in the sediments. Paraonids have no palps and are considered to be subsurface deposit feeders; they have only a simple, soft proboscis. Some genera have a distinctive medial antenna. The number of taxa has increased in recent years through the use of finer mesh screens and the increased exploration of continental shelf and slope depths where they are most abundant.

The family is presently organized into eight genera and approximately 140 described species. The most comprehensive reviews of Paraonidae are by Cerruti (1909), Hartman (1957), Laubier (1967), Laubier and Ramos (1974), Strelzov (1973/1979)[1], Blake (1996), Rouse and Pleijel (2001), and Aguirrezabalaga (2012). Since Strelzov's monograph (1973/1979), numerous new species and taxonomic updates have been described from worldwide locations by Aguado and Lopez (2003), Aguirrezabalaga and Gil (2008, 2009), Arriaga-Hernández *et al.* (2013), Brown (1976), Castelli (1988), Çinar *et al.* (2011), Çinar and Dagli (2013), Gaston (1984), Hartley (1981, 1984), Hartmann-Schröder and Rosenfeldt (1988), Hobson (1972), Katzmann and Laubier (1975), Leon-González *et al.* (2006), Leon-González and Díaz-Casteneda (2011), López (2008), Lovell (2002), Mackie (1991), McLelland and Gaston (1994), Montiel and Hilbig (2004), Sardá *et al.* (2009), and Zhou and Reuscher (2013).

For this chapter, available literature on paraonid external and internal morphology, biology, ecology, phylogeny, and taxonomy has been reviewed. Each of the genera is reviewed and discussed, with numbers of species and geographic distributions reported.

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#### Morphology

##### External morphology

**Body shape and regions.** The Paraonidae include a variety of small polychaetes having bodies ranging from thin and threadlike to large and robust. Paraonids are mostly between 10 and 20 mm in length but may range from 2–3 mm up to 30–40 mm. The body is composed of numerous segments. An anterior thoracic region may appear enlarged and is usually dorsoventrally flattened; abdominal segments are cylindrical in cross-section and are not crowded and sometimes appear moniliform. The body is divided into a head region that includes a well-developed prostomium and reduced and poorly demarcated peristomium, a thoracic region that includes three or more prebranchial segments, and a branchial region of three to many segments (Fig. 7.3.1.1.1 A–F), or branchiae may be absent, and a postbranchial or abdominal region that terminates in a narrow pygidium that usually bears two to three anal cirri (Fig. 7.3.1.1.2 G–H) (eight in *Paraonis pygoenigmatica*).

**Prostomium and peristomium.** The prostomium ranges from long and narrow to short and wide (Fig. 7.3.1.1.1 A–I), with the boundary between the prostomium and peristomium vague and usually difficult to discern. The peristomium appears to be limited to the lips that surround the mouth. Strelzov (1973/1979) described a ciliary band that encircles the head of many Paraonidae and may be a retained larval ciliary field (Fig. 7.3.1.1.4 C); if confirmed with developmental studies, this band might define a boundary between the prostomium and the peristomium. A medial antenna is present or absent. When present, the antenna is of major taxonomic importance and takes on a variety of forms (Fig. 7.3.1.1.1 D–I), from short to long, cirriform to clavate, smooth (*Aricidea claudiae*, Fig. 7.3.1.1.1 F) to articulated (*Aricidea wassi*, Fig. 7.3.1.1.1 G), or even branched (*Aricidea ramosa*, Fig. 7.3.1.1.1 I). Paired eyespots are present or absent (Fig. 7.3.1.1.1 E–F). The tip of the prostomium bears a retractable terminal sense organ or palpode in some taxa (Fig. 7.3.1.1.4 A). Semicircular nuchal slits are usually present at the posterior margins

1 Throughout this chapter, except for taxonomic priority, Strelzov is cited as (1973/1979) due to the 6-year gap, different pagination, and some differences in text arrangement between the original Russian edition (published in 1973) and the English translation (published in 1979). Further, the list of abbreviations in the 1973 edition was not translated or included in the English edition; it has been manually translated by a colleague and will be made available on line in due course.

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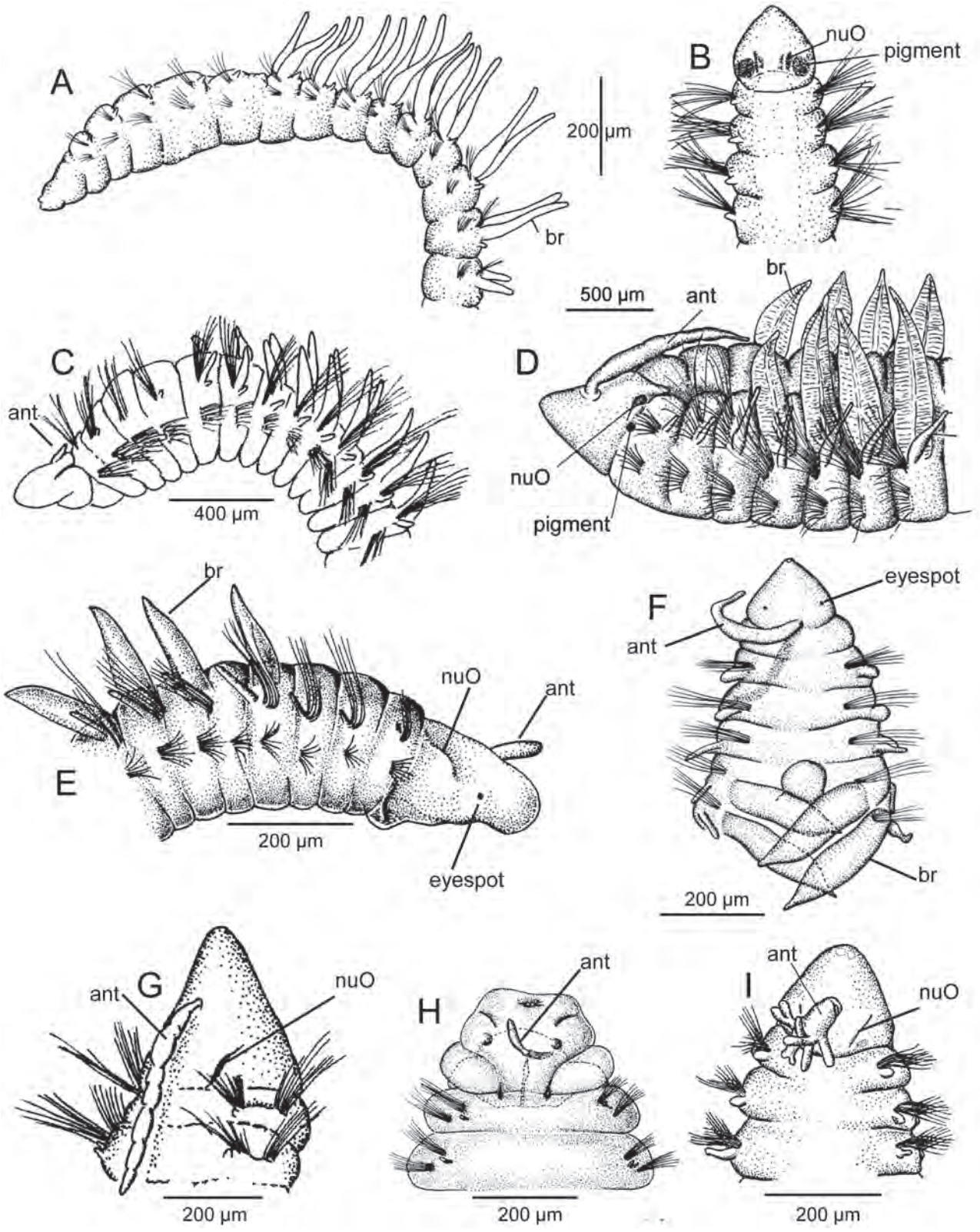


**Fig. 7.3.1.1.1:** Anterior morphology of Paraonidae. A, *Levinsenia oculata*, lateral view; B, dorsal view, anterior end. C, *Cirrophorus branchiatus*, lateral view. D, *Aricidea* (*Acmira*) *lopezi*, lateral view. E, *Aricidea* (*Acmira*) *cerruti*, lateral view. F, *Aricidea* (*Strelzovia*) *claudiae*, dorsal view. G, *Aricidea* (*Aricidea*) *wassi*, dorsolateral view. H, *Aricidea* (*Strelzovia*) *monicae*, dorsal view. I, *Aricidea* (*Strelzovia*) *ramosa*, dorsal view. ant, antenna; br, branchia; nuO, nuchal organ. A–B, D, After Blake (1996); C, G, from Imajima (1973); E–F, H, from Laubier (1967); I, after Strelzov (1973/1979).

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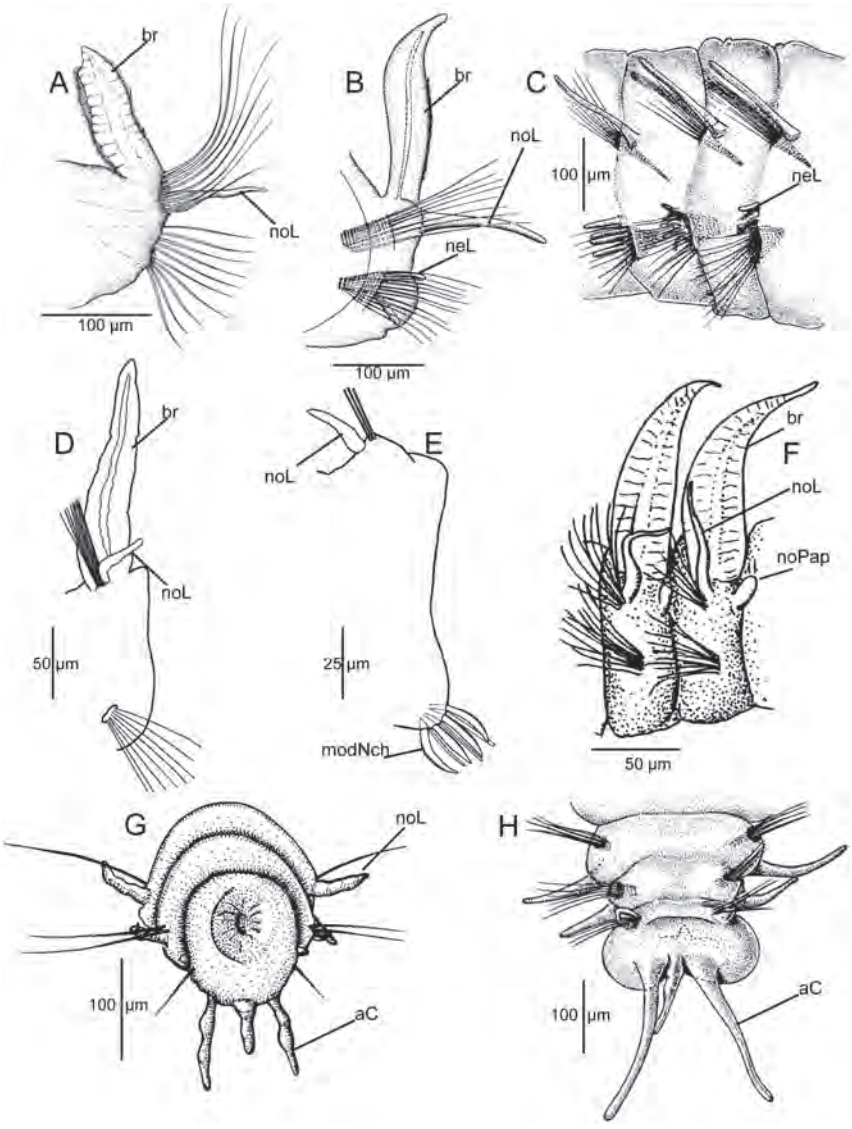


**Fig. 7.3.1.1.2:** Parapodia and pygidia of Paraonidae. A, *Aricidea* sp., branchial parapodium. B, *Aricidea* (*Strelzovia*) *monicae*, branchial parapodium. C, Three middle branchial parapodia. D, *Levinsenia materi*, branchial parapodium. E, Posterior parapodium and modified neurochaetae. F, *Aricidea* (*Acmira*) *rubra*, lateral view of chaetigers 10–11, with extra notopodial papillae. G, *Aricidea* (*Acmira*) *annae*, pygidium, posterior view. H, *Aricidea* (*Strelzovia*) *monicae*, posterior parapodia and pygidium, ventral view. aC, anal cirrus; br, branchiae; neL, neuropodial lamellae; modNch, modified neurochaeta; noL, notopodial lobe; noPap, notopodial papillae. A, Original; B–C, G–H after Laubier (1967); D–E, after Çinar and Dagli (2013); F, after Blake (1996).

of the peristomium (Fig. 7.3.1.1.1 B, D, E, I). The proboscis is a thin, eversible ciliated pouch (Fig. 7.3.1.1. 4 C). The mouth opening is situated ventrally often at the level of chaetiger 1 or 2 and surrounded by four lips, the form of which is sometimes of taxonomic importance.

**Branchiae.** The branchial region is usually the widest part of the body (Fig. 7.3.1.1.1 D–F), with larger parapodia that are often dorsally flattened, and bear heavier chaetal fascicles. Branchiae are thin, flattened, and ciliated (Fig. 7.3.1.1.2 A, B), with two blood vessels connected by capillaries; there is no blood loop as in spionids and many other families. Circulation to and from the branchiae is described in the next section. Branchiae are typically limited to anterior body segments. The shape, length, number, and arrangement of branchiae are of taxonomic importance.

**Parapodia and chaetae.** Parapodia are biramous, with reduced parapodial tori bearing well-developed fascicles of chaetae (Fig. 7.3.1.1.2 A–F). The notopodial postchaetal lobe is usually well developed in the branchial region (Fig. 7.3.1.1.2 A–B, D). It may be an elongate, cirriform structure (Fig. 7.3.1.1.3 O) or broader and more triangular. A similar neuropodial postchaetal lobe may also be present (Fig. 7.3.1.1.2 B, C) but is usually not as well developed as the notopodial lobe. Sometimes, additional short postchaetal lobes are present on some noto- or neuropodia.

Chaetae are limbate capillaries in the prebranchial and branchial regions, with some species having modified chaetae of various types in postbranchial middle and posterior segments (Fig. 7.3.1.1.3 A–Q). Modified chaetae are highly diagnostic and include bayonet or lyrate chaetae (Fig. 7.3.1.1.3 M–N), curved simple spines (Fig. 7.3.1.1.3 E, O), and spines with various types of accessory sheaths,

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mucrons, aristae, or bristles (Fig. 7.3.1.1.3 A–L, P–Q). Strelzov (1973/1979) classified the chaetae of paraonids according to the increasing complexity from the simple capillaries to the various types of modified chaetae.

### Anatomy

The internal anatomy of paraonids is poorly known and represents an important gap in comparing these polychaetes with other taxa. Most observations are relatively old and by standard histological methods; ultrastructural observations are limited to a single study on sense organs by Purschke and Hausen (2007).

**Epidermis.** According to Strelzov (1973/1979), the integument consists of a single layered epithelium consisting of cuboidal cells, glandular cells, and ciliated cells. The thickness of the cuticle varies along the body. The glandular cells occur singly or in groups and are concentrated in different parts of the body depending on species. In *Cirrophorus branchiatus*, Strelzov noticed that the largest glandular accumulations were associated with chaetal sacs, whereas in *Aricidea quadrilobata*, large groups of mucous cells were present in a thickened epithelium on the ventral surface.

**Digestive system.** There appears to be variability in the pharyngeal morphology. Strelzov (1973/1979) described the proboscis as ventral in the paraonids he investigated, whereas Purschke and Tzetlin (1996) described a simple axial proboscis in others. The mouth of paraonids is located ventrally sometimes as far posteriorly as the level of chaetiger 1 or 2 (Fig. 7.3.1.1.4 A, C). *Paraonella nordica* has a nonmuscular axial proboscis and a ciliated foregut but no dorsolateral ciliary folds, whereas *Aricidea* sp. has ventral dorsolateral ciliary folds that lead directly into the esophagus (Purschke and Tzetlin 1996). These authors implied that the difference in observed patterns of ciliation of the proboscis might be a developmental shift from dorsolateral ciliary folds to an axial proboscis. In a later paper, Tzetlin and Purschke (2005) suggested that paraonids have a ciliated nonmuscular proboscis similar to that of orbiniids and some opheliids. When everted, the proboscis of paraonids is heavily ciliated (Fig. 7.3.1.1.4 C, D). Paraonids have a relatively simple tubular gut weakly divided into an esophagus and mid- and posterior intestine (Fig. 7.3.1.1.4 B) (Strelzov 1973/1979, Penry and Jumars 1990). Species with simple guts generally occur in sediments with relatively high organic enrichment and required less through time to process their food source according to Penry and Jumars (1990).

**Body cavities and coelom.** The coelom of paraonids evidently has little in the way of open space, being filled with loose tissue (Strelzov 1973/1979). The space occupied by the digestive tract, however, is free of loose cells. The coelomic cavity of each segment is enclosed by anterior and posterior septa.

**Blood vascular system.** The circulatory system is closed and complete, with major dorsal and ventral vessels clearly evident together with the branchiae well infused with blood flow. Respiration or oxygen exchange is facilitated by beating of cilia on the branchiae and interbranchial cilia. Strelzov (1973/1979) described the circulatory pattern in *C. branchiatus*, which is similar to that reported by Cerruti (1909) for *Aricidea cerruti* (*as A. jeffreysii*). The ventral vessel originates in the posterior part of the body and continues anteriorly. In the branchial region, a branch from the ventral vessel diverges to each gill, and within the gill, capillaries connect the flow to another vessel, which exits to the dorsal vessel flowing posteriorly. Enlarged dilated blood sinuses are sometimes present in the branchial region; but these are absent in *C. branchiatus* according to Strelzov (1973/1979). At the posterior border of the first segment, the ventral vessel sends one branch to the pharynx and another to the posterior part of the brain. Return flow from the anterior end and branchiae is in the dorsal vessel. A simple diagram of the major features of the circulatory system of paraonids is shown in Fig. 7.3.1.1.4 E. Blood is a red or reddish yellow fluid, like hemoglobin, according to Strelzov (1973/1979), and is without cellular elements.

**Nervous system and sensory organs.** The nervous system of paraonids has been described for *Paraonis fulgens* by

▸ **Fig. 7.3.1.1.3:** Chaetae of Paraonidae. A, *Aricidea* (*Strelzovia*) *claudiae*, modified neurochaetae. B, *Aricidea (Acmira) annae*, modified neurochaetae. C, *Aricidea* (*Acmira*) *cerruti*, modified neurochaeta. D, *Aricidea* (*Acmira*) *catherinae*, modified neurochaeta. E, *Arcidea* (*Acmira*) *simplex*, modified neurochaetae. F–G, *Aricidea* (*Acmira*) *assimilis*, modified neurochaeta. H, *Aricidea* (*Acmira*) *lopezi*, modified neurochaetae. I, J, *Aricidea* (*Aricidea*) *wassi*, modified neurochaetae. K, *Aricidea* (*Strelzovia*) *hartleyi*, modified neurochaeta. L, *Levensenia kantaruiensis*, scanning electron microscopy (SEM) image of modified neurochaetae. M, *Cirrophorus branchiatus*, modified notochaeta. N, *Cirrophorus miyakoensis*, furcate notochaeta. O, *Paradoneis spinifera*, modified spinous notochaetae. P, *Levinsenia flava*, modified neurochaetae. Q, *Levinsenia flava*, SEM images of modified neurochaetae. noL, notopodial lobe. A–D, After Laubier (1967); E, after Hartman and Fauchald (1971); F, after Laubier and Ramos (1974); G, M, after Strelzov (1973/1979); H–K, O, after Blake (1996); L, Q after Aguirrezabalaga and Gil (2009); N, after Imajima (1973); P, original.

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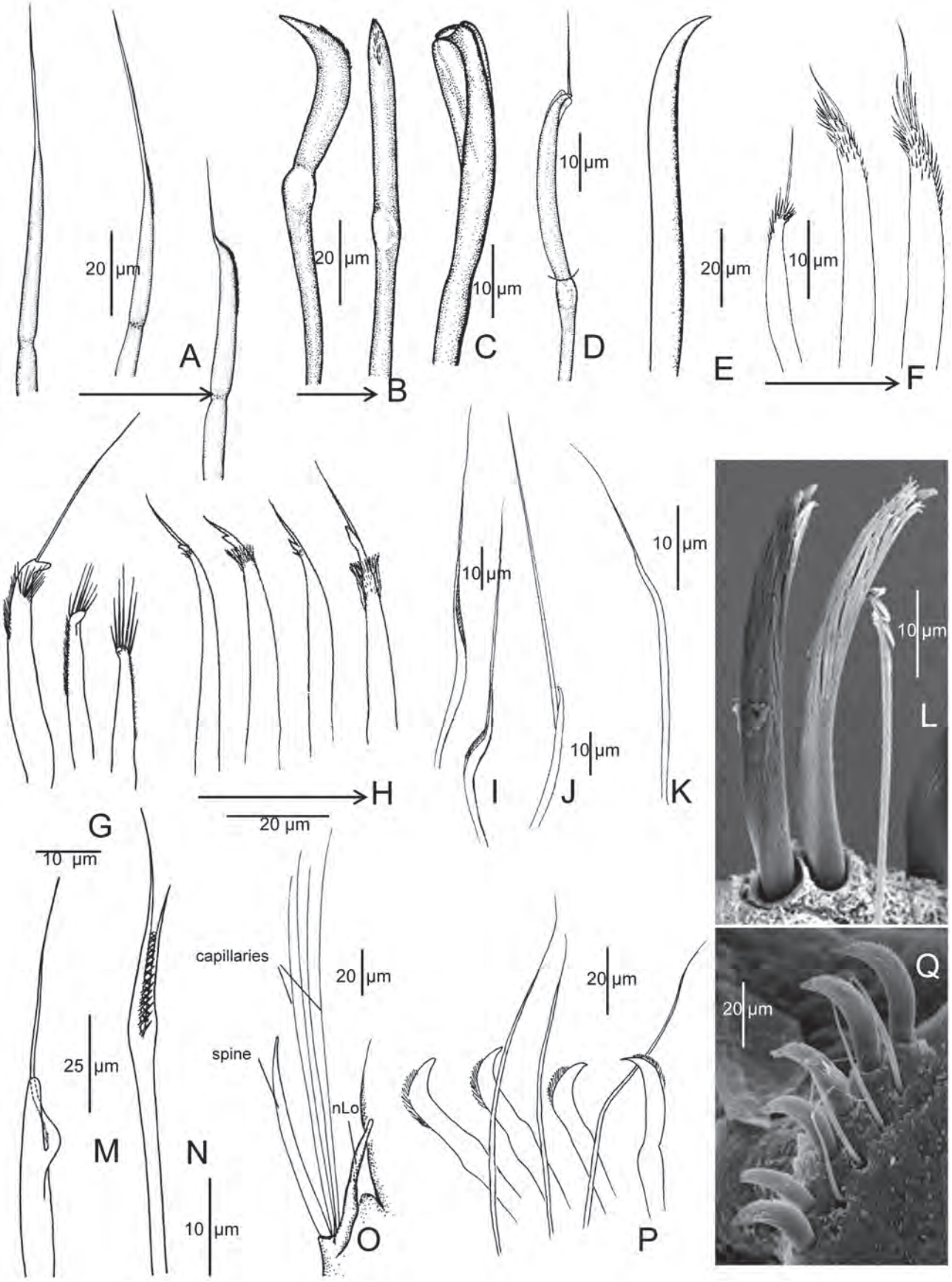


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Mesnil and Caullery (1898), *A. cerruti* (as *A. jeffreysii*) by Cerruti (1909), *Levinsenia gracilis* and *Paradoneis lyra* by Orrhage (1966), and *C. branchiatus* and *A. quadrilobata* by Strelzov (1973/1979). In general, the same overall pattern is evident in all of these species (Strelzov 1973/1979). The brain or circumesophageal ganglion occupies the anterior part of the prostomium and it contains four main commissures: (1) the dorsal and (2) ventral anterior commissures and the (3) dorsal and (4) ventral posterior commissures (Orrhage 1966). Paraonids lack sympathetic nerves emanating from the antero-ventral cerebral commissure. There is no posterior section of the brain as occurs in most polychaetes.

In *Aricidea* species, the medial antenna is innervated and may be sensory (Orrhage 1966). Orrhage (1966, 1993) and Orrhage and Müller (2005) identified nerves in the paraonids *Levinsenia gracilis* and *Paradoneis lyra* that correspond to palp innervations in other polychaetes, but no palps are present in any known paraonid. Out of 12 palp nerve roots, paraonids had one nerve root (no. 6) attached to the ventral nerve and another (no. 9) attached to the dorsal nerve. The only other polychaete family having this arrangement is the Scalibregmatidae. Nuchal nerve innervation is associated with the dorsal root of the circumesophageal ganglion connective in Paraonidae similar to that found in Poecilochaetidae and Apistobranchidae; in Scalibregmatidae, nuchal organs are associated with the dorsal commissure of the dorsal root (Orrhage and Müller 2005).

Sense organs in Paraonidae include (1) eye spots, (2) nuchal organs, (3) eversible palpodes at the tip of the prostomium, (4) lateral tubercle or "cheek" organs on the prostomium of a few species, (5) lateral organs, (6) a variety of ciliary bands, and (7) possibly the medial antenna found on some genera.

Eyespots occur in some species of *Aricidea* (Fig. 7.3.1.1.1 E–F), *Levinsenia*, and *Paradoneis* (Fig. 7.3.1.1.11 H) and consist of a few pigmented cells; in some instances, these may simply be pigmented cells surrounding or incorporated into the nuchal organs.

The nuchal organs of paraonids in life were observed by Strelzov (1973/1979) to be a pair of curved, kidney-shaped ciliated ridges located at the posterior margin of the prostomium. When retracted, as is typical in preserved specimens, they are curved slits (Fig. 7.3.1.1.1 B, D–E, I). In several species of *Aricidea* and *Levinsenia*, the nuchal slits are surrounded by pigmented cells (Strelzov 1973/1979), which have been confused with eyes by some investigators (Figs. 7.3.1.1.1 B and 7.3.1.1.10 E, J, K).

A terminal sense organ or eversible palpode occurs on the tip of the prostomium (Röder 1971, Strelzov 1973/1979) but is often overlooked in preserved specimens (Fig. 7.3.1.1.4 A). Strelzov (1973/1979) suggested that the palpode might be tactile in function and noted that it is capable of retracting by means of a muscle innervated directly from the brain. Lateral "cheek" organs were reported for several species of *Levinsenia* by Strelzov (1973/1979). In *Levinsenia gracilis*, they occur at the widest part of the head (Fig. 7.3.1.1.10 B; Strelzov 1973/1979: Fig. 54 B).

Retractile lateral organs are present below the notopodia on each segment in paraonids (Cerruti 1909, Strelzov 1973/1979). Lateral organs for *Aricidea* sp. and *Paraonis paucibranchiata* are described in detail by Purschke and Hausen (2007). These organs occur between the noto- and neuropodia and consist of large ciliary brushes arranged in three discernable vertical rows (Fig. 7.3.1.1.4 F–I). The length of these cilia may exceed 10 µm. These lateral organs are slightly curved. The details of the ultrastructure, including sensory cells, supportive cells, and musculature, are described by Purschke and Hausen (2007), who found a commonality in cellular morphology of sensory cells, supportive cells, and musculature between paraonids and several other families of the Scolecida they investigated.

A preoral ciliary band was observed by Strelzov (1973/1979) in most species he examined and is clearly evident in scanning electron microscopy images of *P. nordica* (Fig. 4C). In some species of *Levinsenia*, the ciliary band was noted by Strelzov to be reduced to two sensory tubercles on either side of the mouth. Ciliated cells have been reported in various parts of the body by Cerruti (1909) and Strelzov (1973/1979). In some species, these occur in two rows on the branchiae and three rows on the prostomium (two lateral and one ventral).

In *Aricidea* species, the medial antenna is innervated and may be sensory (Orrhage 1966).

▸ **Fig. 7.3.1.1.4:** Morphology. A, *Paraonis fulgens,* sagittal section of the anterior end showing several anatomical characteristics. B, *Cirrophorus branchiatus*, diagram of anterior digestive tract. C, *Paraonella nordica*, anterior end, ventral view with proboscis everted. D, Same, detail of proboscis and cilia. E, Diagram of the vascular system of paraonids. F–I, *Aricidea* sp. showing lateral sensory organs. F, Thoracic chaetiger 11 showing the location of the ciliated, brush-like lateral organ (boxed) positioned between noto- and neuropodia. G, Detail of the lateral organ from F. H, Abdominal chaetiger 35 showing the location of the ciliated lateral organ (boxed) between noto- and neuropodia, anterior row. I, Detail of the cilia of the lateral organ from a posterior chaetiger in posterior view, arrows denote distance of individual cilia in posteriormost row. bV, blood vessel; bSin, blood sinus; brCap, branchial capillaries; brbV, branchial blood vessel; cap, capillaries; comV, commissural vessel; dbV, dorsal blood vessel; dc, dorsal cirrus; eso, esophagus; fGut, foregut; hGut, hind gut; int, intestine; mGut, midgut; nep, neuropodium; nop, notopodium; paPd, palpode; paPd musc, palpode muscle; prob, proboscis; pr, prostomium; piPlex, peri-intestinal plexus; piSin, peri-intestinal sinus; vB, ventral blood vessel. Arrows in I denote widely spaced individual cilia in posterior row. A, Modified from Rouse and Pleijel (2001), originally derived from Röder (1971); B, E, modified from Strelzov (1973/1979); C, D, after Tzetlin and Purschke (2005); F–I, after Purschke and Hausen (2007).

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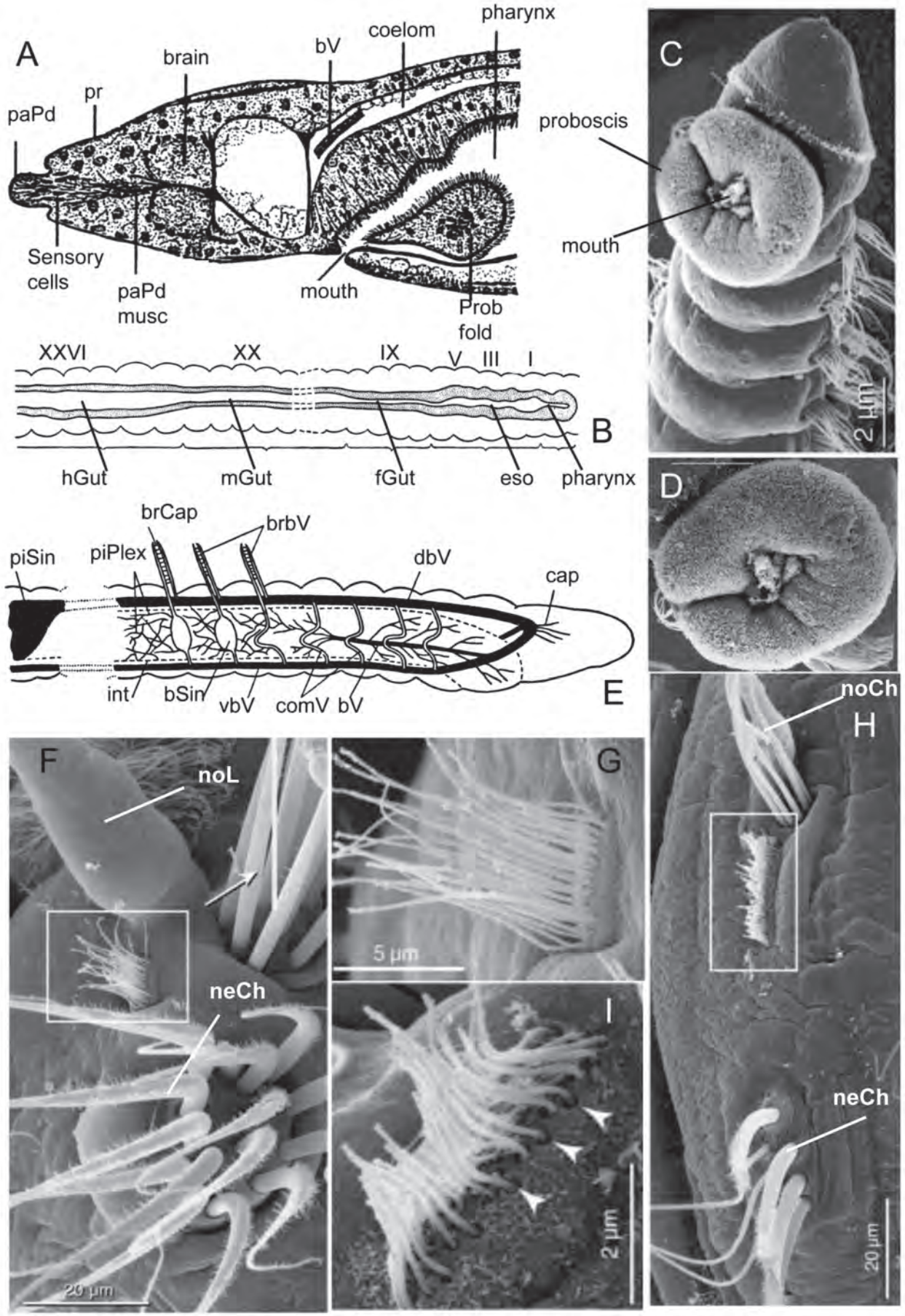


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**Musculature.** The most conspicuous musculature in paraonids are two pairs of longitudinal muscles, dorsal and ventral, that extend along the length of the body (Strelzov 1973/1979). The ventral muscles are larger than the dorsal. They are thin anteriorly, becoming larger in the middle body and then decreasing in size again in posterior segments; they split into small fibers near the pygidium (Strelzov 1973/1979). Circular muscles do not form continuous rings and are best developed in the area of the posterior lip of the mouth and dorsal to the nerve cord in anterior segments. The musculature that controls the movement of parapodia and chaetae has not been described (Strelzov 1973/1979).

**Excretory system and nephridia.** Segmental organs or metanephridia are present in the prebranchial region and branchial region and absent in the posterior region but have been poorly described (Cerruti 1909, Strelzov 1973/1979). Cerruti (1909) described metanephridia in *Aricidea cerruti* (as *A. jeffreysii*). These were reported to consist of a ciliated funnel and a narrow nephridial canal that discharged externally on the anterior borders of segments. Strelzov (1973/1979) described a somewhat different arrangement for *A. quadrilobata*, where a small nephrostome is followed by several narrow loops in the intersegmental groove that discharge externally through a narrow nephridiopore ventral to the parapodia. Strelzov (1973/1979) also noted that long cilia discharge into the nephridial canal and cells containing granules of excreta and vacuoles were present along its length. Nephridia were not present in the reproductive segments of *A. quadrilobata* and *Aricidea hartmani* examined by Strelzov (1973/1979).

**Reproductive organs and gametes.** Paraonids are dioecious or gonochoric, with gametes developing in postbranchial segments (Strelzov 1973/1979), where some workers have found large ova in relatively few numbers (two to eight) in each reproductive segment of a mature female: *Aricidea nolani* by Webster and Benedict (1887), *Cirrophorus lyra* by Southern (1914), *Levinsenia gracilis* by Pettibone (1963), *Paradoneis armata* by López-Jamar (1987), and *Aricidea simplex* by Blake and Baptiste (1985). However, other species of *Aricidea* have been reported with numerous ova (Cerruti 1909, Pettibone 1963). Cerruti (1909) described the sperm as having a pointed nucleus, short middle piece, and elongate tail or flagellum. However, there have been no modern studies of paraonid spermiogenesis or oogenesis.

### Reproduction and development

There have been relatively few reports that deal with the reproduction and development of paraonids. There have been reports of paraonids rising to the water surface during periods of reproduction (Levinsen 1883, Southern 1914, Strelzov 1973/1979). The eggs of paraonids are reported to be large (Hartman 1957, Strelzov 1973/1979, López-Jamar *et al.* 1987), suggesting that development is direct.

López-Jamar (1987) followed seasonal gametogenesis in a population of *Paradoneis armata* at an embayment in NW Spain (1984–1985) using average oocyte diameter as an index of maturity. The first evidence of oogenesis was in January (15 μm); previtellogenic oocytes were observed in February (35 μm); vitellogenic oocytes were observed in April (60 μm); the largest oocytes were observed in June (180 μm). Each gonad-bearing segment had four oocytes, each attached to the body wall by a tubular anchor. No female gametes were present in July, suggesting that spawning occurred in June. For males, spermatocytes were observed in January and February, and by April, free sperm were observed in the coelom; spawning occurred in May–June. The relatively large egg size suggested to López-Jamar (1987) that development was direct, but he had no direct observations, although it was clear that spawning occurred at least once a year in June. López-Jamar (1987) noted the presence of enlarged eyes and natatory chaetae in adults at the time of spawning. He also noted that at least some of the adults died after spawning because population densities declined afterward. There were no confirmed reports of pelagic larvae.

Blake and Baptiste (1985) developed data to assess reproductive timing, settlement, and recruitment of six paraonid species as part of a 3-year benthic monitoring program on Georges Bank, offshore Massachusetts: *Aricidea catherinae, Aricidea* cf. *suecica*, *Aricidea simplex* (as *A. neosueicica*), *Levinsenia gracilis*, *Levinsenia* sp. A (as *Paraonis*), and *Paradoneis* sp. A. The use of 300-μm sieves made it possible to identify the earliest juvenile stages. Data on *A. catherinae* indicated that maximal reproductive activity occurred in the summer. For the three summer collections (July 1981, July 1982, and July 1983), 27.4%, 51.0%, and 32.0% of the population, respectively, were females. A high percentage of males were identified in July 1982 (25%) and July 1983 (23.7%). Size frequency data indicated that juveniles recruited into the population heavily in July and November 1981, with the cohort readily identifiable in February 1982. *A. catherinae* therefore underwent reproduction during late spring and summer, with spawning and recruitment evident in summer and the fall months. The species may have a 2-year life cycle, as evidenced by the total disappearance of the larger size classes during 1982. These larger sizes were present in 1981 and began to reappear in 1983. Data on reproduction of *A.*cf.

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*suecica* indicated that most reproductive activity occurred in the spring and summer months. The highest numbers of females with eggs were found in July 1981 (38.8%), May 1982 (56.2%), July 1982 (58.0%), May 1983 (20%), and July 1983 (52.1%). Size frequency data indicated that a light recruitment occurred in July and November 1981, with a large average size developed by May 1982 (58.95 setigers). This population was largely replaced in July 1982 by smaller animals having an average size of 39.18 setigers. For *A. simplex*, the reproductive data were scanty. Eggs were present in specimens collected in November 1981 (7.1%), February 1982 (1.6%), and May 1982 (8.7%). Natatory chaetae were observed in individuals from November (9.8%) and February (24.2%). Since the presence of eggs and natatory chaetae usually denotes periods of reproductive activity, these data suggest that reproduction and spawning take place at times other than summer months. For *L. gracilis,* data on reproduction indicated that the highest percentage of females having eggs occurred in May 1982 (33.3%), July 1982 (50.2%), May 1983 (40.6%), and July 1983 (62.5%). Males were not observed, although one specimen collected in July 1983 was observed to have both eggs and sperm. Size frequency data indicated that recruitment occurred in July 1981, November 1982, and July 1983. Data for *Levinsenia* sp. A. were also scanty; however, reproductive males and females were observed year-round, with the highest numbers of males and females (combined) present in July 1981 (80.9%), November 1981 (82.7%), and May 1982 (75%). This suggests that most reproductive activity took place over an extended period between spring and fall. No trends were evident from the size frequency data. *Paradoneis* sp. A is a small threadlike species, known only from the outer shelf stations at about 200 m. Although females in various stages of maturation were found year-round, spawning probably took place more regularly in the summer months, since there were a higher percentage of females in the population during those months: July 1982 (19.8%) and July 1983 (21.3%). Egg diameter data for seven of the nine seasons studied show that large eggs were present during most of the year.

There are no reports of paraonid spermatogenesis, oogenesis, embryology, or larval development. Fewkes (1883) described some early pelagic larvae of what he thought were *Aricidea*, but they are clearly spionids, probably a species of *Polydora*. Bhaud (1983) described what he believed to be pelagic larvae of a paraonid, but in a subsequent report changed the identification to *Poecilochaetus* (Bhaud *et al*. 1987). However, the larvae that Bhaud illustrated in his 1983 paper do not bear any resemblance to pelagic larvae of *Poecilochaetus serpens* as described by Hannerz (1956). Further, the hooked neurochaetae with a crest or hood differ from the relatively smooth geniculate hooks of *Poecilochaetus* (Allen 1904). The aristate "sabre" chaetae occur in anterior segments but are of very different structure from the anterior sabre chaetae of *Poecilochaetus*. At this point, the identity of Bhaud's larvae is an open question.

## Biology and ecology

### Distribution

Paraonids are present in all of the world's oceans, including the Arctic and Antarctic. They inhabit soft substrates and appear to be most common in continental shelf and slope depths, where they are frequently among the dominant and characteristic species of infaunal benthic communities. Paraonids are not as common in shallow bays, although species such as *Paradoneis armata* and *Aricidea catherinae* have been reported as dominants in benthic communities in coastal harbors and embayments (e.g., López-Jamar *et al*. 1987, Hilbig and Blake 2000). As part of monitoring a deep-sea disposal site at depths of 2,200–3,200 m offshore San Francisco, seven species of Paraonidae were among the most abundant 20 species out of more than 800 taxa identified with *Levinsenia flava* and *Aricidea simplex* being the two most abundant invertebrate species identified in 10 years of sampling (Blake *et al*. 2009). Off Cape Hatteras, North Carolina, *Aricidea quadrilobata* was the fifth overall most abundant species in depths of ~600–1,500 m out of 280 species identified and at some stations ranked higher (Blake and Hilbig 1994). In most surveys conducted offshore in shelf or slope depths, species of Paraonidae are typically among the top five most abundant families of polychaetes (Blake *et al*. 2009).

### Species richness and diversity

Species richness of Paraonidae is extraordinarily high in deep-water habitats and with numerous species identified in recent surveys that are not yet described in the taxonomic literature. For example, out of more than 1,295 species of benthic invertebrates identified on the continental slope offshore North and South Carolina as part of surveys conducted for the U.S. Department of the Interior (1983–1986, 1992), 21 of 35 species of Paraonidae identified are believed to be new to science (Blake and Grassle 1994, Blake and Hilbig 1994, Hilbig 1994). As part of baseline surveys by the U.S. Environmental Protection Agency and U.S. Navy (1990–1992) offshore San Francisco, CA, intended to identify an offshore dredged material disposal site in depths of 550–2,700 m, 24 of 41 species of Paraonidae identified

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were believed new to science (Hilbig and Blake 2006). Similarly, as part of the 10-year monitoring effort at the deep-sea disposal site off San Francisco that was designated, in 2,200–3,200 m (1995–2004), 27 of 36 species of Paraonidae identified are believed new to science (Blake *et al*. 2009). These results from North America and elsewhere suggest that there are probably as many undescribed species of Paraonidae in deep water as are now currently known for the family. The fact that several of these species are the dominants in their faunal assemblages emphasizes their importance in offshore habitats and deep-water benthic communities.

### Burrowing and feeding

Paraonids appear to live in vertical burrows, often in spirals, and may be able to form temporary fragile mucous tubes. Some species, such as *Levinsenia gracilis*, twist their bodies into a tight vertical corkscrew, and this may facilitate water movement through the burrow. Many paraonids, when preserved in the field, are twisted into spirals. Röder (1971) described the orientation of *P. fulgens* in spiraling burrows that branched with increasing depth; he found the species to feed selectively on diatoms and Foraminifera and did not ingest sediment. Risk and Tunnicliffe (1978) confirmed the burrow traces of *Paraonis fulgens* as consisting of horizontal spirals originating from vertical exploratory shafts and postulated that the spiral and vertical structures served as traps to bring food particles, probably diatoms, to depth. Gaston *et al*. (1992) found the same spiraled orientation in *P. fulgens* in the Gulf of Mexico and noted that the worms moved vertically in the spirals as part of their feeding behavior. *Paraonis fulgens* apparently selects benthic diatoms as part of its subsurface detrital feeding (Röder 1971, Gaston *et al*. 1992). In contrast, Gaston (1987) examined the gut contents of seven species of the genera *Aricidea, Cirrophorus, Levinsenia*, and *Paradoneis* from shelf depths offshore New Jersey to Virginia and determined that all ingest detritus nonselectively. These results led Jumars *et al*. (2015) to conclude that feeding in paraonids includes species that are selective for specific particles such as diatoms and Foraminifera and other species that are nonselective for detrital particles. The discovery of Penry and Jumars (1990) that *Levinsenia oculata* has a simple tubular gut with short through times supports a view that paraonids thrive in sediments that are organically enriched. There also appears to be variability in feeding depth within sediments. Blake (1994) developed vertical distribution data for four species of Paraonidae from the continental slope off Cape Lookout, North Carolina. For *Levinsenia* sp. 1, 80% of all individuals were found from 2 to 10 cm deep; for *L. flava*, 92.5% were found from 0 to 5 cm and only 7.5% deeper than 5 cm; *Paradoneis lyra* was similar to *L. flava* in that 87.5% occurred in the 0–5 cm depth and with only 14.5% deeper than 5 cm. Another species, *Paradoneis brevicirratus*, had 78.9% of individuals in the 2–5 cm depth, but there were fewer specimens available. These results suggest that *L. sp*. 1, by being near the surface, utilizes a different food resource than *L. flava, P. lyra*, and *P. brevicirratus* do. Paraonids are therefore considered to be motile deposit feeders that have species that feed both subsurface and near the surface (Jumars *et al*. 2015).

Spiral burrow structures remarkably similar those described for *Paraonis fulgens* by Röder (1971) and Risk and Tunnicliffe (1978) were identified in early Permian intertidal flat deposits in New Mexico, USA, by Minter *et al*. (2006). These fossils are called graphoglypids and represent trace fossils of biogenic structures of burrowing organisms. As a spiral trace fossil, these were assigned by Minter *et al*. (2006) to a generic category, *Spirorhaphe*. These authors envisioned that like extant *P. fulgens*, the spiral structures of *Spiroraphe* served as traps to bring food to depth. Whether the organisms that constructed these structures were paraonids is not known, but they were most likely a burrowing polychaete that behaved similarly.

## Phylogeny and taxonomy

### Phylogeny

**Morphological studies.** The first major effort to develop a cladistic-based family-level phylogeny of polychaetes using morphological characters was by Rouse and Fauchald (1997). These authors established a phylogeny that arranged the polychaete families into six basic clades. The Paraonidae were grouped with eight other families into a clade termed the Scolecida. The two families most closely grouped with paraonids were Orbiniidae and Questidae, now combined. Other families assigned to the Scolecida were Cossuridae, Arenicolidae, Maldanidae, Capitellidae, Opheliidae, and Scalibregmatidae. All of these families are burrowing deposit feeders that lack palps. In general, this group of families is often treated together in monographic or faunal works (example, Day 1967, Hartman 1969, Hartmann-Schröder 1971, 1996).

Rouse and Pleijel (2001) developed a "Polychaete metatree" based on a variety of sources. In this effort, Paraonidae were a sister group to Orbiniidae and the then family Questidae. However, unlike the other families, the genera of Paraonidae were not separated out. There have been no family-specific cladistic analyses of Paraonidae using morphology.

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**Molecular studies.** Paraonids have rarely been used in molecular phylogenetic studies, which is surprising because many species are available in relatively shallow waters, often in high densities. Further, little effort has been devoted to the relationships of individual species, with most studies simply presenting data at the genus level.

Rousset *et al*. (2007) presented the results of a large data set of over 200 annelid species using four genes: two nuclear ribosomal genes (18S rDNA, 28S rDNA), one nuclear protein coding gene (Histone H3), and one mitochondrial ribosomal gene (16S rDNA). This study was aimed at assessing the monophyly of the major polychaete clades identified morphologically by Rouse and Fauchald (1997); of these, the Scolecida clade includes the Paraonidae. Among the Scolecida, members were scattered over the various trees that were presented. The one paraonid included in their analysis was *Cirrophorus lyra* collected from Sweden. In the results, this species was included in a clade with *Cossura* and all of the opheliids, sequenced including *Travisia*.

Struck *et al*. (2007) presented an analysis for 81 taxa using 11 nuclear and mitochondrial genes intended to examine the position of Sipuncula, Echiura, Siboglinidae, and Clitellata within the Annelida. While their results supported inclusion of these taxa within Annelida and that the latter three taxa were sister taxa to polychaetes, the position of the two paraonids tested was not clear. In one analysis, *Paraonis* sp. formed a clade with a brachiopod; other tests were entirely different from one another.

Struck *et al*. (2008) presented a new analysis of 18S rRNA and of 28S rRNA sequences. This study was aimed at addressing the problem of multiple substitutions in nucleotide positions that tend to obliterate signal, a situation called saturation. In the first maximum likelihood (ML) tree where the possibility of saturation was excluded, *Aricidea* sp. (from off New England) was sister to a group of cirratuliform taxa (flabelligerids, cirratulids, and ctenodrilids) in one clade and another that included three species of Nephtyidae, one polygordiid and a saccocirrid. Nodal support for *Aricidea* sp. and other sister taxa was low. The second ML cladogram, not excluding saturation, placed *Aricidea* sp. in a clade that included seven cirratuliforms (flabelligerids, cirratulids, ctenodrilids, fauveliopsids, and sternaspids), one aeolosomoatid, and a parergodrilid. Nodal support for *Aricidea* sp. and several other sister species was low. Nevertheless, these results, not discussed in the article, suggest a closer relationship of paraonids to cirratuliforms than the Scolecida.

A sister-group relationship with cirratuliforms (flabelligerids and cirratulids) was also identified in a ML tree using a combined 18S rRNA + 28S rRNA + EF-1α by Bleidorn (2009) that had been modified from Struck *et al*. (2007). No discussion of this result was presented.

Zrzavý *et al*. (2009) presented a combined morphological and molecular analysis using 93 morphological characters and six genes. These authors found that Fauveliopsidae, *Sternaspis*, *Cossura*, and Paraonidae consistently placed next to either Cirratuliformia or a clade termed SSC that included (1) Spionida *sensu stricto* (Spionidae, *Trochochaeta*, and *Poecilochaetus*), (2) Sabellidae/Serpulidae, and (3) Sabellariidae.

Several recent efforts to evaluate annelid relationships using phylogenomics by Andrade *et al*. (2015), Lemer *et al*. (2015), Weigert *et al*. (2014), Weigert and Bleidorn (2016), and Struck *et al*. (2011) did not utilize any paraonids in their analysis.

The conclusion from available phylogenetic analyses where paraonids have been included is that there appears to be a relationship between the Paraonidae and taxa of the Cirratuliformia (Cirratulidae, Ctenodrilidae, Flabelligeridae, and Fauveliopsidae) rather than with the Scolecida of Rouse and Fauchald (1997). However, very few species of Paraonidae have been analyzed, and for the molecular work, most taxa have not been identified beyond the genus level. No studies, morphological, or molecular have been developed to confirm the current arrangement and definition of the genera. The lack of modern anatomical studies of paraonids is another gap in understanding the relationships of paraonids with other families.

## Taxonomy

**Taxonomic history.** The most important modern reviews of paraonid systematics are those by Hartman (1957) and Strelzov (1973/1979). Strelzov's monograph was translated into English in 1979, and readers are referred to both of these works for historical aspects of the discovery of paraonids and the early efforts to classify them. Hartman (1957) reviewed and summarized all earlier published names and reevaluated the genera. In conjunction with this study and those published later (Hartman 1959, 1965), seven genera were recognized: *Aricidea, Aedicira, Aparaonis, Cirrophorus, Paradoneis, Paraonis,* and *Paraonides*. This scheme was not universally accepted and many papers subsequently appeared that either rejected this system entirely or objected to definitions of one or more genera (Pettibone 1965, Laubier 1966, Day 1967, Storch 1967, Jones 1968, Strelzov 1968). Strelzov (1973/1979) reviewed, described, and illustrated most of the then known genera and species; this monograph has become an important starting point for studies of Paraonidae. Strelzov (1973/1976) recognized six genera: *Aricidea, Cirrophorus* (includes *Paradoneis*),

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*Paraonella*, *Paraonis*, *Sabidius*, and *Tauberia*, and also revised *Aricidea*, establishing four subgenera: *Aricidea sensu stricto*, *Aedicira* Hartman, *Allia*, and *Acesta*.

Strelzov's monograph stimulated considerable research on paraonids, including further revision to the genera and descriptions of numerous additional new species. Katzmann and Laubier (1975) did not agree with Strelzov's synonymy of *Paradoneis* with *Cirrophorus*, and in most subsequent accounts, these two genera have been maintained separately (e.g., Hartley 1981, Castelli 1988, Mackie 1991, Blake 1996). McLelland and Gaston (1994), however, preferred to follow Strelzov in combining the two genera but did not provide any additional support. Strelzov's separation of *Aricidea* into four subgenera has been accepted. Fauchald (1977), however, elevated all of them to full generic level with no explanation. This has not been followed in subsequent revisions (Blake 1996). Hartley (1981) determined that the subgenus *Acesta* Strelzov was preoccupied in the Mollusca and replaced it with *Acmira*. More recently, Aguirrezabalaga (2012) determined that *Allia* Strelzov was a homonym in the Lepidoptera and replaced it with *Strelzovia*. The debate regarding the use and validity of *Paraonides* Cerruti, 1909 versus *Paraonella* Strelzov, 1973 is discussed in detail further in the chapter.

In order to stabilize the family name Paraonidae Cerruti, 1909, the International Commission of Zoological Nomenclature (ICZN) ruled that the Paraonidae would be the family group name over Levinseniidae Mesnil & Caullery, 1898 (Melville 1979). The type species of *Paraonis* was designated as *Aonides fulgens* Levinsen, 1883. The type species of *Levinsenia* was designated as *Aonides gracilis* Tauber, 1879. In this same ruling, the genus *Tauberia* Strelzov, 1973 was referred to synonymy with *Levinsenia*.

Following these revisions, there are eight currently accepted genera: *Aparaonis*, *Aricidea* (with four subgenera), *Cirrophorus*, *Levinsenia*, *Paradoneis*, *Paraonella*, *Paraonis*, and *Sabidius*.

### Genera diagnosis

### Family Paraonidae Cerruti, 1909

### Type genus *Paraonis* Cerruti, 1909

**Diagnosis:** Body elongate, thread-like, often coiled, smooth, epidermis lacking papillae. Prostomium forming a distinct bluntly conical "head"; with single medial antenna present or absent; papilla-like sensory organ often present on the tip of prostomium; nuchal organs ciliated curved, comma-shaped slits limited to posterior margins of prostomium; eyes present or absent; palps absent, but palpal nerves identified. Peristomium limited to ventral lip of the mouth. Segments distinct, biramous, generally similar along body; parapodia with simple papillate or ridged podia; postchaetal notopodial lobes or lamellae present or absent; dorsal and ventral cirri absent. Branchiae dorsal to notopodia, flattened, usually limited to few or many anterior segments or entirely absent. Ciliated lateral organs present between noto- and neuropodia. Aciculae absent; chaetae include capillaries and a variety of modified noto- and/or neurochaetae; lyrate chaetae present in the notopodia of some species; aristate, hooked, smooth, or fimbriated spines in neuropodia of many species, rarely in notopodia. Pygidium with three or more cirri.

**Remarks:** As presently defined, the Paraonidae include eight genera and about 140 species. Two genera, *Aparaonis* and *Sabidius*, are monotypic; six other genera include the bulk of the known species, with more than half of those belonging to the genus *Aricidea* currently partitioned into four subgenera. Each genus is diagnosed in the following, with the currently known species listed together with their known geographic distributions and depth ranges. As noted in the "Biology and Ecology" section, paraonids are species rich in deep-sea habitats and numerous species await descriptions, which should bring the species total for the family to well over 200 based on provisional identifications published thus far from the east and west coasts of North America alone (Blake and Grassle 1994, Blake and Hilbig 1994, Hilbig 1994, Hilbig and Blake 2006, Blake *et al.* 2009).

### Genus *Aparaonis* Hartman, 1965 (one species)

**Type species:** *Aparaonis abyssalis* Hartman, 1965, by monotypy

**Diagnosis** (emended, based on holotype LACM-AHF Poly 661): Body long, slender, anterior five segments weakly expanded, rest of body with segments narrow, longer than wide (Fig. 7.3.1.1.5 A). Prostomium triangular without medial antenna, ciliary bands, or distinct terminal sense organ; eyes absent; nuchal organs not observed. Branchiae entirely absent. Parapodia with distinct rounded lobes throughout, largest in far posterior segments. Parapodia lateral in all segments except far posterior chaetigers, where noto- and neuropodia shifted dorsally (Fig. 7.3.1.1.5 B). Chaetigers 1–4 with elongate, flattened postchaetal lamellae (Fig. 7.3.1.1.5 A). Chaetae include smooth capillaries from chaetiger 1 in both noto- and neuropodia, mostly replaced by numerous elongate spines (Fig. 7.3.1.1.5 C) in far posterior chaetigers where parapodia shift dorsally. Pygidium unknown.

**Remarks:** *Aparaonis abyssalis* is known from a single, mostly complete, specimen from off New England in 4,436 m (Hartman 1965). The holotype is fragile, with a

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narrow, elongate body; it has 27 chaetigers broken into three pieces that collectively measure 5.16 mm long and 0.3 mm wide. In the original description, branchiae were said to be present on chaetigers 2–4. However, these are not branchiae; they are notopodial postchaetal lamellae with one also visible on the right side of chaetiger 1 (broken off on the left side) and well developed on both sides of chaetigers 2–4 (Fig. 7.3.1.1.5 A). The noto- and neuropodia include prominent rounded podial lobes, sometimes weakly stalked that bear fascicles of long, smooth capillaries. These podial lobes are laterally placed along most of the body but become larger and shifted dorsally in the posteriormost segments (Fig. 7.3.1.1.5 B) transitioning from segments with all capillaries to modified segments that bear fascicles of up to eight long curved brass-colored spines producing a unique posterior armature not known for other paraonids.

These new observations on the holotype of *A. abyssalis* describe an entirely unique paraonid. Although the absence of branchiae has been reported in some paraonid species, the elongate postchaetal lamellae of chaetigers 1–4 and the presence of modified posterior parapodia that are shifted dorsally and that bear numerous long curved spines are not known for other paraonids. The dorsally shifted parapodia of posterior segments is reminiscent of orbiniids, but *Aparaonis* lacks a distinct peristomium, aciculae, and camerated or bristled capillaries characteristic of Orbiniidae. Among other paraonids, *A. abyssalis* is perhaps most similar to *Levinsenia uncinata* (Hartman 1965), known from the same and adjacent locations off New England, in lacking branchiae and having thick spines in posterior neuropodia. However, *A. abyssalis* has elongate notopodial lamellae in some anterior segments and modified posterior spines in both noto- and neuropodia of posterior segments instead of only neuropodia. Unfortunately, the remote abyssal habitat likely precludes any recollection of this species in the near future.

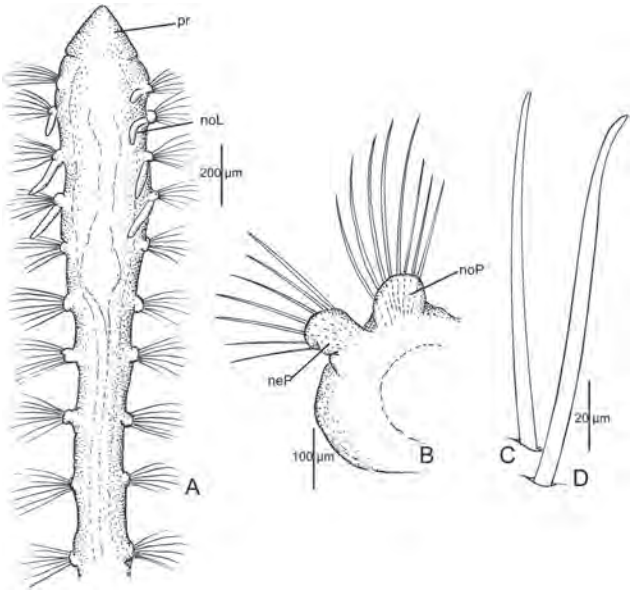


**Fig. 7.3.1.1.5:** *Aparaonis abyssalis*. Holotype (LACM-AHF Poly 661). A, Anterior end, dorsal view. B, Far posterior parapodium, anterior view. C, modified notochaeta. D, Modified neurochaeta. neP, neuropodium; noL, notopodial lamellae; noP, notopodium; pr, prostomium. All original.

**Genus *Aricidea* Webster, 1879 (~75 species)**

**Type species:** *Aricidea fragilis* Webster, 1879, by monotypy

**Description:** Body long, slender, threadlike, cylindrical in cross-section, with numerous segments. Prostomium more or less conical; median antenna present (Fig. 7.3.1.1.6 A, E); pair of nuchal slits present; terminal sensory organ present. Peristomium more or less fused to prostomium, ventrally forming lateral lips of the mouth; ventral part of first two segments forming posterior lip. Three prebranchial segments. Branchiae simple, located dorsal to notopodia, paired, strap-like, ciliated, with variable shape and size along body (Fig. 7.3.1.1.6 B) or branchiae absent. Parapodia biramous, lacking distinct chaetal lobes, but with digitiform to filiform postchaetal notopodial lobes (=dorsal cirri); with or without postchaetal neuropodial lobes on some anterior segments (=ventral cirri). Chaetae include simple capillaries in both noto- and neuropodia and modified neurochaetae of various types in postbranchial segments (Fig. 7.3.1.1.6 C–D, F–H, K). Pygidium with two to three filiform anal cirri.

**Remarks:** The genus *Aricidea* is the largest in the Paraonidae, with more than 75 known species. Strelzov (1973) divided the genus into four subgenera: *Aricidea sensu stricto, Aedicira* Hartman, 1957, *Allia* Strelzov, 1973, and *Acesta* Strelzov, 1973. The basis for Strelzov's separation of *Aricidea* into subgenera was the nature of the modified neurochaetae, wherein he was able to organize species into discrete groupings. These subgenera have largely been accepted by subsequent workers. However, Hartley (1981) pointed out that chaetal differences are too indistinct to justify full generic status for the four subgenera. Hartley also pointed out that the name *Acesta* was preoccupied in the Mollusca and renamed the homonym *Acmira* Hartley, 1981 Recently, Aguirrezabalaga (2012) established *Strelzovia*, replacing *Allia* Strelzov, 1973, after determining it was a homonym of *Allia* Walker, 1868 in the Lepidoptera. Most recent papers have used these four subgenera in their treatment of *Aricidea*.

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**Subgenus *Aricidea sensu stricto***

**Type species:** *Aricidea fragilis* Webster, 1879

**Diagnosis:** Prostomium elongate; prostomial antenna cirriform, often articulate (Fig. 7.3.1.1.6 A). Posterior lip of the mouth extending onto the ventral sides of two anterior setigerous segments. Parapodia of the branchial region bear well-developed notopodial lobes, typical for genus (Fig. 7.3.1.1.6 B). Modified neurochaetae pseudocompound or hooked typically with subterminal spine attached on concave side of shaft (Fig. 7.3.1.1.6 D, F–H).

**Remarks:** The long appendage on the modified neurochaetae are characteristic of the stem subgenus. Several species in this subgenus have an articulated antenna.

1. *Aricidea* (*Aricidea*) *capensis* Day, 1961. Africa, southern coast, 3–10 m; also recorded from the Adriatic.
2. *Aricidea* (*Aricidea*) *fragilis* Webster, 1879. U.S. mid-Atlantic coastal waters, intertidal to shallow shelf depths.
3. *Aricidea* (*Aricidea*) *longicirrata* Hartmann-Schröder, 1965. Chile, shelf depths, 136–264 m; western Mexico.
4. *Aricidea* (*Aricidea*) *longobranchiata* Day, 1961. Coastal waters of South Africa, 5–95 m.
5. *Aricidea* (*Aricidea*) *minima* Strelzov, 1973. Off Argentina, 142 m; western Mexico, shelf depths.
6. *Aricidea* (*Aricidea*) *minuta* Southward, 1956. Northern Europe, Irish Sea, North Sea, Kattegat, Oresund, low water to ca. 60 m.
7. *Aricidea* (*Aricidea*) *multiantennata* Lovell, 2002. Off Thailand, Andaman Sea, 19–79 m.

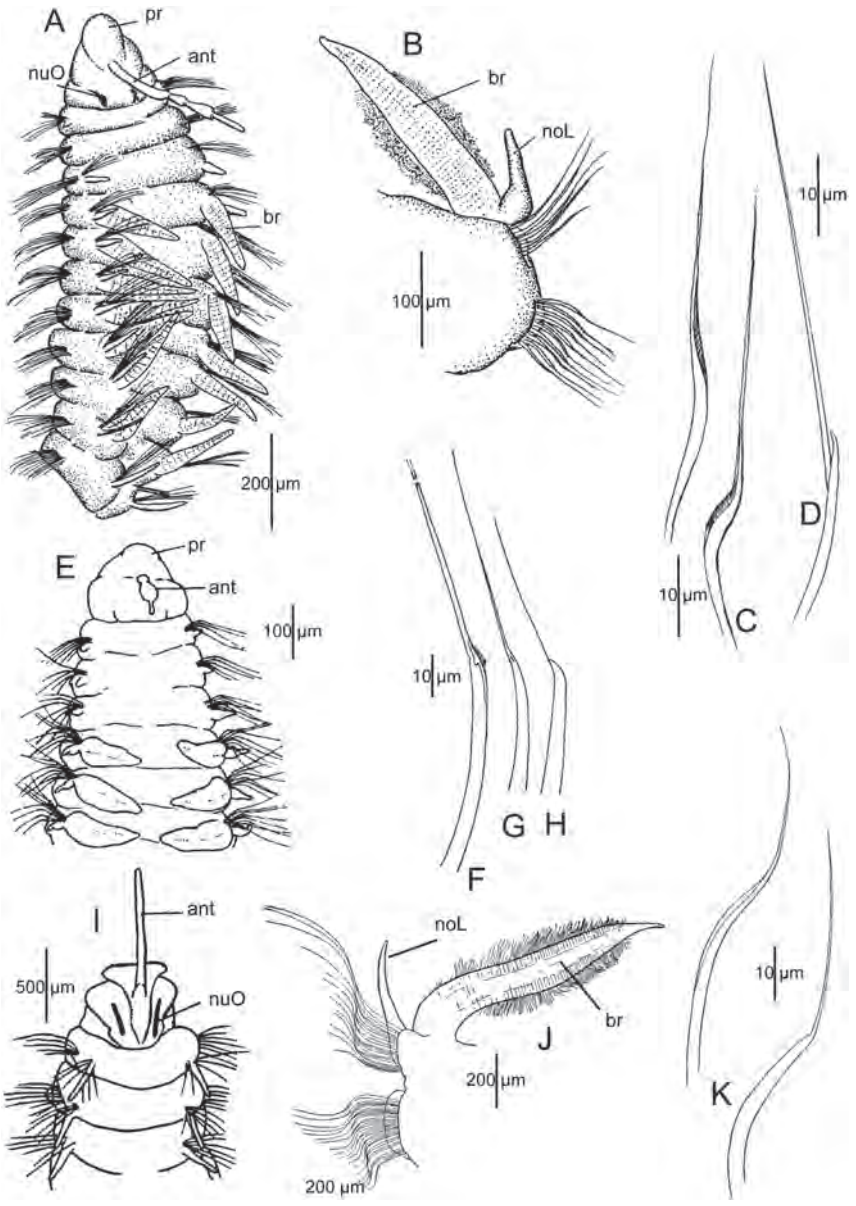


**Fig. 7.3.1.1.6:** Examples of *Aricidea* (*Aricidea*) and *Aricidea* (*Aedicira*) species. A–D, *Aricidea* (*Aricidea*) *wassi*: A, anterior end, dorsal view; B, parapodium from fourth branchial segment; C, capillaries from branchial noto- and neuropodia; D, modified neurochaeta. E–H, *Aricidea* (*Aricidea*) *pseudoarticulata*: E, anterior end, dorsal view; F–H, modified neurochaetae. I–K, *Aricidea* (*Aedicira*) *pacifica*: I, anterior end, dorsal view; J, branchial segment; K, posterior neurochaetae. ant, antenna; br, branchia; noL, notopodial lamella; nuO, nuchal organ; pr, prostomium. A–D, After Imajima (1973); E–H, after Hobson (1972); I, after Strelzov (1973/1979); J–K, after Hartman (1944).

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8. *Aricidea* (*Aricidea*) *petacalcoensis* León-González, Hernández-Guevara & Rodríguez-Valencia, 2006. Western Mexico, shelf depths.
9. *Aricidea* (*Aricidea*) *pseudoarticulata* Hobson, 1972. Off California, 80–90 m; Gulf of Mexico, off Florida, 27 m; northeast Atlantic, off Portugal, 25–50 m.
10. *Aricidea* (*Aricidea*) *rosea* Reish, 1968. Western Mexico, Bahía de los Angeles, subtidal.
11. *Aricidea* (*Aricidea*) *sanmartini* Aguado & López, 2003. Pacific Panama, intertidal.
12. *Aricidea* (*Aricidea*) *similis* Fauchald, 1972. Western Mexico, shelf depths.
13. *Aricidea (Aricidea) thailandica* Lovell, 2002. Off Thailand, Andaman Sea, 32–65 m.
14. *Aricidea* (*Aricidea*) *wassi* Pettibone, 1965. U.S. Atlantic coastal waters, 10–45 m; Gulf of Mexico, 15–36 m; off California, 80–1,480 m; Western Mexico, shelf depths; Adriatic Sea, 54–111 m; North Sea off England, 143 m; Japan, 45–50 m.

**Subgenus *Aedicira* Hartman, 1957**

**Type species:** *Aricidea pacifica* Hartman, 1944

**Diagnosis:** Prostomium small, somewhat flattened dorsally, truncate along anterior margin; antenna cirriform (Fig. 7.3.1.1.6 I). Posterior lip of the mouth extending onto the venter of first setigerous segment and bearing a small medial posterior lobe continuing onto setiger 2. Modified neurochaetae entirely absent; all chaetae capillaries without fringe or basal enlargement (Fig. 7.3.1.1.6 K).

**Remarks:** *Aricidea* (*Aedicira*) *pacifica* Hartman, 1944 has been reported from southern California (Hartman, 1944, 1957, 1969), the Yellow Sea (Strelzov 1973), and Japan (Imajima 1973). Hartley (1984) questioned the validity of *A. pacifica* because the posterior end had never been observed, precluding confirmation that modified chaetae might not actually be present in the far posterior segments; however, the reports by Strelzov (1973/1979) and Imajima (1973) clearly imply the absence of modified neurochaetae. Apart from the absence of modified neurochaetae, species of *Aricidea* (*Aedicira*) represent typically appearing *Aricidea* species in the nature of the medial antenna, parapodia, branchiae, and notopodial lamella (Fig. 7.3.1.1.6 J). All five species assigned to this subgenus are poorly known.

1. *Aricidea* (*Aedicira*) *alisetosa* Fauchald, 1972. Mexico, Gulf of California, 2334–3,111 m.
2. *Aricidea* (*Aedicira*) *antarctica* Hartmann-Schröder & Rosenfeldt, 1988. Off Antarctic Peninsula, type locality, Joinville Island group, 220+ m. Transferred to subgenus *Aedicira* by Hartmann-Schröder and Rosenfeldt (1990).
3. *Aricidea* (*Aedicira*) *ascensionensis* Hartmann-Schröder, 1992. South Atlantic Ocean, Ascension Island, intertidal.
4. *Aricidea* (*Aedicira*) *oregonensis* Fauchald & Hancock, 1984. Off Oregon, 2,400 m.
5. *Aricidea* (*Aedicira*) *pacifica* Hartman, 1944. Eastern Pacific, California to Baja California, Mexico; intertidal to shallow subtidal; also recorded from Yellow Sea, Japan.

**Subgenus *Acmira* Hartley, 1981**

**Type species:** *Aricidea catherinae* Laubier, 1967. Designated by Hartley (1981).

**Synonym:** *Acesta* Strelzov, 1973. Homonym of *Acesta* H. & A. Adams, 1858 in the Mollusca. *Fide* Hartley 1981.

**Diagnosis:** Prostomium pear shaped to oval, with rounded anterior margin; antenna simple, unbranched, not articulate (Fig. 7.3.1.1.7 A, C, E, G, I). Posterior lip of the mouth on ventral surface of first two setigers (Fig. 7.3.1.1.7 E). Capillary noto- and neurochaetae of postbranchial segments same thickness. Modified neurochaetae heavy, curved spines with or without accessory filaments, teeth, bristles, or sheaths (Fig. 7.3.1.1.7 B, D, F, H, J); these chaetae always thicker than notochaetae and accompanying capillary neurochaetae.

**Remarks:** Species of *Aricidea* (*Acmira*) are readily recognized by having a wide variety of modified neurochaetae. Some of these species are among the most common and well-known paraonids including: *A. catherinae, Aricidea cerrutii,* and *A. simplex*.

1. *Aricidea* (*Acmira*) *annae* Laubier, 1967. France, Mediterranean, 30–55 m.
2. *Aricidea* (*Acmira*) *assimilis* Tebble, 1959. Mediterranean Sea; Red Sea, shelf depths; Western Mexico, Baja, California; off Thailand, Andaman Sea, 19–1,155 m.
3. *Aricidea* (*Acmira*) *bispinata* Cantone, 1995. Antarctica, Ross Sea, Terra Nova Bay, 568 m.
4. *Aricidea* (*Acmira*) *brevicornis* (Hartmann-Schröder, 1962). Peru, 9 m.
5. *Aricidea* (*Acmira*) *catherinae* Laubier, 1967. Widespread in northern hemisphere, intertidal to shelf depths. [*Aricidea eximia* Imajima, 1973]. *Fide* Lovell, 2002. [*Aricidea elongata* Imajima, 1973]. *Fide* Lovell, 2002.
6. *Aricidea* (*Acmira*) *cerrutii* Laubier, 1966. Widespread globally, chiefly in the northern hemisphere, low water to shelf depths.
7. *Aricidea* (*Acmira*) *crassicapitis* Fauchald, 1972. Off Western Mexico, Cedros Island to Acapulco, shelf and slope depths.
8. *Aricidea* (*Acmira*) *finitima* Strelzov, 1973. South Africa; Uruguay; Scotia Sea; California; shelf depths.

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9. *Aricidea* (*Acmira*) *flava* Zhou & Reuscher, 2013. China, coastal waters of Bohai and Yellow Seas, 14–41 m.
10. *Aricidea (Acmira) hirsuta* Arriaga-Hernández, Hernández-Alcántara & Solís-Weiss, 2013. Southern Gulf of Mexico, shallow water.
11. *Aricidea* (*Acmira*) *horikoshii* Imajima, 1973. Japan, central California; low water to 90 m.
12. *Aricidea (Acmira) jeanetese* Langeneck, Busoni, Aliani & Castelli, 2017. Mediterranean Sea, 600–2,100 m. New name for *Arcidea trilobata* Laubier & Ramos, 1974. Homonym of *A. triblobata* Imajima 1973.
13. *Aricidea* (*Acmira*) *laubieri* Hartley, 1981. Northeast Atlantic, Celtic Sea to North Sea; Portugal, Bay of Biscay.
14. *Aricidea* (*Acmira*) *lopezi* Berkeley & Berkeley, 1956. Eastern Pacific, British Columbia to Mexico; Mediterranean, South Africa, Sea of Japan, 12–1,100 m.
15. *Aricidea* (*Acmira*) *mirifica* Strelzov, 1973. Antarctica, 2,948 m; off New Guinea, 799 m.
16. *Aricidea* (*Acmira*) *philbinae* Brown, 1976. East and west coasts of Florida, intertidal to 1 m.
17. *Aricidea* (*Acmira*) *pigmenta* Carrasco, 1976. Chile, Concepción Bay, 12–50 m.
18. *Aricidea* (*Acmira*) *punctata* (Hartmann-Schröder 1962). Peru, 9 m.
19. *Aricidea* (*Acmira*) *rubra* Hartman, 1963. Off California, shelf and upper slope depths, 98–600 m.
20. *Aricidea* (*Acmira*) *simonae* Laubier & Ramos, 1974. Mediterranean, Adriatic, North Sea; Cape Breton Canyon, Bay of Biscay, 30–1,113 m.
21. *Aricidea* (*Acmira*) *simplex* Day, 1963. Widespread globally in continental slope depths, 100–3,000 m.
22. *Aricidea* (*Acmira*) *strelzovi* Hartmann-Schröder & Rosenfeldt, 1990. Antarctica; type-locality off Elephant Island, 363 m.
23. *Aricidea* (*Acmira*) *tetrabranchia* Hartman & Fauchald, 1971. Western North Atlantic, slope and abyssal depths.
24. *Aricidea* (*Acmira*) *trilobata* Imajima, 1973. Japan, shelf depths; off California, slope depths.

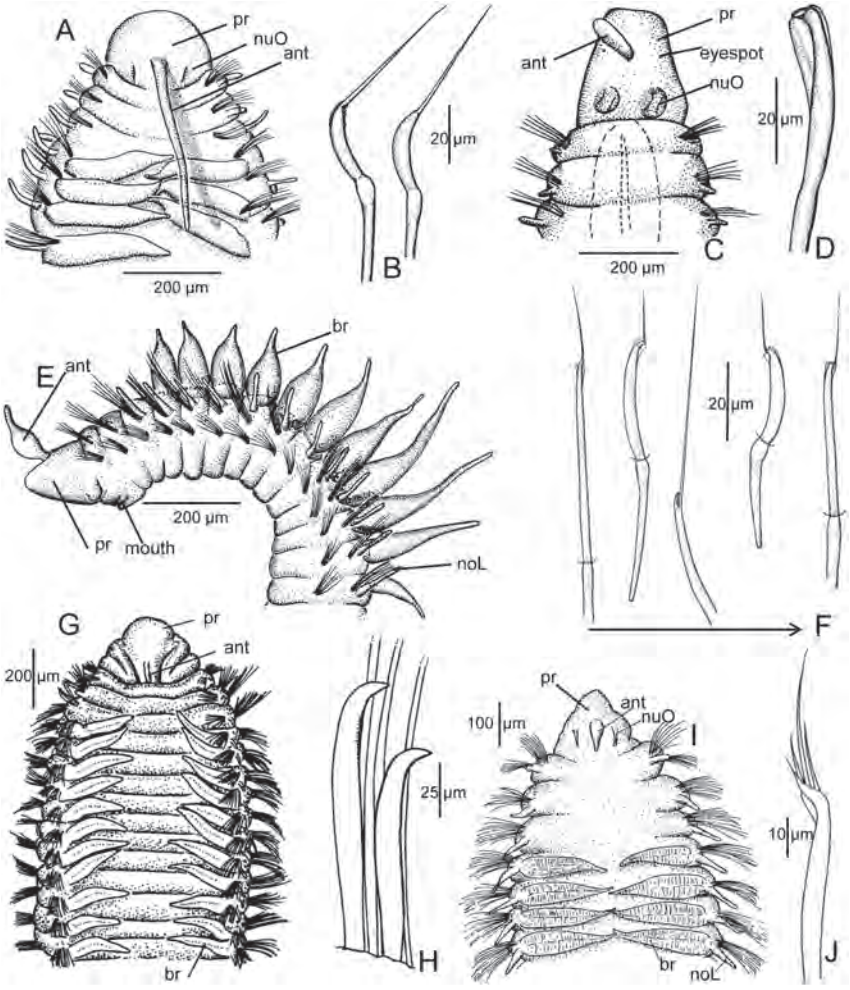


**Fig. 7.3.1.1.7:** Examples of *Aricidea* (*Acmira*) species. A, B, *Aricidea* (*Acmira*) *annae*: A, anterior end, dorsal view; B, modified neurochaetae. C, D, *Aricidea* (*Acmira*) *cerruti*: C, anterior end, dorsal view; D, modified neurochaeta. E, F, *Aricidea* (*Acmira*) *catherinae*: E, anterior end, lateral view; F, modified neurochaetae. G, H, *Aricidea* (*Acmira*) *simplex:* G, anterior end, dorsal view; H, modified neurochaetae. I, J, *Aricidea* (*Acmira*) *rubra*: I, anterior end, dorsal view; J, modified neurochaeta. ant, antenna; br, branchia; noL, notopodial lamella; nuO, nuchal organ; pr, prostomium. A–F, After Laubier (1967); G–J, after Blake (1996).

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**Subgenus *Strelzovia* Aguirrezabalaga, 2012**

**Type species:** *Aricidea albatrossae* Pettibone, 1957. Designated by Aguirrezabalaga, 2012

**Synonym:** *Allia* Strelzov, 1973. Homonym of *Allia* Walker, 1868 in the Lepidoptera.

**Diagnosis:** Prostomium short, often pear shaped, flattened, or rounded along anterior margin (Fig. 7.3.1.1.8 A, C, G, E); antenna simple or branched (Fig. 7.3.1.1.8 E), not articulate; often very long (Fig. 7.3.1.1.8 A, G). Posterior lip of the mouth on ventral surface of first two chaetigers or only on first; in latter case, chaetiger 2 forms anteriorly directed protuberance bisected by longitudinal groove (Fig. 7.3.1.1.8 C). Branchiae present (Fig. 7.3.1.1.8 H) or absent. Chaetae include simple capillaries (Fig. 7.3.1.1.8 I) and modified neurochaetae (Fig. 7.3.1.1.8 B, D, J, F). Postbranchial capillary neurochaetae thicker than corresponding notochaetae, transitioning to modified neurochaetae along the body; modified chaetae include enlarged capillaries with elongate terminal spine or mucron, or shorter, curved chaetae with or without terminal extension.

**Remarks:** Species of the subgenus *Strelzovia* are difficult to distinguish based on the morphology of modified chaetae because if the thin terminal extension is missing or broken, the resulting chaeta appear simple and curved. Consequently, the nature of the antenna, form of the branchiae, and prostomium are important characters for species recognition.

1. *Aricidea* (*Strelzovia*) *aberrans* Laubier & Ramos, 1974. Mediterranean, 2,090–2,292 m.
2. *Aricidea* (*Strelzovia*) *abranchiata* Hartman, 1965. Off New England, slope depths 1,500–2,000; Barents Sea, 452–586 m.
3. *Aricidea* (*Strelzovia*) *abyssalis* Laubier & Ramos, 1974. Mediterranean Sea, 90–827 m.
4. *Aricidea* (*Strelzovia*) *albatrossae* Pettibone, 1957. Western North Atlantic, off Massachusetts to Chesapeake Bay, 1,434–2,900 m.
5. *Aricidea* (*Strelzovia*) *alisdairi* Hasan, 1960. Indian, Karachi coast, intertidal.
6. *Aricidea* (*Strelzovia*) *antennata* Annenkova, 1934. Eastern Pacific, western Canada to Mexico; western Pacific, off Japan, Sea of Okhotsk; Atlantic Ocean, Capebreton Canyon; 492–113 m.
7. *Aricidea* (*Strelzovia*) *australiensis* Hartmann-Schröder, 1990. Australia, Queensland, near Maryborough, Great Sandy Strait, low water.
8. *Aricidea* (*Strelzovia*) *belgicae* (Fauvel 1936). Antarctica, 426–1,432 m.
9. *Aricidea* (*Strelzovia*) *bifurcata* Aguirrezabalaga & Gil, 2009. Capebreton Canyon, Bay of Biscay, 492–495 m.
10. *Aricidea* (*Strelzovia*) *bryani* Gaston & McLelland, 1996. Gulf of Mexico, coastal Mississippi, shallow subtidal.
11. *Aricidea* (*Strelzovia*) *bulbosa* Hartley, 1984. Gulf of Suez, 34 m.
12. *Aricidea* (*Strelzovia*) *claudiae* Laubier, 1967. Mediterranean and Black Sea; Capebreton Canyon, Bay of Biscay, 15–576 m.
13. *Aricidea* (*Strelzovia*) *curviseta* Day, 1963. South Africa, shelf depths, 79–183 m.
14. *Aricidea* (*Strelzovia*) *facilis* Strelzov, 1973. Pacific Ocean, slope and abyssal depths, 1,952–5,030 m; Southern Ocean, 3,076 m.
15. *Aricidea* (*Strelzovia*) *hartleyi* Blake, 1996. Off California, 49–98 m; off Thailand, Andaman Sea, 19–98 m.
16. *Aricidea* (*Strelzovia*) *hartmanae* (Strelzov, 1968). Barents Sea, 105–195 m.
17. *Aricidea* (*Strelzovia*) *longisetosa* Sardá, Gil, Taboada & Gili, 2009. NW Mediterranean canyons off Spain and France, 30–500 m.
18. *Aricidea* (*Strelzovia*) *maialenae* Aguirrezabalaga & Gil, 2009. Capebreton Canyon, Bay of Biscay, 480–968 m.
19. *Aricidea* (*Strelzovia*) *mariannae* Katzmann & Laubier, 1975. Adriatic Sea, 111–225 m.
20. *Aricidea* (*Strelzovia*) *mediterranea* (Laubier and Ramos, 1974). Mediterranean, shallow subtidal.
21. *Aricidea* (*Strelzovia*) *mirunekoa* Aguirrezabalaga & Gil, 2009. Capebreton Canyon, Bay of Biscay, 492–1,113 m.
22. *Aricidea* (*Strelzovia*) *monicae* Laubier, 1967. Western Mediterranean Sea, 200–300 m; California, 600 m.
23. *Aricidea* (*Strelzovia*) *nekanae* Aguirrezabalaga & Gil, 2009. Capebreton Canyon, Bay of Biscay, 492–495 m.
24. *Aricidea* (*Strelzovia*) *oculata* Hartmann-Schröder & Rosenfeldt, 1990. Antarctica; type locality off Elephant Island, 290 m.
25. *Aricidea (Strelzovia) parabelgicae* López & Sikorski, 2017. Off Norway, 252–300 m.
26. *Aricidea* (*Strelzovia*) *pisanoi* Montiel & Hilbig, 2004. Off Southern Chile, Strait of Magellan; Drake Passage; 14–382.
27. *Aricidea* (*Strelzovia*) *pseudannae* Katzmann & Laubier, 1975. Adriatic Sea, 66–645 m.
28. *Aricidea* (*Strelzovia*) *pulchra* Strelzov, 1973. Pacific Ocean, slope and abyssal depths, 1,602–5,511 m.
29. *Aricidea* (*Strelzovia*) *quadrilobata* Webster & Benedict, 1887. Western North Atlantic, shallow subtidal to shelf depths; reported widely elsewhere, but likely refer to other species.
30. *Aricidea* (*Strelzovia*) *ramosa* Annenkova, 1934. Eastern Pacific, Puget Sound to western Mexico, 10–2,000 m; western Pacific, Japan, 44–2,400 m.

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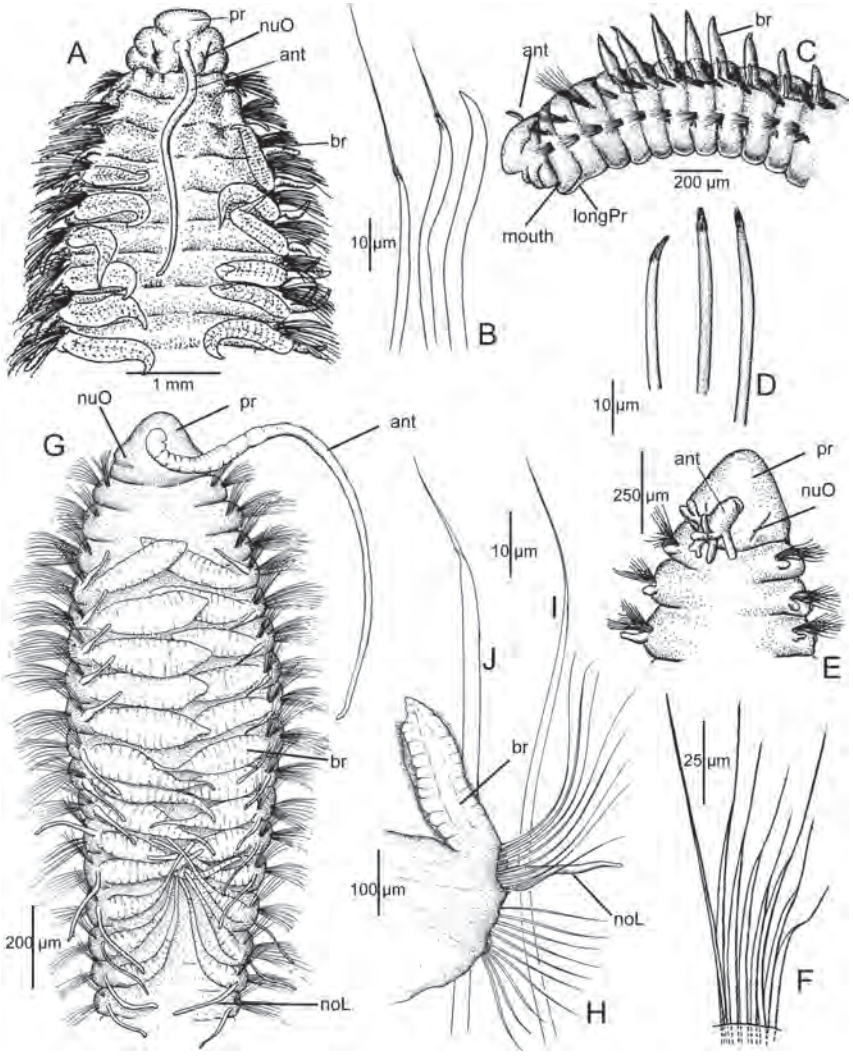


**Fig. 7.3.1.1.8:** Examples of *Aricidea* (*Strelzovia*) species. A, B, *Aricidea* (*Strelzovia*) *antennata*: A, anterior end, dorsal view; B, modified neurochaetae. C, D, *Aricidea* (*Strelzovia*) *monicae*: C, anterior end, dorsal view; D, modified neurochaetae. E, F, *Aricidea* (*Strelzovia*) *ramosa*: E, anterior end, dorsal view; F, modified neurochaetae; G, H, *Aricidea* (*Strelzovia*) sp. (eastern Pacific hydrothermal vents): G, anterior end, dorsal view; H, branchial parapodium, anterior view. I, Thoracic notochaeta. J, Posterior modified neurochaeta. ant, antenna; br, branchia; longPr, longitudinal protuberance; noL, notopodial lobe; nuO, nuchal organ; pr, prostomium. A–B, After Imajima (1973); C, D, after Laubier (1967); E, F, after Strelzov (1973/1979); G–J, originals.

31. *Aricidea* (*Strelzovia*) *sardai* Aguirrezabalaga & Gil, 2009. Capebreton Canyon, Bay of Biscay, 1,000 m.
32. *Aricidea* (*Strelzovia*) *suecica* Eliason, 1920. North Sea, British Isles, shelf depths.
33. *Aricidea* (*Strelzovia*) *taylori* Pettibone, 1965. Gulf of Mexico, Florida coast, intertidal.

**Genus *Cirrophorus* Ehlers, 1908 (nine species)**

**Type species:** *Cirrophorus branchiatus* Ehlers, 1908, by monotypy

**Diagnosis:** Body long, thin, but thickened and somewhat robust anteriorly. Prostomium with median antenna (Fig. 7.3.1.1.9 A, E, F); prostomial ciliary bands absent; longitudinal nuchal grooves present, distinctly separated from short peristomial ring, posterior margin of prostomium sometimes overlapping peristomium (Fig. 7.3.1.1.9 F); eyes present or absent. Three to five prebranchial segments. All notopodia with postchaetal lobes (Fig. 7.3.1.1.9 B, C); neuropodial lobes absent. Notochaetae include capillaries and either lyrate chaetae (Fig. 7.3.1.1.9 G) or modified spines (Fig. 7.3.1.1.9 D); neurochaetae include capillaries and sometimes heavier, curved ventral sabre chaetae; capillaries without lateral fringe. Branchiae from chaetigers 4–6, numbering 6–30 or more pairs. Pygidium rounded terminally, with three anal cirri.

**Remarks:** Species of *Cirrophorus* were reviewed by Strelzov (1973/1979), who combined the genus with *Paradoneis* Hartman (1965). Most subsequent authors except McLelland and Gaston (1994) have retained the separation of the two genera, and that concept is followed here. The presence of the median antenna in *Cirrophorus* and its absence in *Paradoneis* are a consistent and reliable character within a species and provides a convenient point of

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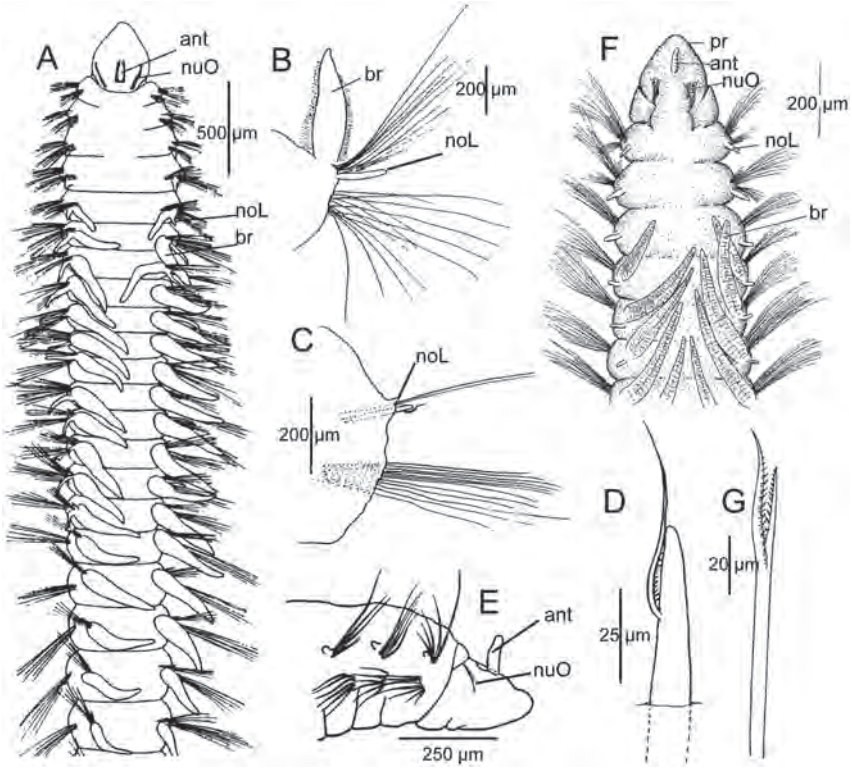


**Fig. 7.3.1.1.9:** Examples of species of *Cirrophorus*. A–D, *Cirrophorus branchiatus*: A, anterior end, dorsal view; B, parapodium from branchial region; C, posterior parapodium; D, modified notopodial spine. E–G, *Cirrophorus furcatus*: E, anterior end, lateral view; F, anterior end, dorsal view; G, furcate notochaetae. ant, antenna; br, branchia; noL, notopodial lamella; nuO, nuchal organ; pr, prostomium. A, After Glémarec (1966); B, after Imajima (1973); C, G, after Hartman (1957); D, F, after Blake (1996); E, after Strelzov (1973/1979).

separation between the two genera. Furthermore, there is also a qualitative difference in the size of *Cirrophorus* and *Paradoneis* species; the latter have thinner, less robust bodies than the former. In addition, most species of *Cirrophorus* have a reddish pigment caste to their bodies, whereas species of *Paradoneis* are generally unpigmented.

1. *Cirrophorus aciculatus* (Hartman, 1957). Southern California, shelf depths.
2. *Cirrophorus americanus* Strelzov, 1973. Western North Atlantic; off Uruguay, shelf and slope depths.
3. *Cirrophorus branchiatus* Ehlers, 1908. Widespread globally, shelf and slope depths.
4. *Cirrophorus brevicirratus* Strelzov, 1973. Off New England, 300–832 m; Scotia Sea, 400 m.
5. *Cirrophorus furcatus* (Hartman, 1957). Off California, shelf depths; also reported from the U.S. Atlantic and Gulf coasts.
6. *Cirrophorus longifurcata* (Hartmann-Schröder, 1965). Chile, Isla Mocha, 26–84 m.
7. *Cirrophorus miyakoensis* Imajima, 1973. Japan, Miyako Bay, 28 m.
8. *Cirrophorus nikebianchii* Langeneck, Barbieri, Maltagliatai & Castelli, 2017. Mediterranean Sea, 0.5–100 m. See also Erdoğan-Dereli *et al.* (2017).
9. *Cirrophorus turcicus* Erdoğan-Dereli, Çinar & Dağli, 2017. Mediterreanean Sea, Sea of Mamara, Agegean Sea, and Levantine Sea, intertidal to 500 m.

**Genus *Levinsenia* Mesnil, 1897 (22 species)**

**Type species:** *Aonides gracilis* Tauber, 1879, designated by the ICZN (Melville, 1979)

**Synonym:** *Tauberia* Strelzov, 1973

**Type species:** *Aonides gracilis* Tauber, 1879, Designated by Strelzov, 1973. *Fide* Melville (1979)

**Synonym:** *Periquesta* Brito & Núñez, 2002

**Type species:** *Periquesta canariensis* Brito & Núñez, 2002, by monotypy. *Fide* Giere *et al.* (2008) for synonymy.

**Diagnosis:** Body long, thin, threadlike. Prostomium lacking antenna (Fig. 7.3.1.1.10 A, D, H); with terminal sensory organ (Fig. 7.3.1.1.10 A); prostomial ciliary bands absent; nuchal organs along posterior prostomial margin (Fig. 7.3.1.1.10 B, D–E, H, J, K); lateral sensory organs (cheek organs) present or absent on the sides of prostomium. Prebranchial segments numbering 4–7; branchial segments few or many (Fig. 7.3.1.1.10 A, D, H). All notopodia with postchaetal lobes (Fig. 7.3.1.1.10 F, L); neuropodial postchaetal lobes absent. Notochaetae all capillaries; neurochaetae include capillaries and thick,

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curved modified spines; spines often curved with distinct fringe on convex side (Fig. 7.3.1.1.10 C, G); bidentate spines known (Fig. 7.3.1.1.10 I). Pygidium tapering, with two anal cirri.

**Remarks:** Species of *Levinsenia* are among the most abundant polychaetes in continental shelf and slope sediments, and many undescribed species are known (Blake *et al*. 2009). Several species such as *L. flava*, *L. gracilis*, and *L. oculata* have exceptionally wide geographic ranges and likely represent complexes of species.

1. *Levinsenia acutibranchiata* (Strelzov, 1973). Uruguayan shelf, 90–175 m.
2. *Levinsenia antarctica* (Strelzov, 1973). Antarctica, off Kemp and Mawson Coast, 1,340 m.
3. *Levinsenia brevibranchiata* (Strelzov, 1973). Off New Guinea, 1,790 m.
4. *Levinsenia canariensis* (Brito & Núñez, 2002). Canary Islands, shallow subtidal.
5. *Levinsenia demiri* Çinar, Dagli & Acik, 2011. Sea of Marmara and Mediterranean Seas, 10–200 m.
6. *Levinsenia duodecimbranchiata* Cantone, 1995. Antarctica, Terra Nova Bay, 668 m.
7. *Levinsenia flava* (Strelzov, 1973). Widespread globally in slope depths; type locality off New Guinea, 1,790 m.
8. *Levinsenia gracilis* (Tauber, 1879). Widespread globally, shallow water to slope depths, likely a complex of species.
9. *Levinsenia hawaiiensis* Giere, Ebbe & Erséus, 2007. Hawaii, subtidal, 5–75.6 m.
10. *Levinsenia japonica* Imajima, 1973. Japan, Sagami Bay, 145 m. (as subspecies of *L. gracilis*).
11. *Levinsenia kantauriensis* Aguirrezabalaga & Gil, 2009. Capebreton Canyon, Bay of Biscay, 492–1,113 m.

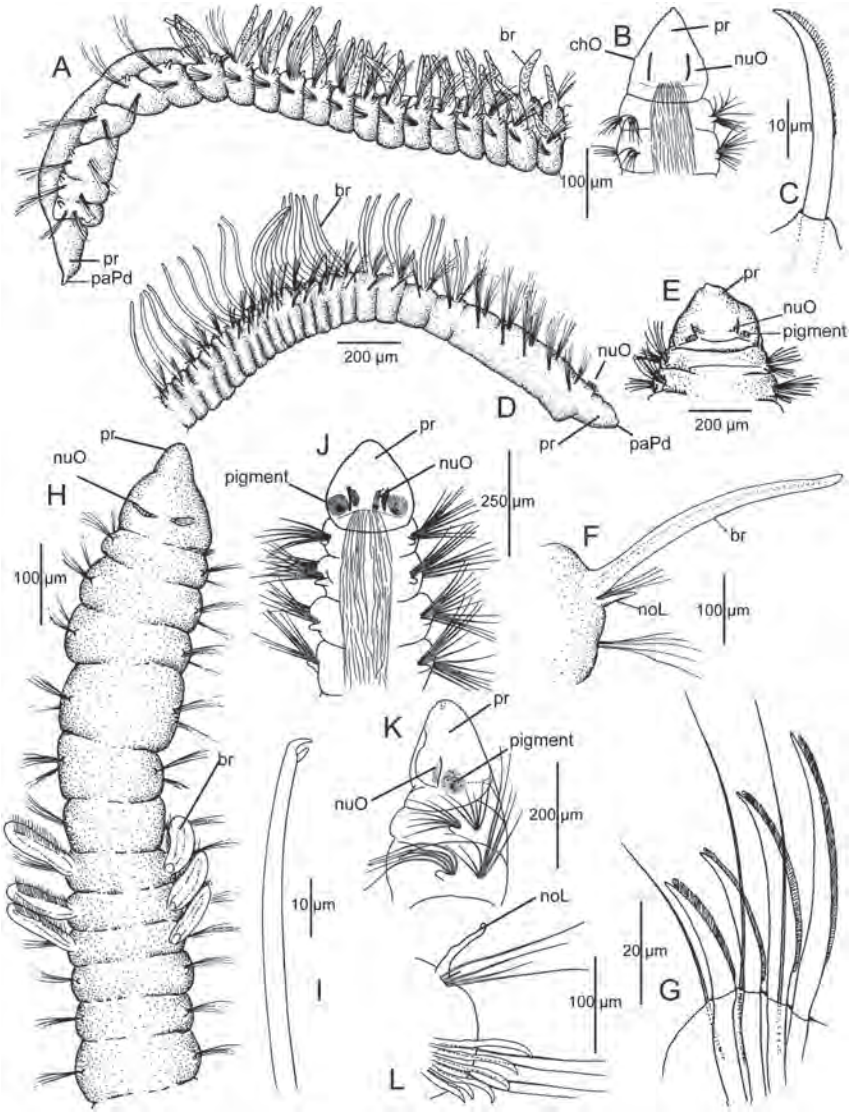


**Fig. 7.3.1.1.10:** Examples of species of *Levinsenia*. A–C, *Levinsenia gracilis*: A, anterior end, lateral view; B, anterior end, dorsal view; C, modified neurochaeta. D–G, *Levinsenia multibranchiata*: D, anterior end, lateral view; E, anterior end, dorsal view; F, parapodium from branchial region; G, modified neurochaetae and capillaries. H, I, *Levinsenia sp.* (eastern Pacific hydrothermal vents): H, anterior end, dorsal view; I, modified hooked neurochaeta. J–L, *Levinsenia oculata*: J, anterior end, dorsal view; K, same, lateral view; L, posterior parapodium, posterior view. br, branchia; chO, cheek organ; noL, notopodial lamella; nuO, nuchal organ; paPd, palpode; pr, prostomium. A, C–D, F–G, After Blake (1996); B, E, J–L after Strelzov (1973/1979); H–I originals.

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12. *Levinsenia kirbyae* Lovell, 2002. Off Thailand, Andaman Sea, 42–63 m.
13. *Levinsenia kosswigi* Çinar, Dagli & Acik, 2011. Sea of Marmara and Mediterranean Sea, 66–70 m.
14. *Levinsenia marmarensis* Çinar, Dagli & Acik, 2011. Sea of Marmara, 17–54 m.
15. *Levinsenia materi* Çinar & Dagli, 2013. Aegean Sea, 23 m.
16. *Levinsenia multibranchiata* (Hartman, 1957). Off California, 475–555 m.
17. *Levinsenia oculata* (Hartman, 1957). California to Mexico, shelf and slope depths; records globally likely refer to other species.
18. *Levinsenia oligobranchiata* (Strelzov, 1973). Pacific Ocean, in deep water, 3,388–3,860 m.
19. *Levinsenia pycnobranchiata* (Fauchald, 1972). Western Mexico, Gulf of California, 2,449 m, new combination.
20. *Levinsenia reducta* (Hartman, 1965). South Atlantic, 520–1,500 m.
21. *Levinsenia tribranchiata* Çinar, Dagli & Acik, 2011. Sea of Marmara and Mediterranean Sea, 17–100 m.
22. *Levinsenia uncinata* (Hartman, 1965). Atlantic and Pacific Oceans in slope and abyssal depths.

**Genus *Paradoneis* Hartman, 1965 (20 species)**

**Type species:** *Paraonis lyra* Southern, 1914, by monotypy

**Diagnosis:** Body long, thin, slightly enlarged anteriorly (Fig. 7.3.1.1.11 H). Median antenna absent; prostomial ciliary bands absent; longitudinal nuchal grooves along posterior prostomium margin (Fig. 7.3.1.1.11 A, H);

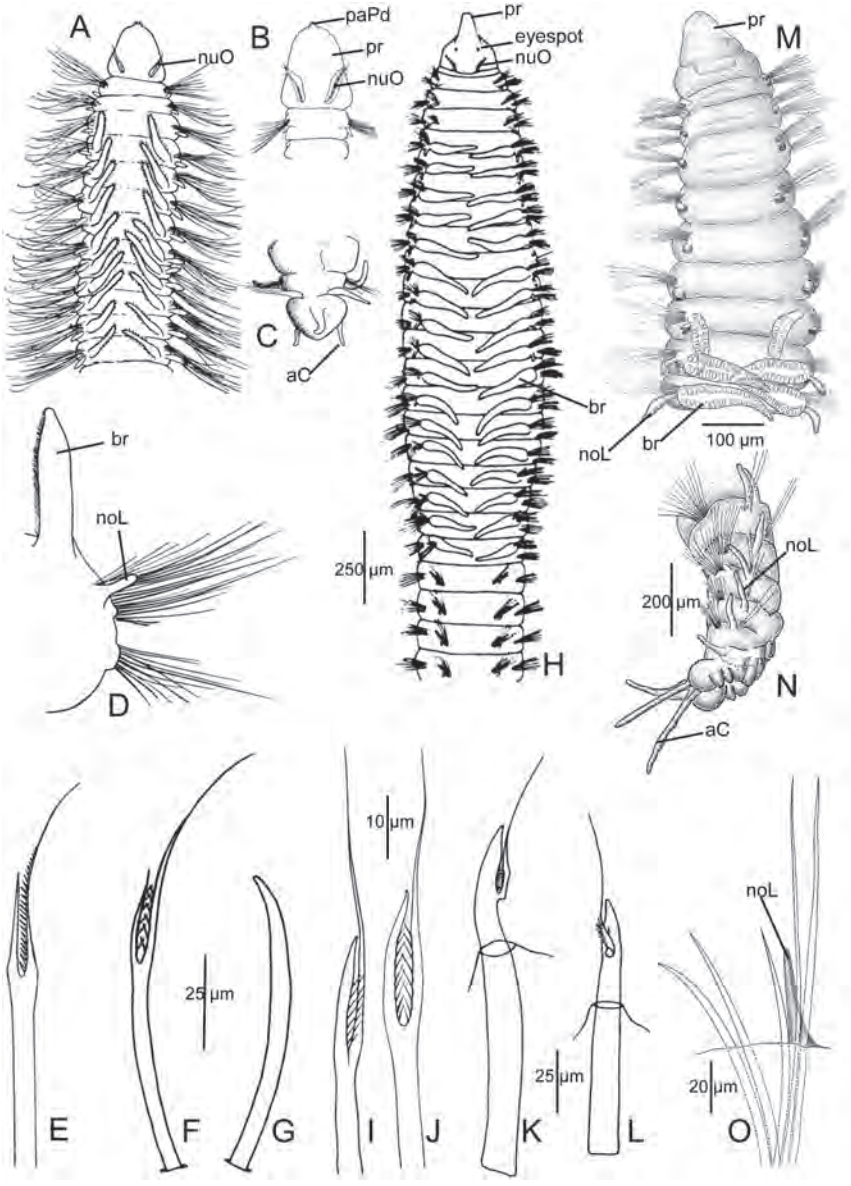


**Fig. 7.3.1.1.11:** Examples of species of *Paradoneis*. A–E, *Paradoneis lyra*: A, anterior end, dorsal view; B, same detail of prostomium; C, pygidium; D, thoracic branchiate parapodium, posterior view; E, furcate notochaeta. F, G, *Paradoneis eliasoni*: F, furcate notochaeta; G, modified neuropodial spine. H–L, *Paradoneis armata*: H, anterior end, dorsal view; I–J, furcate notochaetae; K–L, modified furcate spinous notochaetae. M–O, *Paradoneis drachi*: M, anterior end, dorsal view; N, posterior end with pygidium, lateral view; O, notopodium, with notopodial spines, capillaries, and notopodial lamella. aC, anal cirrus; br, branchia; noL, notopodial lamella; nuO, nuchal organ; paPd, palpode; pr, prostomium. A–E, After Southern (1914); F, G, after Mackie (1991); H–L, after Glémarec (1967); M–O, after Laubier and Ramos (1973).

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peristomium indistinct; eyes present or absent. Three to six prebranchial segments (Fig. 7.3.1.1.11 A, H, M); branchiae from setigers 4–7, numbering 6–30 or more pairs. All segments with notopodial postchaetal lobes (Fig. 7.3.1.1.11 A, D, M, N); neuropodial lobes absent. Notochaetae include capillaries and either lyrate chaetae (Fig. 7.3.1.1.11 E–F, I–J) modified spines (Fig. 7.3.1.1.11 K, L) or simple curved spines (Fig. 7.3.1.1.11 O); neurochaetae capillaries, without lateral fringe; a few species with one to two curved neuropodial spines in posterior segments (Fig. 7.3.1.1.11 G). Pygidium rounded terminally, with three anal cirri (Fig. 7.3.1.1.11 C, N).

**Remarks:** *Paradoneis* is differentiated from *Cirrophorus* chiefly by lacking a median antenna, having a more slender body, and by lacking any pigment. In contrast, species of *Cirrophorus* have an antenna, and their bodies are often robust and with a reddish or otherwise dark pigment. *Paradoneis armata* described by Glémarec (1966) and *P. lyra* recently redescribed by Mackie (1991) have been reported widely are among the best known species of the genus.

1. *Paradoneis abranchiata* Hartman, 1965. Western North Atlantic, slope and abyssal depths; Pacific Ocean, deep water.
2. *Paradoneis armata* Glémarec, 1966. Northeast Atlantic, shelf and slope depths; Mediterranean Sea, shelf depths; Andaman Sea, shelf depths.
3. *Paradoneis bathyilvana* Aguirrezabalaga & Gil, 2009. Northeast Atlantic, Cape Britton Canyon, 492–576 m.
4. *Paradoneis brunnea* (Hartmann-Schröder and Rosenfeldt, 1988).
5. *Paradoneis carmelitensis* Arriaga-Hernández, Hernández-Alcántara & Solís-Weiss, 2013.
6. *Paradoneis drachi* Laubier & Ramos, 1974. Mediterranean Sea, 115 m.
7. *Paradoneis eliasoni* Mackie, 1991. Northern Europe, 140–680 m.
8. *Paradoneis forticirrata* (Strelzov, 1973). Off California, 3,260 m; Slope of Kuril Basin, 2,780 m.
9. *Paradoneis harpagonea* (Storch 1967). Red Sea; Indian Ocean.
10. *Paradoneis hirsuta* Sardá, Gil, Taboada & Gili, 2009. Mediterranean Sea, Foix submarine canyon off Spain, 990 m.
11. *Paradoneis ilvana* Castelli, 1985. Mediterranean Sea, 30 m; Northeast Atlantic, Bay of Biscay, 35–50 m.
12. *Paradoneis lyra* (Southern, 1914). North Atlantic coastal waters, shelf depths; also reported widely in North America, South America, and South Africa.
13. *Paradoneis magdalenaensis* (León-González, Hernández-Guevara & Rodríguez-Valencia, 2006). Western Mexico, Baja California, 26–74 m.
14. *Paradoneis mikeli* Aguirrezabalaga & Gil, 2009. Northeast Atlantic, Cape Breton Canyon, 492–1,113 m; likely includes some records of *P. lyra* from Mediterranean Sea; Adriatic Sea; and North America.
15. *Paradoneis neapolitana* (Cerruti, 1909). Bay of Naples, 5 m. [No evidence of any re-description of the species since Cerruti].
16. *Paradoneis nipponica* (Imajima, 1973). Japan, intertidal to 500 m.
17. *Paradoneis perdidoensis* (McLelland and Gaston, 1994). Gulf of Mexico, Northwest Florida, Perdido Key, shallow subtidal.
18. *Paradoneis perkinsi* (McLelland and Gaston, 1994). Gulf of Mexico, Northwest Florida, Perdido Key, shallow subtidal.
19. *Paradoneis spinifera* (Hobson, 1972). Eastern Pacific, Puget Sound, Washington, 27–40 m; central California, 150 m.
20. *Paradoneis strelzovi* de León-González & Diaz-Castañeda, 2011. Western Mexico, Baja California, 30–78 m.

### Genus *Paraonella* Strelzov, 1973 (eight species)

**Type species:** *Paraonides nordica* Strelzov, 1968. Designated by Strelzov, 1973.

**Diagnosis:** Body long and thin; middle body segments may be moniliform (Fig. 7.3.1.1.12 A). Median antenna absent; eyes present or absent; nuchal grooves at posterior margin of prostomium (Fig. 7.3.1.1.12 D); peristomium indistinct. Prebranchial segments 3–4 (Fig. 7.3.1.1.12 D), with number and shape of branchiae variable; or branchiae entirely absent. All segments with notopodial postchaetal lobes (Fig. 7.3.1.1.12 B); neuropodial lobes absent. Noto- and neurochaetae all capillaries (Fig. 7.3.1.1.12 E), modified chaetae entirely absent. Pygidium rounded terminally, with two to three anal cirri (Fig. 7.3.1.1.12 C).

**Remarks:** The genus *Paraonella* is characterized by lacking a medial antenna and the complete absence of any type of chaeta other than capillaries. There is considerable disagreement, however, over the validity of *Paraonella* in that Strelzov (1973/1979) established the genus to replace *Paraonides* Cerruti, 1909, which he considered to be a synonym of *Paradoneis* (as *Cirrophorus*). Strelzov came to this conclusion because Cerruti (1909) only had a single specimen from the Bay of Naples of his type-species *P. neapolitana* that he had preserved in Canada balsam on a prepared slide. The original description and illustrations were prepared from this mounted specimen. Cerruti (1909:

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Plate 18, Fig. 21) illustrated a type of notochaeta with an expanded, leaf-like wing, which Day (1967) considered to be a kind of modified broad-winged capillary. Such a chaeta has not been reported for any other paraonid. Strelzov (1973/1979) was unable to locate Cerruti's original slide in the National Museum of Paris, and there were no other type specimens available or other more recent collections to confirm the presence or entire absence of modified chaetae. Strelzov (1973/1979) was able, however, to examine a prepared slide of a specimen that had been identified by M. Glémarec as *Paraonides neopolitana* from the Bay of Biscay, Glenan Islands, and discovered lyrate chaetae among the notochaetae. From this, he concluded that the light refraction coefficient of the mounting medium may have led Cerruti to confuse the two branches of the lyrate chaetae as single expanded chaeta. Strelzov (1973/1979) went on to refer the genus *Paraonides* and its type species, *P. neapolitana*, to *Paradoneis*, included by him in *Cirrophorus*, and prepared an illustrated description (Strelzov 1973/1979: Fig. 48) based largely on the Glémarec specimen and specimens from South Africa described by Day (1955, 1967) as *P. lyra capensis* Day, 1955 archived in the British Museum of Natural History.

Subsequent workers have either accepted Strelzov's revision and used *Paraonella* as a valid genus, with *Paraonides* referred to synonymy with *Paradoneis,* or disagreed with the revision and continued to use *Paraonides* as valid with *Paraonella* as a junior synonym. This is the current arrangement in WoRMS.

The first paper to appear supporting *Paraonides sensu* Cerruti (1909) was by Katzmann and Laubier (1975), who described a new species, *Paraonides myriamae* Katzmann & Laubier, 1975 from the Adriatic. In discussing Strelzov's (1973) revision, these authors offered no evidence to support or reject Strelzov's synonymy of *Paraonides* with *Paradoneis* (as *Cirrophorus*), except to state that it was questionable. These authors also made no effort to compare their new species with *P. neopolitana* despite listing it as one of seven species of *Paraonides* and that was originally described from the Bay of Naples on the other side of Italy. Additional papers supporting continued use of the genus *Paraonides* include Laubier and Ramos (1974), Castelli (1988), Aguirrezabalaga and Gil (2008, 2009), and Aguirrezabalaga (2012). However, no new collections or redescription of *P. sensu* Cerruti (1909) have been presented since the original account. In contrast, Fauchald (1977), Fauchald and Hancock (1981), Gaston (1984), Blake (1996), and Gillet (1999) used *Paraonella* as a valid genus.

The problem is that there has been no documented rediscovery and redescription of Cerruti's species since 1909. The species is either a stand-alone species of *Paraonides* with no modified chaetae or a species of *Paradoneis* with lyrate notochaetae. Until specimens are recollected, preferably from the type locality (the Bay of Naples), and a neotype established to define the species, there can be no justification for rejecting *Paraonella* as a valid genus. Indeed, as part of the recent list of polychaetes from Italian seas by Castelli *et al.* (2008) that included most of the active Italian polychaete experts as coauthors, both the genus *Paraonides* and the species *P. neopolitana* were listed as doubtful.

In this chapter, *Paraonella* is treated as a valid genus, with Strelzov (1973/1979) as the authority. Eight species are here considered valid.

1. *Paraonella andreae* (López & Sikorski), 2017. Norway, 38–88 m.
2. *Paraonella cedroensis* (Fauchald, 1972). Western Mexico, off Cedros Island, 1,723–1,750 m.
3. *Paraonella monilaris* (Hartman & Fauchald, 1971). Western North Atlantic, lower slope and abyssal depths; equatorial Atlantic, abyssal; 2,864–4,825 m; off California, lower slope depths.

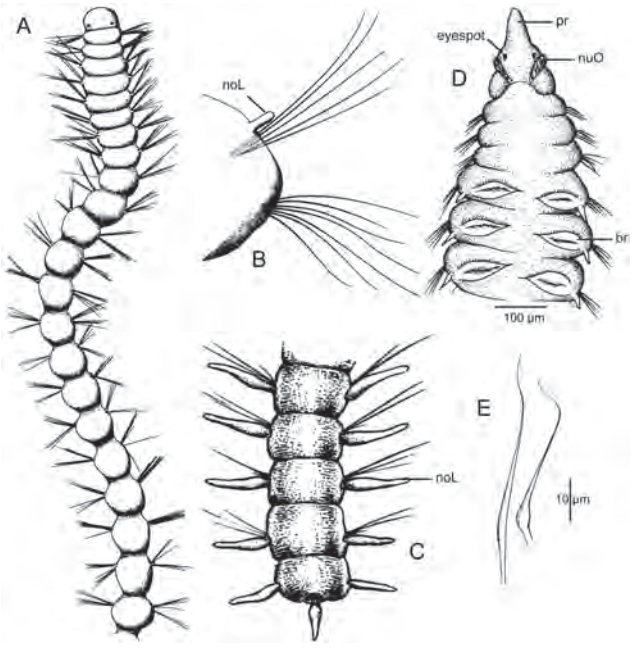


**Fig. 7.3.1.1.12:** Examples of *Paraonella*. A–C, *Paraonella monilaris*: A, anterior and middle body segments, dorsal view; B, middle body segment, anterior view; C, posterior end; D–E, *Paraonella platybranchia*: D, anterior end, dorsal view; E, posterior neurochaetae. br, branchia; cB, noL, notopodial lamella; nuO, nuchal organ; pr, prostomium. A–C, After Hartman and Fauchald (1971); D–E, after Blake (1977).

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4. *Paraonella myriamae* (Katzmann and Laubier, 1975). Adriatic Sea, 10–180 m; Capebreton Canyon, Bay of Biscay, 1,026–1,036 m.
5. *Paraonella nordica* (Strelzov, 1968). Barents Sea, 6–92 m.
6. *Paraonella platybranchia* (Hartman, 1961). California, intertidal to low water.
7. *Paraonella rubriceps* (Hartman & Fauchald, 1971). Western North Atlantic, slope and abyssal depths, 1,102–3,753 m.
8. *Paraonella subantarctica* Gillett, 1999. Subantarctic Marion and Prince Edward Islands, 30–210 m.

### Genus *Paraonis* Cerruti, 1909 (six species)

**Type species:** *Aonides fulgens* Levinsen, 1883. Designated by the ICZN (Melville 1979).

**Diagnosis:** Body long, slender, sometimes coiled. Prostomium generally longer than wide, with one or more bands of cilia (Fig. 7.3.1.1.13 A, C, E); medial antennae absent; terminal sensory organ well developed (Fig. 7.3.1.1.13 A, C); nuchal organs elongate slits joining posterior margin of prostomium (Fig. 7.3.1.1.13 A, C); eyes present or absent. Three or more prebranchial segments present. Branchiae from chaetiger 4 continuing for 20 or more segments. Dorsal ciliary bands present (Fig. 7.3.1.1.13 A). Noto- and neuropodia reduced to small rounded lobes; postchaetal lobes or lamellae absent. Chaetae include capillaries throughout often with distinct fringe of fibrils along one edge; modified chaetae present in posterior segments consisting of curved spines often with subterminal rows of stiff fibrils on concave side of chaeta (Fig. 7.3.1.1.13 F); other types of spines with tooth-like protuberance at the base of long tapering shaft (Fig. 7.3.1.1.13 B). Pygidium rounded typically with three anal cirri (eight or more in *P. pygoenigmatica*).

**Remarks:** *Paraonis fulgens* and *P. pygoenigmatica* are the best known species of the genus, with both having broad geographic distributions and the subject of several studies of morphology and ecology. The other four species are not well known. In particular, *P. dubius,* and *P. paucibranchiata* do not appear to have been reported since their original descriptions. *Paraonis pycnobranchiata* Fauchald, 1,972 from deep-water off Western Mexico, is transferred to the genus *Levinsenia*. *Paradoneis strelzovi* may also belong to *Levinsenia*.

1. *Paraonis dubius* (Augener, 1914). West Australia, Sharks Bay, 2–4 m; ?Antarctica.
2. *Paraonis fulgens* (Levinsen, 1883). Widespread in the North Atlantic, England, French coast, Irish Sea, North Sea; coastal waters of North America, Eastern Canada to Massachusetts; Gulf of Mexico; intertidal to shallow subtidal.
3. *Paraonis multibranchiata* Hartman, 1957. Off California, 475–558 m.

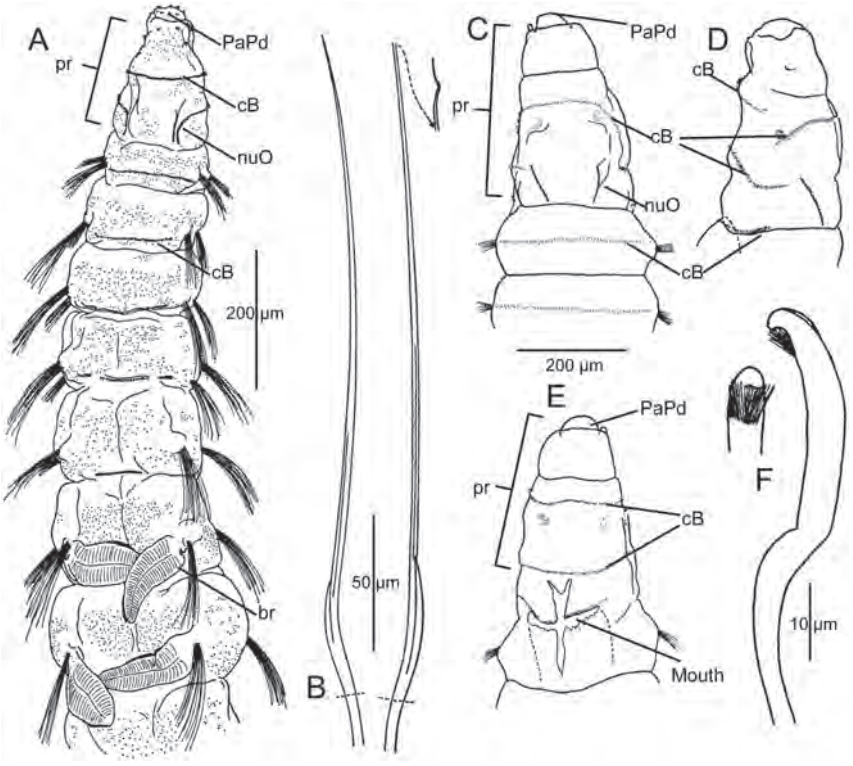


**Fig. 7.3.1.1.13:** Examples of species of *Paraonis*. A, B, *Paraonis pygoenigmatica*: A, anterior end, dorsal view; B, modified neurochaetae. C–F, *Paraonis fulgens*: C, anterior end dorsal view; D, anterior end, lateral view; E, anterior end, ventral view; F, modified neurochaetae. br, branchia; cB, ciliary band; noL, notopodial lamella; nuO, nuchal organ; paPd, palpode; pr, prostomium. A–B, after Jones (1968); C–F, after Strelzov (1973/1979).

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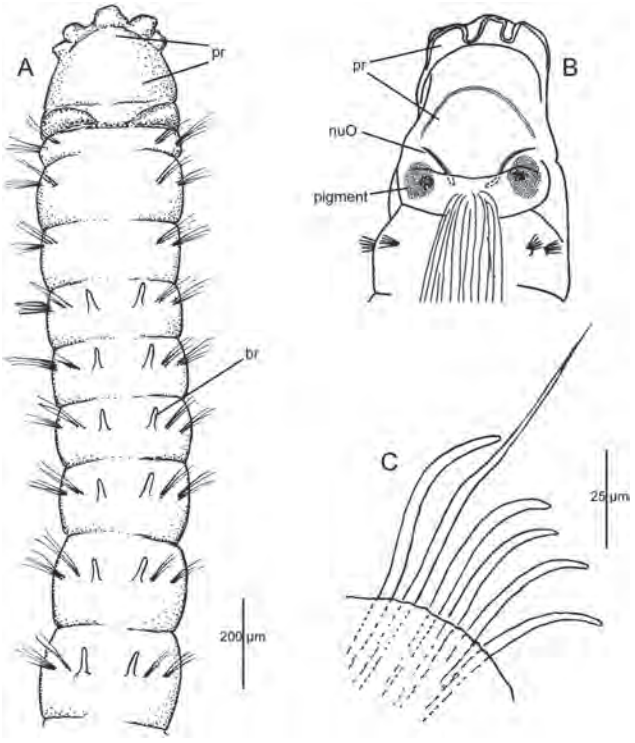


**Fig. 7.3.1.1.14:** Examples of *Sabidius* species. A–C, *Sabidius cornatus*. A, Anterior end, dorsal view. B, Detail of the head region, prostomium, and first chaetiger, dorsal view. C, Posterior modified neurochaetae. br, branchia; nuO, nuchal organ; pr, prostomium. A, C, After Hartman (1965); B, after Strelzov (1973/1979).

4. *Paraonis paucibranchiata* Cerruti, 1909. Mediterranean Sea.
5. *Paraonis pygoenigmatica* Jones, 1968. New England, coastal waters; east coast of Florida, northern Gulf of Mexico, northwest Florida coast, intertidal to shallow subtidal.
6. *Paraonis strelzovi* Hartmann-Schröder, 1980. West Australia, Port Samson, mangroves, intertidal.

### Genus *Sabidius* Strelzov, 1973 (one species)

**Type species:** *Paraonis cornatus* Hartman, 1965, by monotypy

**Diagnosis:** Body long and slender, fragile with numerous segments, often tightly coiled. Prostomium with distinctive thick, trilobed cuticle on anterior margin (Fig. 7.3.1.1.14 A, B); medial antenna, ciliated bands, terminal sensory organ, and cheek organs absent; nuchal organs curved slits on posterior margin (Fig. 7.3.1.1.14 B) associated with two areas of dark reddish-brown pigment often fused and extending across dorsum. Three prebranchial segments present; branchiae short, narrow, limited to few segments. Noto- and neuropodia without podial lobes. Chaetae include slender capillaries in notopodia; enlarged curved modified spines present in postbranchial neuropodia, at least one to two per fascicle with long arista (Fig. 7.3.1.1.14 C). Pygidium an expanded lobe, anal cirri not observed.

**Remarks:** Only a single species, *Sabidius cornatus* (Hartman, 1965), is known. The species is readily recognized by the sculptured anterior margin of the prostomium, short, fingerlike branchiae, and unique dark reddish pigment associated with the nuchal organs and that sometimes extends completely across the dorso-posterior margin. Morphologically, *S. cornatus*, apart from the nature of the anterior margin on the prostomium, is similar to species of *Levinsenia*. The pygidium is usually broken and missing. An examination of numerous specimens from the continental slope off the U.S. Atlantic coast suggests that the body terminates in a simple swollen segment that lacks anal cirri. Many specimens are tightly coiled as reported for other paraonids.

The species was originally reported by Hartman (1965) and Hartman and Fauchald (1971) from off New England in slope and abyssal depths (400–2,900 m). The species was subsequently found in slope depths all along the U.S. Atlantic slope from the Canadian boundary to off the Carolinas (Blake *et al*. 1987) and has recently been identified in surveys from slope depths in the Gulf of Mexico off Louisiana (Blake unpublished). Strelzov (1973/1979) reported the species from the western Pacific.

## References

Aguirrezabalaga, F. (2012): Family Paraonidae. In: Parapar, J., Alos, C., Nunez, J., Moreira, J., Lopez, E., Aguirrezabalaga, F., Besteiral, C. & Martinez, A., *Fauna Iberica, 36. Annelida Polychaeta III*. National Museum de Ciencias Naurales Consejo Superior de Investigaciones Cientificos: 160–272. Madrid.

Aguirrezabalaga, F. & Gil, J. (2008): Paraonidae (Annelida: Polychaeta) of the inlet of Zarautz (Basque Coast, Bay of Biscay), with new records from the Atlantic and Iberian coasts. *Cahiers de Biologie Marine* 49: 37–57.

Aguirrezabalaga, F. & Gil, J. (2009): Paraonidae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with the description of eight new species. *Scientia Marina* 73(4): 631–666.

Aguado, M.T. & López, E. (2003): Paraonidae (Annelida: Polychaeta) del Parque Nacional de Coiba (Pacífic, Panamá), con la descripción de una nueva especie de Aricidea Webster, 1879. *Revista Chilena de Historia Natural* 76: 363–370.

Allen, E.J. (1904): The anatomy of *Poecilochaetus*. *Quarterly Journal of Microscopical Science, London, New Series* 48: 79–151, 6 plates.

Andrade, S.C.S, Novo, M., Kaauchi, G.Y., Worsaae, K., Pleijel, F., Girbet, G. & Rouse, G.W. (2015): Articulating "Archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32(11): 2860–2775.

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Arriaga-Hernández, S., Hernández-Alcantra, P. & Solís-Weiss, V. (2013): Description and distribution of two new species of Paraonidae (Annelida: Polychaeta) from a lagoon-estuarine ecosystem of the southern Gulf of Mexico. *Zootaxa* 3686(1): 5–64.

Bhaud, M. (1983): Premières observations de la larve planctonique récolte en haute mer d'un représentant de Paraonidae (Annélide Polychète). *Vie et Milieu* 33(1): 41–48.

Bhaud, M., Cazaux, C., Watson Russell, C. & Lefevre, M. (1987): Description and identification of polychaete larvae: their implications in current biological problems. *Oceanis* 13(6): 596–753.

Blake, J.A. (1994): Vertical distribution of benthic invertebrates from the continental slope off Cape Lookout, North Carolina. *Deep-Sea Research II* 41:919–927.

Blake, J.A. (1996): Chapter 2. Family Paraonidae Cerruti, 1909. In: Blake, J.A., Hilbig, B., and Scott, P.H. (eds.) *Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History: 27–70. Santa Barbara, California.

Blake, J.A. & Baptiste, E.M. (1985): Chapter 6. Life history studies on dominant polychaete species from Georges Bank. In: Maciolek-Blake, N., Grassle, J.F. & Neff, J.M. (eds.) *Georges Bank Benthic Infauna Monitoring Program, Final Report for Third Year of Sampling*. U.S. Department of the Interior, Minerals Management Service, Herndon, VA: 140–178. [http://marinecadastre.gov/espis/#/search/study/9111]

Blake, J.A. & Grassle, J.F. (1994): Benthic community structure in the U.S. South Atlantic off the Carolinas: spatial heterogeneity in current dominated system. *Deep-Sea Research II*. 41:835–874.

Blake, J.A., Hecker, B., Grassle, J.F., Brown, B., Wade, M., Boehm, P., Baptiste, E., Hilbig, B., Maciolek, N., Petrecca, R., Ruff, R.E., Starczak, V. & Watling, L.E. (1987): Study of biological processes on the U.S. South Atlantic slope and rise. Phase 2. U.S. Department of the Interior, Minerals Management Service, Washington, D.C. *OCS Study MMS 86-0096*: Volume 1. Executive Summary, ii + 58 pp.; Final Report. ii + 414 pp. and 13 Appendices. National Technical Information Service (NTIS) No. PB 87-214342 and PB 87-214359. [http://marinecadastre.gov/espis/#/search/study/9007]

Blake, J.A. & Hilbig, B. (1994): Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. *Deep-Sea Research II* 41:875–899.

Blake, J.A., Maciolek, N.J., Ota, A.Y. & Williams, I.P. (2009): Long-term benthic infaunal monitoring at a deep-ocean dredged material disposal site off Northern California, *Deep-Sea Research II* 56: 1775–1803.

Blake, J.A. and Walton, C.P. (1977): New species and records of Polychaeta from the Gulf of the Farallones, California. In: Reish, D.J., and K. Fauchald (eds.), *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*. University of Southern California Press, Los Angeles: 307–321.

Bleidorn, C. (2009): Chapter 2. Annelid phylogeny—Molecular analysis with an emphasis on model animals. In: Shain, D.H. (ed.) *Annelids in Modern Biology*. Wiley-Blackwell: 13–30. New Jersey.

Brito, M.C. & Núñez, J. (2002): A new genus and species of Questidae (Annelida: Polychaeta) from the central Macaronesian region and cladistic analysis of the family. *Sarsia* 87: 281–289.

Brown, B. (1976): A new species of *Aricidea* (Polychaeta: Paraonidae) from Florida. *Proceedings of the Biological Society of Washington* 89: 433–438.

Castelli, A. (1988): Censimento dei Policheti dei mare Italiani: Paraonidae Cerruti, 1909. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie B* 94: 319–340.

Castelli, A. Bianchi, C.N., Cantone, G., Çinar, M.E., Gambi, M.C., Giangrande, A., Sareri, D.I., Lanera, P., Licciano, M., Musco, L., Sanfilippo, R. & Simonini, R. (2008): Annelida Polychaeta. In: Relini, G. (ed.). Checklist of the flora and fauna of the deep Italian Part I. *Mediterranean Marine Biology* 15 (s1): 323–373.

Cerruti, A. (1909): Contributo all'anatomia, biologia e sistematica delle Paraonidae (Levinsenidae) con partiolare riguardo alle specie del golf di Napoli. *Mitteilungen aus der zoologischen Station zu Neapel* 19: 459–512, pls. 18–19.

Çinar, M.E. & Dagli, E. (2013): Polychaetes (Annelida: Polychaeta) from the Aegean and Levantine coasts of Turkey, with descriptions of two new species. *Journal of Natural History* 47(13–14): 911–947.

Çinar, M.E., Dagli, E. & Acik, S. (2011): Annelids (Polychaeta and Oligochaeta) from the Sea of Marmara, with descriptions of five new species. *Journal of Natural History* 45(33–34): 2105–2143.

Day, J.A. (1955): The Polychaeta of South Africa. Part 3. Sedentary species from Cape Shores and estuaries. *Journal of the Linnean Society of Zoology* 42: 407–452.

Day, J.H. (1967): *A Monograph on the Polychaeta of Southern Africa*. British Museum of Natural History, Publication No. 656: 1–878.

Erdoğan-Dereli, D., Çinar, M.H. & Dağli, E. (2017): *Cirrophorus* species (Annelida: Polychaeta: Paraonidae) in the Sea of Mamara, with description of a new species. *Zootaxa* 4347: 137–150.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–190.

Fauchald, K. & Hancock, D.R. (1981): Deep-water polychaetes from a transect off Oregon. *Allan Hancock Foundation Monograph* No. 11: 1–73.

Fewkes, J.W. (1883): On the development of certain worm larvae. *Bulletin of the Museum of Comparative Zoology at Harvard College* 11(9): 167–208.

Gaston, G. (1984): Chapter 2. Family Paraonidae Cerruti, 1909. In: Uebelacker, J.M. & Johnson, P.G. (eds.) *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico*. Vol. 1. Barry A. Vittor & Associates, Inc. Mobile, AL: 2-1–2-53.

Gaston, G.R. (1987): Benthic Polychaeta of the Middle Atlantic Bight: feeding and distribution. *Marine Ecology Progress Series* 36:251–262.

Gaston, G., McLelland, J.A. & Heard, R.W. (1992): Feeding biology, distribution, and ecology of two species of benthic polychaetes: *Paraonis fulgens* and *Paraonis pygoenigmatica* (Polychaeta: Paraonidae). Gulf Research Reports 8: 395–399.

Giere, O., Ebbe, B. & Erséus, C. (2008): *Questa* (Annelida, Polychaeta, Orbiniidae) from Pacific regions — new species and reassessment of the genus *Periquesta*. *Organisms, Diversity & Evolution* 7: 304–319.

Gillet, P. (1999): A new species of *Paraonella* (Paraonidae: Polychaeta) from Marion and Prince Edward Islands, Indian Ocean. *Beaufortia* 49: 10: 109–113.

Glémarec, M. (1966): Paraonidae de Bretagne. Description de *Paradoneis armata* nov. sp. *Vie et Milieu, Séries A, Biologie Marine* 17(2A): 1045–1052.

Hannerz, L. (1956): Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetiae n. fam.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

in the Gullmar Fjord (Sweden). *Zoologiska Bidråg fran Uppsala* 31: 1–204.
Hartley, J.P. (1981): The family Paraonidae (Polychaeta) in British waters: a new species and new records with a key to species. *Journal of the Marine Biological Association of the United Kingdom* 61: 133–149.
Hartley, J.P. (1984): Cosmopolitan polychaete species: the status of *Aricidea belgicae* (Fauvel, 1936) and notes on the identify of *A. suecica* Eliason, 1920 (Polychaeta; Paraonidae). In: Hutchings, P.A. (ed.) *Proceedings of the First International Polychaete Conference, Sydney*. Linnean Society of New South Wales: 7–20. Sydney, Australia.
Hartman, O. (1944): Polychaetous annelids Part VI. Paraonidae, Magelonidae, Longosomidae, Ctenodrilidae, and Sabellariidae. Allan *Hancock Pacific Expeditions* 10: 311–389.
Hartman, O. (1957): Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pacific Expeditions* 15(3): 211–393, pls. 20–44, 1 chart.
Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation Occasional Paper* 23: 1–628.
Hartman, O. (1965): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Publications, Occasional Paper* 28: 1–378.
Hartman, O. (1969): *Atlas of the Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles.
Hartman, O. & Fauchald, K. (1971): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Part II. *Allan Hancock Monographs in Marine Biology* 6: 1–327.
Hartmann-Schröder, G. (1971): Annelida, Borstenwürmer, Polychaeta. *Die Tierwelt Deutschlands* 58:1–594.
Hartmann-Schröder, G. (1996): Annelida, Borstenwürmer, Polychaeta. *Die Tierwelt Deutschlands (2nd Edition)*: 58, 1–648.
Hartmann-Schröder, G. & Rosenfeldt, P. (1988): Die Polychaeten der "Polarstern" Reise ANT III/2 in the Antarktis 1984. Teil 1: Euphrosinidae bis Chaetopteridae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 85: 25–72.
Hartmann-Schröder, G. & Rosenfeldt, P. (1990): Die Polychaeten der "Walter Herwig"–Reise 68/1 nach Elephand Island (Antarktis) 1985. Teil 1: Aphroditidae bis Cirratulidae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 87: 89–122.
Hilbig, B. (1994): Faunistic and zoogeographical characterization of the benthic infauna on the Carolina continental slope. *Deep-Sea Research II* 41(4–6): 929–950.
Hilbig, B. & Blake, J.A. (2000): Long-term Analysis of polychaete-dominated benthic infaunal communities in Massachusetts Bay. *Bulletin of Marine Science* 67:147–164.
Hilbig, B. & Blake, J.A. (2006): Deep-sea polychaete communities in the Northeast Pacific Ocean off the Gulf of the Farallones, California. *Bulletin of Marine Science* 78: 243–269.
Hobson, K.D. (1972): Two new species and two new records of the Family Paraonidae (Annelida, Polychaeta) from the northeastern Pacific Ocean. *Proceedings of the Biological Society of Washington* 85: 549–556.
Imajima, M. (1973): Paraonidae (Polychaeta) from Japan. *Bulletin of the National Science Museum* 16: 253–292.
Jones, M.L. (1968): *Paraonis pygoenigmatica* new species, a new annelid from Massachusetts (Polychaeta: Paraonidae). *Proceedings of the Biological Society of Washington* 81: 323–334.
Jumars, P.A., Dorgan, K.M. & Lindsey, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. Annual Review of Marine Science 7: 497–520 + Supplemental Appendix A. Family-by-Family Updates: A1–A350 + Supplemental Table of Guild Characteristics: 1–14.
Katzmann, W. & Laubier, L. (1975): Paraonidae (Polychètes sédentaires) de l'Adriatique. *Annales des Naturhistorischen Museums in Wien* 79: 567–588.
Langeneck, J., Barbieri, M., Maltagliati, F. & Castelli, A. (2017): A new species of *Cirrophorus* (Annelida: Paraonidae) from Mediterranean organically enriched environments, with taxonomic notes on the family. *Journal of the Marine Biological Association of the United Kingdom* 97(5): 871–880.
Langeneck, J., Busoni, G., Aliani, S. & Castelli, A. (2017): Deep-sea polychaetes from the Malta Escarpment (western Ionian Sea). *The European Zoological Journal* 84(1): 142–152.
Laubier, L. (1966): Sur la présence du genre *Cirrophorus* (Polychètes, Paraonidae) en Méditerranée. *Bulletin de la Societé Zoologique de France* 90: 469–477.
Laubier, L. (1967): Sur quelques *Aricidea* (Polychaeta, Paraonidae) de Banyuls-sur-Mer. *Vie et Milieu, Series A: Biologie Marine* 18(1A): 99–132.
Laubier L. & Ramos, J. (1974): Paraonidae (Polychètes sédentaires) de Méditerranée. Bulletin du Muséum National d'Historie Naturelle, 3e séries, No. 168, *Zoologie* 113: 1097–1148 (dated 1973, but printed 30 March 1974).
Lemer, S., Kawauchi, G.Y., Andrade, S.C.S, González, V., Boyle, M.J. & Girbert, G. (2015): Re-evaluating the phylogeny of Sipuncula through transcriptomics. *Molecular Phylogenetics and Evolution* 83: 174–183.
de Leon-Gonzáles, J.A. & Díaz-Castañeda, V. (2011): A new species of Paraonidae (Polychaeta: Paraonidae) from the western coast of Baja California, Mexico. *Proceedings of the Biological Society of Washington* 124: 40–44.
de Leon-Gonzáles, J.A., Guevera, N.A.H. & Rodríquez-Valencia, J.A. (2006): Paraonidae (Polychaeta) from western Mexico, with description of two new species. *Journal of the Marine Biological Association of the United Kingdom* 86: 253–262.
Levinsen, G.M.R. (1883): Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra den Dansk Naturhistorisk Forening i Kjøbenhavn* Pt. 2: 92–350.
López, E. (2008): Redescription of *Aricidea beligicae* (Fauvel, 1936), an Antarctic Paraonidae (Annelida: Polychaeta), with reassessment of its taxonomic status based on new material. *Proceedings of the Biological Society of Washington* 121: 297–307.
López, E. & Sikorski, A. (2017): The Paraonidae (Annelida: Sedentaria) from Norway and adjacent seas, with two new species, four new records, and a redescription of *Paraonides nordica* Strelzov, 1968 based on type material. *Zootaxa* 4320: 41–67.
López-Jamar, E., O'Connor, B. & González, G. (1987): Demography and gametogenic cycle of *Paradoneis armata* Glémarec (Polychaeta, Paraonidae) in Ría de la Coruña, north-west Spain. *Ophelia* 27: 127–136.
Lovell, L.L. (2002): Paraonidae (Annelida: Polychaeta) of the Andaman Sea, Thailand. *Phuket Marine Biological Center Special Publication* 24: 33–56.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

McLelland, J.A. & Gaston, G.R. (1994): Two new species of *Cirrophorus* (Polychaeta: Paraonidae) from the northern Gulf of Mexico. *Proceedings of the Biological Society of Washington* 107: 524–531.

Mackie, A.S.Y. (1991): *Paradoneis eliasoni* sp. nov. (Polychaeta: Paraonidae) from northern European waters, with a redescription of *Paradoneis lyra* (Southern, 1914). *Ophelia Supplement* 5: 147–155.

Melville, R.V. (1979): Opinion 1139. *Paraonis* Grube, 1873. (Polychaeta, Paraonidae). Designation of a type species under the plenary powers. *Bulletin of Zoological Nomenclature* 36: 114–118.

Mesnil, F. & Caullery, M. (1898): Étude de morphologie externe chez les Annélides. IV. La famille nouvelle des Levinseniens. Révision des Ariciens. Affinités des deux familles. Les Apistobranchiens. *Bulletin Biologique de la France et de la Belgique* 31: 126–150, pl. 6.

Minter, N.J., Buatois, L.A., Lucas, S.G., Braddy, S.J. & Smith, J.A. (2006): Spiral-shaped graphglyptids from an early Permian intertidal flat. *Geology* 34(12): 1057–1060. Geological Society of America.

Montiel, A. & Hilbig, B. (2004*): Aricidea pisanoi* (Annelida: Polychaeta), a new species of Paraonidae from the southernmost waters of South America (Chile). *Journal of the Marine Biological Association of the United Kingdom* 84: 43–45.

Orrhage, L. (1966): Über die Anatomie des zentralen Nervensystems der sedentären Polychaeten. *Archiv fur Zoologi* 19: 99–133.

Orrhage, L. (1993): On the microanatomy of the cephalic nervous system of Nereidae (Polychaeta), with a preliminary discussion of some earlier theories on the segmentation of the polychaete brain. *Acta Zoologica (Stockholm)* 74: 145–172.

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

Penry, D.L. & Jumars, P.A. (1990): Gut architecture, digestive constraints and feeding ecology of deposit-feeding and carnivorous polychaetes. *Oecologia* 82: 1–11.

Pettibone, M.H. (1963): Marine polychaete worms of the New England region I. Aphroditidae through Trochochaetidae. *Bulletin of the United States National Museum* 227(1): 1–356.

Pettibone, M.H. (1965): Two new species of *Aricidea* (Polychaeta, Paraonidae) from Virginia and Florida, and redescription of Aricidea fragilis Webster. *Proceedings of the Biological Society of Washington* 78: 127–140.

Purschke, G. & Hausen, H. (2007): Lateral organs in sedentary polychaetes (Annelida) – ultrastructure and phylogenetic significance of an insufficiently known sense organ. *Acta Zoologica* 88: 23–39.

Purschke, G. & Tzetlin, A.B. (1996): Dorsolateral ciliary folds in the polychaete foregut: structure, prevalence and phylogenetic significance. *Acta Zoologica* 77: 33–49.

Risk, M.J. & Tunnicliffe, V.J. (1978): Intertidal spiral burrows: *Paraonis fulgens* and *Spiophanes wigleyi* in the Minas Basin, Bay of Fundy. *Journal of Sedimentary Petrology* 48(4): 1287–1292.

Röder, H. (1971): Gangsystem von *Paraonis fulgens* Levinsen 1883 (Polychaeta) in ökologischer, ethologischer und actuopaläontologischer Sicht. *Senckenbergiana. Maritime* 3: 3–51.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and polychaetes. *Zoologica Scripta* 26(2): 139–204.

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

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

Sardá, R., Gil, J., Taboada, S. & Gili, J.M. (2009): Polychaeta species captured in sediment traps moored in northwestern Mediterranean submarine canyons. *Zoological Journal of the Linnaean Society* 155: 1–21.

Southern, R. (1914): Archiannelida and Polychaeta. In: Clare Island Survey, Pt. 47. *Proceedings of the Royal Irish Academy, Dublin* 31: 1–160.

Storch, V. (1967): Neue Polychaeten aus der Sandfauna des Roten Meeres. Zoologischer Anzeiger 178: 102–110.

Strelzov, V.E. (1968): Polychaetous annelids of the family Paraonidae (Polychaeta, Sedentaria) of the Barents Sea. *Trudy Murmanskogo Morskogo Biologicheskogo Instituta* 17: 74–95 [In Russian].

Strelzov, V.E. (1973): Polychaete worms of the family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria). *Akademiya Nauk SSSR, Leningrad*: 1–169, plates I–IX [In Russian].

Strelzov, V.E. (1979): *Polychaete Worms of the Family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria)*. English translation of the 1973 Russian edition, published by the Smithsonian Institution and U.S. National Science Foundation, Washington, DC.

Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–545.

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

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

Tzetlin A. & Purschke G. (2005): Pharynx and intestine. *Hydrobiologia* 535: 199–225.

Webster, H.E. & Benedict, J.E. (1887): The Annelida Chaetopoda from Eastport, Maine. *Reports of the U.S. Fish Commission for 1885*: pp. 707–755.

Weigert, A. & Bleidorn, D. (2016): Current status of annelid phylogeny. *Organisms, Diversity & Evolution*. DOI: 10.1007/s13127-016-0265-7.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31(6): 1391–1401.

Zhou, J. & Reuscher, M.G. (2013): Description of a new species of *Aricidea* (Polychaeta: Paraonidae) from Chinese Seas. *Proceedings of the Biological Society of Washington* 126(3): 276–283.

Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189. DOI: 10.1186/1471-21-48-9-189.

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Brigitte Ebbe and James A. Blake

## 7.3.1.2 Cossuridae Day, 1963

### Introduction

Cossuridae is one of the smaller families of polychaetes that are easily recognized despite their lack of intricate morphological features such as prostomial or parapodial appendages. The diagnostic character for the family is a single branchial filament arising mid-dorsally from one of the anteriormost segments. Cossuridae occur in muddy and sandy sediments, where they live in burrows without producing tubes. The bathymetric distribution of cossurids reaches from shallow subtidal waters to lower slope depths. In some instances, individual species constitute a large percentage of total infaunal abundance (Blake and Hilbig, 1994).

### Morphology

#### External morphology

Cossurids are rather thin and fragile, with numerous segments, typically only about 15 mm long, less than 1 mm wide, with about 60 to 150 chaetigers. The body is indistinctly separated into two or three regions (Fig. 7.3.1.2.1 A, D), depending on the authors. The anterior thoracic region is characterized by a slightly flattened cross-section, segments that are wider than long and chaetal fascicles emerging near the anterior segmental border (Fig. 7.3.1.2.1 B–C, E–F), whereas the posterior abdominal region consists of more fragile, thin-walled segments that are often beadlike and about as long as wide, and chaetal fascicles emerge near the middle of the segments (Fig. 7.3.1.2.1 A, D). The border between the thorax and the abdomen can be obvious in some species but hardly distinguishable in others. Within the last few segments, which are again becoming progressively shorter and sometimes viewed as a separate posterior region (e.g., Fournier and Petersen 1991, Liñero-Arana and Diaz-Diaz 2010), the body tapers toward a small pygidium. The only appendages are the mid-dorsal branchial filament, emerging from one of the anteriormost segments (2 to 5) (Figs. 7.3.1.2.1 B–C, E and 7.3.1.2.2 A, B), and anal cirri, which are long and threadlike, three in number (Fig. 7.3.1.2.1 G), and may be accompanied by a circlet of papillae or fingerlike processes as in *Cossura pygodactylata* Jones, 1956 (Fig. 7.3.1.2.1 G).

**Prostomium and Peristomium.** The prostomium is usually conical, more or less rounded anteriorly (Figs. 7.3.1.2.1 A–C, D–F and 7.3.1.2.2 A, B) (except for *Cossura ginesi* Liñero-Arana & Diaz-Diaz, 2010, which shows anterolateral horns), and bears paired retractable nuchal organs (Fig. 7.3.1.2.2 A–C), usually visible as ciliated grooves near the posterior edge of the prostomium but more anteriorly located than in most polychaetes (Zhadan *et al*. 2012); eyes are absent. The delineation of the prostomium and peristomium has been subject to debate essentially since the first cossurid was described. Thulin (1921) was the first to determine that the so-called first achaetous segment was indeed part of the prostomium, and consequently, the second achaetous segment constituted the peristomium, with the mouth opening located between the two rings (Figs. 7.3.1.2.1 C, D and 7.3.1.2.2 A, B). Nonetheless, the "number of anterior achaetous segments" was used widely to discriminate one species from another (e.g., Fauchald 1972). Nearly a century after Thulin's observations, Zhadan *et al*. (2012) confirmed that the first of the two rings belonged to the prostomium based on an investigation of a growth series of juvenile to adult specimens of *C. pygodactylata*. The authors observed that the heavily ciliated prototroch in juveniles defined the posterior border of the prostomium and is located posterior to the nuchal organs. The posterior prostomial ring was found to be a result of a muscle contraction and thus not seen in relaxed specimens (Zhadan *et al*., 2012, 2014, Zhadan, 2015).

**Pharynx.** The proboscis is ciliated and armed with a variable, age-dependent even-number of buccal tentacles originating on the dorsal surface of the buccal cavity, near the transition to the esophagus. Tzetlin (1994) first described the buccal tentacles in detail and observed their activity on living specimens. In contrast to some opheliids that have extensive coelomic space within the buccal tentacles, those of *Cossura* are muscular and have little coelomic space (Tzetlin and Zhadan 2009). Recently, Zhadan *et al*. (2015) described the structure of the buccal tentacles based on light and electron microscopy (EM) methods, including confocal laser scanning microscopy, and the authors proposed a mechanism of protraction.

**Parapodia.** Parapodia are strongly reduced so that chaetae emerge directly from the body wall. In the first chaetiger, parapodia are uniramous and biramous in all the following segments; notopodial and neuropodial rami are barely separated in the thoracic region and wider apart in the abdominal region.

**Chaetae.** Chaetae are simple throughout, anterior chaetae typically with thickened shafts bearing numerous bristles tapering to long, narrow capillary tips (Figs 7.3.1.2.1 I and 7.3.1.2.2 D–F), appearing limbate in light microscopy. Chaetae of abdominal fascicles are thin hirsute capillaries; rarely, blunt, acicular spines are present in species, formerly referred to the genera *Cossurella* and *Heterocossura*. Fournier and Petersen (1991) emphasized the striations

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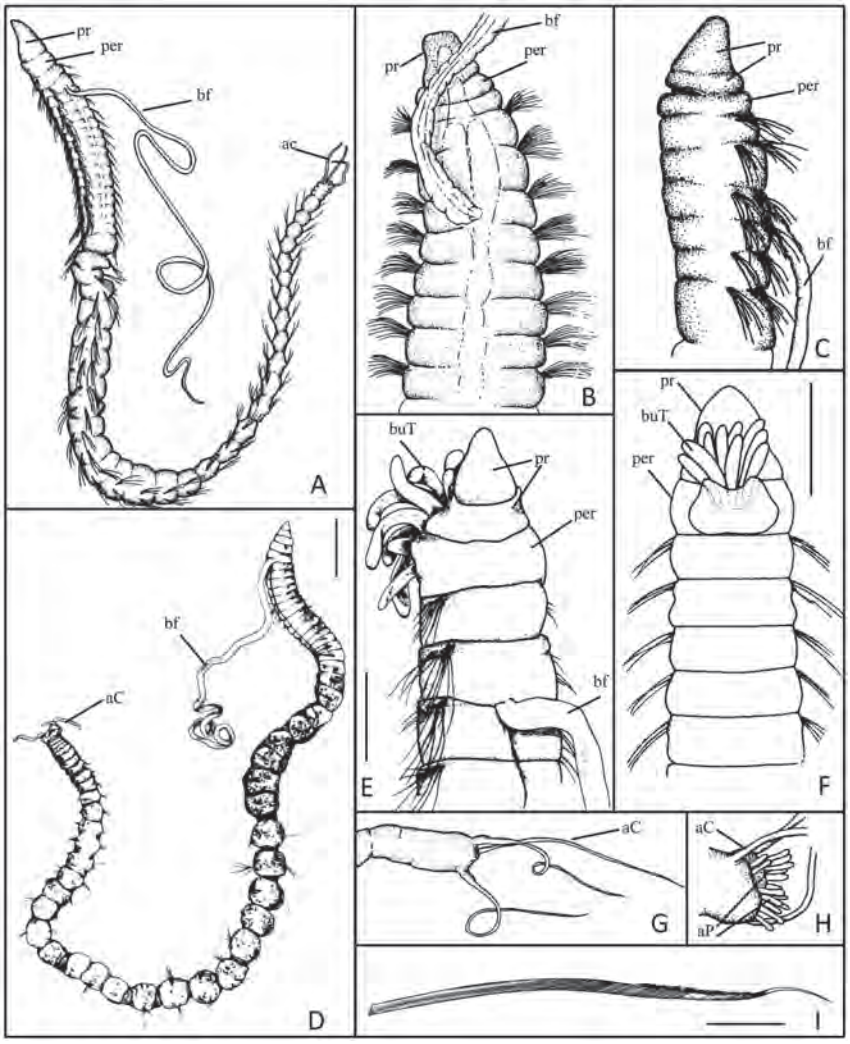


**Fig. 7.3.1.2.1:** Morphology of Cossuridae. A, *Cossura pygodactylata*, whole animal, dorsolateral view. B, C, *Cossura brunnea* anterior ends, in dorsal (B) and lateral (C) views. D–F, *Cossura longocirrata*. D, Whole animal in dorsolateral view. E, Anterior end, dorsal view. F, Anterior end, ventral view. G–H, Pygidia of *Cossura brunnea* (G) and *Cossura pygodactylata* (H). I, *C. longocirrata*, anterior thoracic neurochaetae. aC, anal cirri; aP, anal papillae; bf, branchial filament; buT, buccal tentacles; per, peristomium; pr, prostomium. Scales: D, 500 µm; E, 250 µm; F, 250 µm; I, 50 µm. A–C, G–H, not to scale. A, B, C, G, H, from Hilbig (1996); D, E, F, I, from Fournier and Petersen (1991).

in the shaft together with the fimbriated or bristled edge (Fig. 7.3.1.2.1 I).

**Branchiae.** The single mid-dorsal branchial filament is the most conspicuous character of cossurids. It arises between the second and sixth segments and in life rests in a shallow mid-dorsal groove. The location of the filament is an important taxonomic character and develops very early in ontogeny (Bachelet and Laubier 1994). When Day (1963) established the family Cossuridae to accommodate the genus *Cossura*, he viewed the structure as a single tentacle (vs. paired tentacles in cirratulids). It has since been shown that the appendage is not involved in feeding, but rather respiration.

Species-specific patterns of certain glands in the integument of the thorax result in characteristic methyl green staining patterns that can be used as additional taxonomic characters (Hilbig 1996), although they do not work with all species and are less distinct in older museum material (Zhadan 2015). Examples of species-specific staining patterns in four species from the eastern Pacific are shown in Fig. 7.3.1.3.3.

## Anatomy

Cossurids, like many burrowing polychaetes, lack a coelomic cavity in thoracic segments, as the noncontractile parts of the muscular cells occupy the entire space between the body wall and the intestinal tract. The only exception, reported for *Cossura longocirrata*, is a small dorsal space in the third chaetiger (Rouse and Tzetlin 1997). In abdominal segments, the coelom is spacious and contains coelomocytes.

**Digestive system.** The digestive tract is a simple tube with an axial nonmuscular pharynx. The heavily ciliated tentacles originating from the roof of the buccal cavity, shown to belong to the dorsal part of the axial nonmuscular proboscis by Zhadan *et al.* (2014, 2015), are specific to the family. Blood vessels are weakly developed, except for the intestinal vascular plexus in the abdominal region

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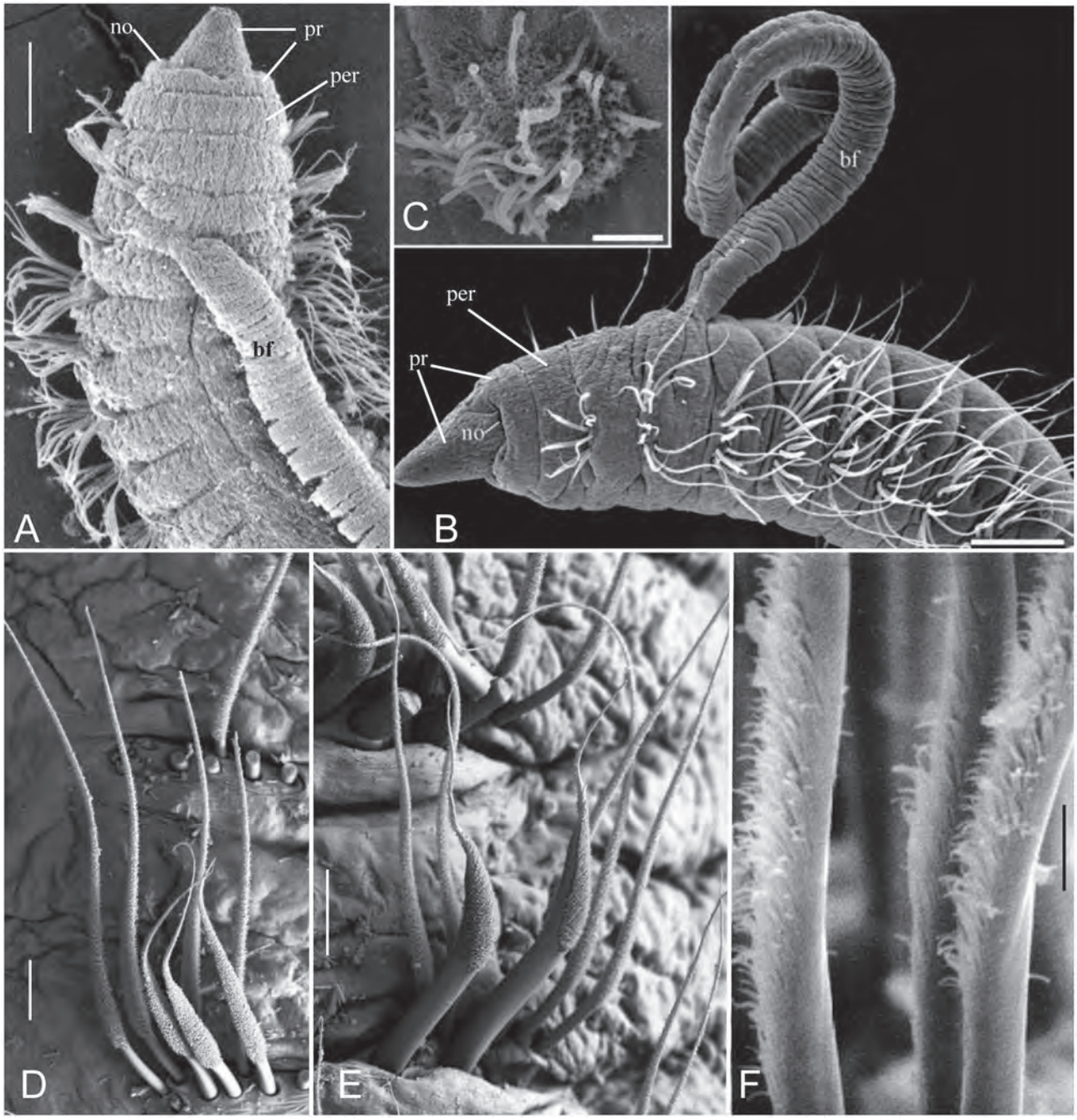


**Fig. 7.3.1.2.2:** Morphology of Cossuridae. A–C, *Cossura pygodactylata*. A, Anterior end, dorsal view. B, Anterior end, lateral view. C, Detail of nuchal organ. D–F, Chaetae of *Cossura* species. D–E, *Cossura hutchingsae*, notochaetae (D), neurochaetae (E). F, *Cossura pygodactylata*, notochaetae. A, F After Bachelet and Laubier (1994); B–C, after Zhadan *et al*. (2012); D–E, after Zhadan (2015). bf, branchial filament, per, peristomium, pr, prostomium, no, nuchal organ. Scales: A, B, 100 µm; C, 3 µm; D, 20 µm; E, 40 µm; F, 3 µm.

(Rouse and Tzetlin 1997) and the muscular heart in anterior segments (Zhadan *et al*., 2015). Little is known about the excretory system. Gametogenesis has been described for *C.* cf. *longocirrata* by Rouse and Tzetlin (1997). The authors describe some features in oogenesis that are unusual, mainly the presence of inactive follicle cells surrounding each oocyte during vitellogenesis, which is extraovarian.

**Musculature.** The most extensively studied aspect of the internal anatomy of cossurids is the musculature, most recently examined by Zhadan *et al*. (2014) in *C. pygodactylata*. The authors provide a three-dimensional reconstruction of the muscles in the body wall, parapodia, prostomium and peristomium, and internal organs, based on confocal laser scanning microscopy. From the

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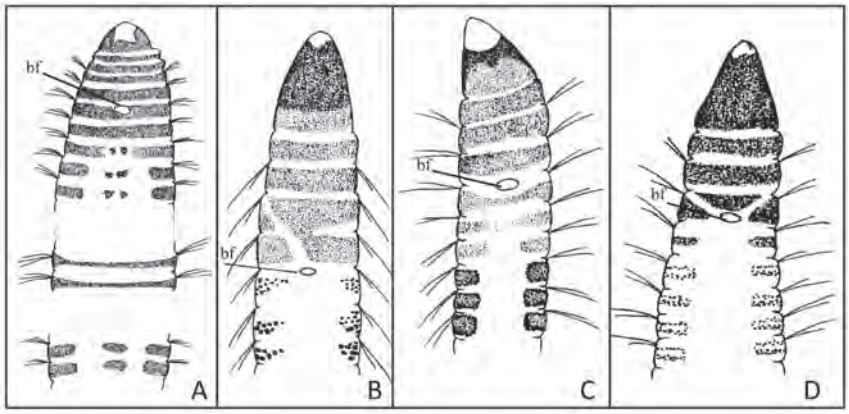


**Fig. 7.3.1.2.3:** Methyl Green staining patterns. A, *Cossura brunnea*. B, *Cossura modica*. C, *Cossura rostrata*. D, *Cossura pygodactylata*. All after Hilbig (2000). bf, branchial filament.

distribution of different muscle fibers, they infer that forward movement in the sediment is accomplished with the anterior (thoracic) region, while the muscles in the thin-walled abdominal region are used to close the coelomic cavity after fragmentation. The branchial filament is not capable of any substantial movement as it is equipped with only longitudinal muscle fibers. The same is true for the buccal tentacles that can be withdrawn by relatively strong muscles, but not actively be pushed forward as they lack circular fibers.

**Nervous system and sense organs.** Knowledge of the cossurid nervous system is almost nonexistent even though investigations on the nervous system of polychaetes are quite numerous, including studies to elucidate the phylogenetic significance of segmentation (Orrhage and Müller 2005 and references therein). The only sense organs noted in most descriptions are the nuchal organs, ciliated pits located in the posterior half of the prostomium. Zhadan *et al*. (2012) found segmental lateral organs in *C. pygodactylata* and described them as ciliated pits lying slightly behind the notopodial fascicle. In a subsequent investigation, the author found lateral organs also in other species of *Cossura* (Zhadan 2015).

## Reproduction and development

Knowledge of the life history of cossurids is sparse. Blake and Baptiste (1985) and Blake (1993) presented data on the size frequency distributions of *C. longocirrata* on the shelf ("mud patch" on Georges Bank, 70 m depth) off Massachusetts and upper slope off Cape Hatteras, North Carolina, USA (600 m depth). In both areas, recruitment was reported to occur most likely in the spring and summer, although at least at the deeper site, *C. longocirrata* seems to reproduce year-round. Both Fournier and Petersen (1991) and Blake (1993) observed a swelling of the posteriormost chaetigers of the thorax during oogenesis and a pronounced beaded appearance of the abdomen during sexual maturity.

Bachelet and Laubier (1994) described heavy recruitment of *C. pygodactylata* in shallow channels near Arcachon (Bay of Biscay) during spring. The authors also presented descriptions of early juveniles with 4 to 24 chaetigers (Fig. 7.3.1.2.4 A–D). The branchial filament was already present in a four-chaetiger juvenile, whereas pygidial cirri did not appear until the animals were 26 chaetigers long. The early development of the branchial filament is therefore a marker to readily identify postlarval. During development, the number of thoracic segments increases gradually through the change of abdominal into thoracic chaetigers. The same species was investigated with SEM by Zhadan *et al*. (2014), who observed the ciliated prototroch for the first time. This very prominent ciliary band persisted until the 21-chaetiger stage (Fig. 7.3.1.2.4 E). At that stage, there were no pygidial cirri present (Fig. 7.3.1.2.4 F), with these not appearing until the 30-chaetiger stage (Fig. 7.3.1.2.4 G). In the same manner, the buccal tentacles do not develop until 30 chaetigers are present. The different developmental rates of key morphology such as pygidial cirri, precludes species confirmation of small specimens of some taxa unless a growth sequence is available. However, the location of the branchial filament, which develops very early, can serve to narrow the species within those known to occur locally. A special mode of dispersal in early juveniles was proposed by Read (2000) for *Cossura consimilis* Read, 2000. Abdominal chaetae were extremely prolonged, suggesting a function as natatory chaetae in a 27-chaetiger specimen.

Year-round reproduction and a maximum age of 2 years are indicated by Zhadan *et al*. (2014). Nothing else is known about reproductive cycles in cossurids. Fournier and Petersen (1991) suggested the possibility of hermaphroditism, but this view has not been supported by other authors.

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## Biology and ecology

### Distribution

Cossurids typically inhabit the upper few centimeters in mud and fine sand biotopes. They do not form permanent tubes, although the mucous tunic that covers the body of the abyssal species, *C. flabelligera* may represent a form of tube (Zhadan 2017). Cossurids are commonly present in benthic samples but rarely as dominant species, with the exception of two deep-sea sites off the USA. One of these sites is on the continental slope off Cape Hatteras (U.S. east coast) in 600–2000 m depth, where *C. longocirrata* (down to 800 m) and *C. pygodactylata* (below 800 m) constituted up to 35% and 17%, respectively, of the total infaunal abundance (Blake and Hilbig 1994). The other deep site is located off the Farallon Islands (northeast Pacific), where three species of *Cossura* together accounted for more than 50% of the total polychaete abundance (Hilbig and Blake 1996). Some species exhibit an unusually large depth range from the shallow subtidal to the lower slope. Whether or not single individuals have such a wide range is not known, but because of different physiological conditions, it is likely that separate populations occupying narrower depth zones exist.

The geographical range of the family (and therefore the genus *Cossura*) is basically worldwide, with the number of species with a restricted distribution being very different from ocean to ocean. Many species have been described from the northeast and southeast Pacific between British Columbia and Chile, some from the Gulf of Mexico and Caribbean Sea, and a few records and new species have been added very recently from Australia, Indonesia, and the Philippines (Zhadan 2015). Just one type locality lies in European waters, and there is a single unnamed species known from the Southern Ocean (unpublished data). The type-species *C. longocirrata* is considered a cold-temperate arctic-boreal species, missing only from in the Russian Arctic (Fournier and Petersen 1991). At least in the White Sea, *C. pygodactylata* is distributed (Zhadan *et al.* 2014). It can, however, be expected that this picture may change as distributional patterns of widely reported species are assessed more carefully and cryptic species may be revealed using morphological and molecular data. As abundances are usually low, the number of records and species essentially reflects the position of sampling stations.

### Feeding

Although live observations are very rare, Cossuridae are considered to be subsurface deposit feeders (Fauchald and Jumars 1979, Jumars *et al.* 2015), burrowing through soft sediment and using the ciliated buccal tentacles to collect particles. Bachelet and Laubier (1994) reported sand grains and diatoms in the guts of *C. pygodactylata*. The species appeared to prefer the top 2 cm of sediment. Blake (1994) documented the vertical distribution of cossurid polychaetes in soft sediments from depths of 600 to 3,000 m off North Carolina and found them throughout the top 10 cm, but most frequently below 2 cm. This finding suggests that in suitable environments, they live and feed below the sediment surface.

Tzetlin (1994) hypothesized that the buccal tentacles cannot perform strong movements but are rather spread over the sediment, while the cilia are used for the actual feeding. In contrast, Jumars *et al.* (2015) were confident, based on fracture mechanics during burrowing observed by Dorgan *et al.* (2006) and Jumars *et al.* (2007) and on the reported depth-frequency distributions by Jumars (1978), Blake (1994), and others, that cossurids rarely fed at the sediment-water interface but instead used their buccal tentacles to collect particles from fractured surfaces during their burrowing activities.

## Phylogeny and taxonomy

### Phylogeny

**Morphological phylogeny.** The first cossurid described was *C. longocirrata* Webster & Benedict, 1887 and was then placed in the family Cirratulidae by the authors. It was not until 1963 that Dales erected a separate family for the genus. Perhaps owing to the paucity of external morphological characters, studies dealing with the phylogenetic position of Cossuridae and their relation to other polychaete families were virtually absent until the turn of the century. In a phylogenetic tree based on morphological characters, Rouse and Fauchald (1997) placed the family as a basal group in the Scolecida, a taxon that has since been shown to be polyphyletic. Zhadan *et al.* (2014) applied confocal laser scanning microscopy as a novel method to describe internal morphological features. The authors studied the musculature of *C. pygodactylata* in great detail, identifying characters unique to cossurids especially around the anterior end, including the foregut and associated buccal tentacles. The latter were studied extensively and considered nonhomologous to buccal tentacles of, e.g., Terebellidae and Ampharetidae (Tzetlin 1994). Zhadan *et al.* (2014) suggested comparable studies of the musculature of other families recently considered close relatives of Cossuridae, such as Paraonidae and Fauveliopsidae (Zrzavy *et al.* 2009). The very sophisticated method of confocal laser scanning microscopy revealing highly informative images of inner structures may help to give new insights to morphological

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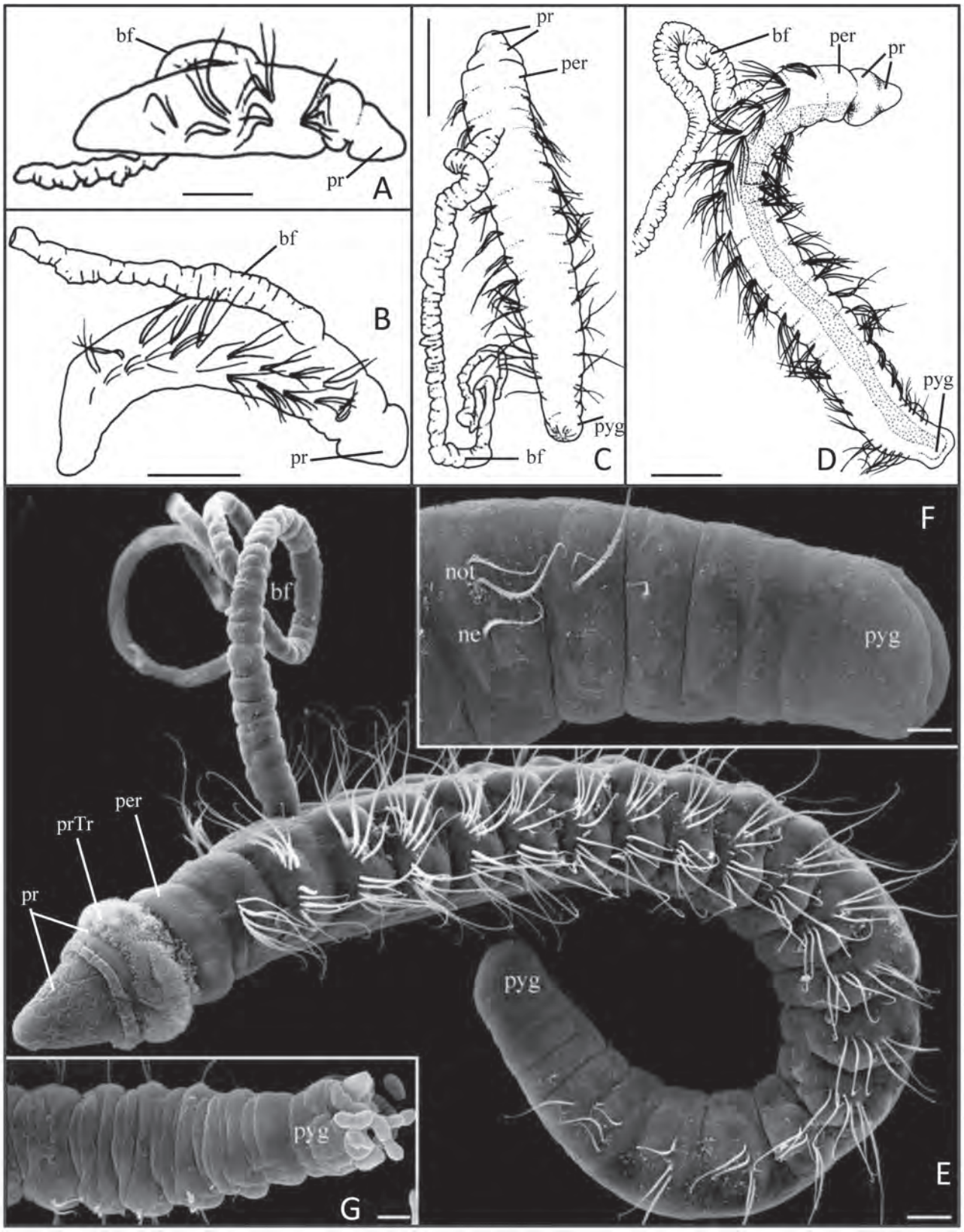


**Fig. 7.3.1.2.4:** Postlarvae and juveniles of *Cossura pygodactylata.* A, Four-chaetiger stage. B, 11-chaetiger stage. C, 14-chaetiger stage. D, 24-chaetiger juvenile. E, 21-chaetiger juvenile, entire worm, lateral view. F, Same, posterior end, lateral view. G, 30-chaetiger juvenile, posterior end, dorsal view. aC, anal cirri; bf, branchial filament; ne, neuropodium; not, notopodium; per, peristomium; pr, prostomium; prTr, prototroch; pyg, pygidium. Scales: A, 50 µm; B, 100 µm; C, D, 200 µm; E, 30 µm; F–G, 10 µm. A–D, From Bachelet and Laubier (1994); E–F, from Zhadan *et al.* (2012).

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research aimed at shedding light on the relationship of polychaete families.

**Molecular studies.** Although the use of molecular genetic methods to elucidate the phylogeny of polychaetes has resulted in a wealth of literature, Cossuridae are rarely addressed. Zrzavy *et al*. (2009) included the family in their total-evidence analysis of relationships among polychaete families and several taxa originally thought to belong to separate phyla. Their analysis was based on 93 morphological characters and six gene sequences. Cossuridae formed a clade together with Fauveliopsidae and Paraonidae, the sister group being a clade formed by Cirratulidae and Ctenodrilidae. The total-evidence analysis may provide very helpful information and resolve some problems coming from conflicting or inconclusive results based on morphology or genetics alone.

### Taxonomy

**Taxonomic history.** The first cossurid, *C. longocirrata* Webster & Benedict, 1887, was placed in the family Cirratulidae, where it remained until 1963, when Day (1963) established the family Cossuridae. The genus was monotypic until 1955, when Hartman (1955) described *Cossura candida* from Los Angeles Harbor. Two decades later, Hartman (1976) established a second genus, *Cossurella* Hartman, 1976, to accommodate a cossurid from the Indian Ocean that differed from other cossurids in bearing spines along with capillary chaetae in abdominal chaetigers. Wu and Chen (1977) described a species from Chinese waters, also bearing spines in abdominal chaetigers, and placed it in a new genus *Heterocossura*, which was synonymized with *Cossurella* only 2 years later (Gardiner and Wilson 1979). Read (2000) noticed that the cossurids assigned to *Cossurella* (including the former *Heterocossura aciculata* Wu & Chen, 1977), apart from the acicular- or spine-like chaetae in the abdomen, shared no additional characters justifying the genus and consequently synonymized *Cossurella* with *Cossura*. The family therefore contains only a single genus again, currently with 28 valid species (Read 2010).

### Taxonomy and distribution

#### Family Cossuridae Day, 1963

#### Type Genus *Cossura* Webster & Benedict, 1887

**Type species:** *Cossura longocirrata* Webster & Benedict, 1887
**Diagnosis:** Small, threadlike polychaetes with numerous segments, anterior (thoracic) region dorsoventrally flattened and rigid, posterior (abdominal) region fragile, breaking easily during collection, with beadlike segments; last few preanal segments more crowded, defined as a separate body region by some authors. Prostomium typically conical, tapering, rarely with short lateral horns; includes first and narrowest of two achaetous rings; eyes absent, ciliated nuchal organs in slits. Peristomium includes second and largest achaetous ring. Single branchial filament inserting middorsally on an anterior chaetiger. All chaetae simple, arising from inconspicuous parapodia, the latter uniramous on chaetiger 1, biramous on subsequent chaetigers. Appendages lacking except for anal cirri, usually three. Foregut with eversible paired buccal tentacles.

#### Genus *Cossura* Webster & Benedict, 1887

**Type species:** *Cossura longocirrata* Webster & Benedict, 1887.
**Synonym:** *Cossurella* Hartman, 1976: 234
**Type species:** *C. dimorpha* Hartman, 1976
**Synonym:** *Heterocossura* Wu & Chen, 1977: 100
**Type species:** *C. aciculata* Wu & Chen, 1977
**Diagnosis:** Same as for the family (see earlier discussion)
**Species:** Distributional data are mostly from the World Registry of Marine Species (Read 2010). Twenty-eight species are currently recognized and have been reported globally. Species range from intertidal to abyssal depths.
*Cossura abyssalis* Hartman, 1967. Off Valparaiso, Chile, in 3655–3651 m (type locality)
*Cossura aciculata* (Wu & Chen, 1977). East China Sea (type locality), Borneo, Philippines, in 5.5 m
*Cossura alba* Hartman, 1967. Off southwest Chile, in 957 m (type locality), Gulf of Mexico
*Cossura bansei* Hilbig, 1996. British Columbia to California, in 18–160 m
*Cossura brunnea* Fauchald 1972. Gulf of California (type locality), Oregon to western Mexico, New England to North Carolina, in 1600–2200 m
*Cossura candida* Hartman, 1955. Los Angeles Harbor (type locality); Mexico, Gulf of California, southern and central California, in 11–2400 m
*Cossura chilensis* Hartmann-Schröder, 1965. Off Chile, in 124–2060 m
*Cossura coasta* Kitamori, 1960. Japan
*Cossura consimilis* Read, 2000. New Zealand, in 0–2330 m
*Cossura dayi* Hartman, 1976. Indian Ocean, in 16–1006 m
*Cossura delta* Reish, 1958. Mississippi delta (type locality), Gulf of Mexico, inshore; New England, Brazil
*Cossura dimorpha* (Hartman, 1976). Mozambique (type locality), Indian Ocean, in 34–110 m
*Cossura flabelligera* Zhadan, 2017. South-east Atlantic Ocean, Congo deep-sea fan, 4719–4846 m.
*Cossura ginesi* Liñero-Arana & Diaz-Diaz, 2010. Caribbean Sea, Venezuela, in 4 m
*Cossura heterochaeta* Orensanz, 1976. Argentina, in 150–310 m

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*Cossura hutchingsae* Zhadan, 2015. Australia, New South Wales, in 6–20 m
*Cossura keablei* Zhadan, 2015. Fiji (type locality), Philippines, nearshore
*Cossura laeviseta* Hartmann-Schröder, 1962. Peru, in 676 m
*Cossura longocirrata* Webster & Benedict, 1887. Maine (type locality), U.S. Atlantic, Denmark, Arctic, in 7–887 m
*Cossura modica* Fauchald & Hancock, 1981. Oregon (type locality) to California, in 985–2955 m
*Cossura pettiboneae* (Ewing, 1987). Puerto Rico, in 257–530 m
*Cossura platypus Zhadan*, 2017. South-east Atlantic Ocean, Congo deep-sea fan, abyssal, 3154–3285 m.
*Cossura pseudakaina* (Ewing, 1987). Gulf of Mexico, Caribbean Sea, in 104–570 m
*Cossura pygodactylata* Jones, 1956. central California (type locality), British Columbia, Japan, North Atlantic, White Sea, in 20–2720 m
*Cossura queenslandensis* Zhadan, 2015. Australia, Queensland, in 1–2 m
*Cossura rostrata* Fauchald, 1972. western Mexico (type locality), Oregon to western Mexico, in 6–3348 m
*Cossura sima* Fauchald, 1972. Central American Trough (type locality), in 2307–3544 m
*Cossura soyeri* Laubier, 1964. Mediterranean Sea (type locality), northern Gulf of Mexico, in 35 m

## References


Bachelet, G. & Laubier, L. (1994): Morphology, ecology, and juvenile development of *Cossura pygodactylata* Jones (Polychaeta, Cossuridae) in Arcachon Bay, SW France, with a reassessment of the geographic distribution of *C. pygodactylata* and *C. soyeri* Laubier. *Mémoires du Muséum National d'Histoire Naturelle* 162: 355–370.

Blake, J.A. (1993): Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. *Journal of the Marine Biological Association of the United Kingdom* 73:123–141.

Blake, J.A. (1994): Vertical distribution of benthic infauna in continental slope sediments off Cape Lookout, North Carolina. *Deep-Sea Research II* 41: 919–927.

Blake, J.A. & Baptiste, E.M. (1985): Chapter 6. Life history studies on dominant polychaete species from Georges Bank. In: Maciolek-Blake, N., Grassle, J.F. & Neff, J.M. (eds.) *Georges Bank Benthic Infauna Monitoring Program, Final Report for Third Year of Sampling*. U.S. Department of the Interior, Minerals Management Service, Herndon, VA: 140–178.

Blake, J.A. & Hilbig, B. (1994): Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. *Deep-Sea Research II* 41: 875–899.

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

Dorgan, K.M., Jumars, P.A., Johnson, B.D. & Boudreau, B.P. (2006): Macrofaunal burrowing: the medium is the message. *Oceanography and Marine Biology Annual Review* 44: 85–121.

Ewing, R.M. (1987): Review of the genus *Cossurella* (Polychaeta: Cossuridae) including descriptions of two new species and a key to the species of the world. *Bulletin of the Biological Society of Washington* 7: 3–10.

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

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

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

Fournier, J.A. & Petersen, M.E. (1991): *Cossura longocirrata*: redescription and distribution, with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta: Cossuridae). *Ophelia Supplement* 5: 63–80.

Gardiner, S.L. and Wilson, W.H. (1979): New records of polychaete annelids from North Carolina with the description of a new species of *Sphaerosyllis* (Syllidae). *Journal of the Elisha Mitchell Scientific Society* 93: 159–172.

Hartman, O. (1955): Endemism in the North Pacific Ocean, with emphasis on the distribution of marine annelids, and description of new or little known species. In: *Essays in the Natural Sciences in Honor of Captain Allan Hancock on the Occasion of His Birthday*. University of Southern California Press, Los Angeles: 39–40.

Hartman, O. (1976): Polychaetous annelids of the Indian Ocean including an account of species collected by members of the International Indian Ocean Expeditions, 1963–64 and a catalogue and bibliography of the species from India. *Journal of the Marine Biological Association of India* 16: 191–252.

Hartmann-Schröder, G. (1962): Zweiter Beitrag zur Polychaetenfauna von Peru. *Kieler Meeresforschungen* 18(1): 109–147.

Hartmann-Schröder, G. (1965): Die Polychaeten des Sublitorals. In: Hartmann-Schröder, G. & Hartmann, G. (eds.) *Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. (Mit Bemerkungen über den Einfluss sauerstoffarmer Strömungen auf die Besiedlung von marinen Sedimenten.)*. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 62 (Ergänzungsband): 59–305.

Hilbig, B. (1996): Chapter 9: Family Cossuridae Day, 1963. In: Blake, J.A., Hilbig, B. & Scott, P.H. (eds.) *Taxonomic Atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 6 The Annelida Part 3, Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara, CA: 385–404.

Hilbig, B. & Blake, JA. (1996): Deep-sea polychaete communities in the northeast Pacific Ocean off the Gulf of the Farallones, California. *Bulletin of Marine Science* 78: 243–269.

Jones, M.L. (1956): *Cossura pygodactylata*, a new annelid from San Francisco Bay (Polychaeta, Cirratulidae). *Journal of the Washington Academy of Sciences* 46: 127–130.

Jumars, P.A. (1978). Spatial autocorrelation with RUM (Remote Underwater Manipulator): vertical and horizontal structure of a bathyal benthic community. *Deep-Sea Research* 25: 589–604.

Jumars, P.A., Dorgan, K.M. and Lindsey, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520 [+ supplemental appendix A. Family-by-family updates: A1–A350 + supplemental table of guild characteristics: 1–14].


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Jumars, P.A., Dorgan, K.M., Mayer, L.M., Boudreau, B.P. & Johnson, B.D. (2007): Physical constraints on infaunal lifestyles: may the persistent and strong forces be with you. In: Miller, W. III (ed.) *Trace Fossils: Concepts, Problems, Prospects 26*. Elsevier, Amsterdam: 442–457.

Kitamori, R. (1960): Two new species of cirratulid and Nephtyidae (Annelida: Polychaeta). *Bulletin of the Japanese Society for Scientific Fisheries* 26(11): 1082–1085.

Laubier, L. (1963): Découverte du genre *Cossura* (polychète, Cossuridae) en Méditerranée: *Cossura soyeri* sp. n. *Vie et Milieu* 14(4): 833–842.

Liñero-Arana, I. & Diaz-Diaz, O. (2010): A new species of Cossuridae (Annelida: Polychaeta) from Venezuela. *Interciencia* 35(19): 789–792.

Orensanz, J.M. (1976): Los anelidos poliquetos de la provincia biogeographica Argentina. IX. Poecilochaetidae y Cossuridae. *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo* 10(140): 1–8.

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

Read, G.B. (2000). Taxonomy and distribution of a new *Cossura* species (Annelida: Polychaeta: Cossuridae) from New Zealand. *Proceedings of the Biological Society of Washington* 113(4): 1096–1110.

Read, G. (2010): Cossuridae Day, 1963. In: Read, G.; Fauchald, K. (Ed.) (2017). World Polychaeta database. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=908 on 2018-01-12

Reish, D.J. (1958): Description of a new species of *Cossura* (Annelida: Polychaeta) from the Mississippi Delta. *Journal of the Washington Academy of Sciences* 48: 53–55.

Rouse, G.W. & Fauchald, K. (1997): Cladistics and Polychaetes. *Zoologica Scripta* 26(2): 139– 204.

Rouse, G.W. & Tzetlin, A. B. (1997): Ultrastructure of the body wall and gametogenesis in *Cossura* cf. *longocirrata* (Cossuridae Polychaeta). *Invertebrate Reproduction and Development* 32: 41–54.

Thulin, G. (1921): Biologisch-faunistische Untersuchungen aus dem Öresund. IV. Über *Cossura longocirrata* Webster und Benedict und über die Röhren von *Disoma multisetosum* Örsted. *Lunds Universitets Årsskrift N.F. Avd*. 2 17(10): 3–7.

Tzetlin, A.B. (1994): Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta, Cossuridae) from the White Sea. *Mémoires du Muséum National d'Histoire Naturelle* 162: 137–144.

Tzetlin, A.B. & Zhadan, A. (2009): Morphological variation of axial non-muscular proboscis types in the Polychaeta. *Zoosymposia* 2: 415–427.

Webster, H.E. & Benedict, J.E. (1887): The Annelida Chaetopoda, from Eastport, Maine. *U.S. Commission of Fish & Fisheries. Report of the United States Commissioner of Fisheries. 1885. part 13, II. Appendix to Report of Commissioner* D.22, pp. 707–758, pls. 1–8.

Wu, B.L. & Chen, M. (1977): *Heterocossura*, a new genus of the Cossuridae (Polychaeta: Sedentaria). *Acta Zoologica Sinica* 23: 97–101.

Zhadan, A. (2015): Cossuridae (Annelida: Polychaeta: Sedentaria) from Australian and adjacent waters: the first faunistic survey. *Records of the Australian Museum* 67: 1–24.

Zhadan, A. (2017): Two new species of *Cossura* (Cossuridae, Annelida) from the terminal lobes of the Congo River deep-sea fan. *Journal of the Biological Association* of the United Kingdom 97(5): 881–888.

Zhadan, A.E., Vortsepneva, E.V. & Tzetlin, A.B. (2012): Redescription and biology of *Cossura pygodactylata* Jones, 1956 (Polychaeta; Cossuridae) in the White Sea. *Invertebrate Zoology* 9: 115–125.

Zhadan, A., Vortsepneva, E. & Tzetlin, A. (2014): Three-dimensional reconstruction of the musculature of *Cossura pygodactylata* Jones. 1956 (Annelida: Cossuridae). *Zoologischer Anzeiger* 253: 181–191.

Zhadan, A., Vortsepneva, E. & Tzetlin, A. (2015): Ontogenetic development and functioning of the anterior end of *Cossura pygodactylata* Jones, 1956 (Annelida: Cossuridae). *Zoomorphology,* DOI: 10.1007/s00435-015-0282-7.

Zrzavy, J., Říha, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189. DOI:10.1186/1471-21-48-9-189.

Anna E. Zhadan and Sergio I. Salazar-Vallejo

### 7.3.1.3 Fauveliopsidae Hartman, 1971

#### Introduction

The name of the family is derived from *Fauveliopsis* McIntosh, 1922. The genus name was dedicated to Pierre Fauvel (1866–1958), a famous French polychaetologist, and the type species *Fauveliopsis challengeriae* McIntosh, 1922 was described with some specimens collected during the famous RV Challenger expedition.

The history of classification of Fauveliopsidae is part of a recurrent process for some other abyssal organisms having a simplified morphology. Thus, *Fauveliopsis* was firstly considered as an aberrant flabelligerid, and then, as a part of a compilation for the abyssal polychaetes, Hartman (1971), proposed to erect a new family. At that point of time, Fauveliopsidae contained some genera which were regarded as being closely related to Flabelligeridae: *Bruunilla* Hartman, 1971, *Fauveliopsis*, *Flabelligella* Hartman, 1965, and *Flota* Hartman, 1967. However, in a subsequent publication (Hartman 1974), the author apparently changed her view, since she again placed *Fauveliopsis* in Flabelligeridae.

On the other hand, the other genera being originally regarded as belonging to Fauveliopsidae have been transferred elsewhere. Thus, Pettibone (1979) demonstrated that *Bruunilla* belongs in Polynoidae, Orensanz (1974) indicated that *Flabelligella* is a member of Acrocirridae, and *Flota* was used to propose an independent family by Buzhinskaya (1996). However, for the latter, it has recently been demonstrated to be a junior synonym to *Buskiella* McIntosh, 1885 and thus part of Flabelligeridae (see Salazar-Vallejo and Zhadan 2007).

Currently, the family comprises only two genera: *Fauveliopsis* McIntosh, 1922 and *Laubieriopsis* Petersen, 2000. These genera differ in the integument, being opaque and variously rugose or papillate in *Fauveliopsis* or transparent and smooth in *Laubieriopsis*. The chaetae are typically directed forward in the whole body of

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*Fauveliopsis* species, while in *Laubieriopsis* species, only the first few chaetigers have chaetae in such an orientation. The number of chaetigers and their relative length also differ: in *Fauveliopsis*, the number of chaetigers shows intraspecific variation, and their relative length can change throughout the body, whereas *Laubieriopsis* species have a fixed number of chaetigers and their length is much less variable throughout the body.

There are no published accounts on fossil fauveliopsids. However, since several species have been found to be associated with foraminferans, gastropods, or scaphopods, one could expect some records once the fossils of the latter groups, which are very well represented among the fossil taxa, have been more carefully evaluated.

Fauveliopsidae is a family entirely composed of benthic species that usually attain a low density in the silty bottoms that they inhabit. Most of the species come from the deep sea being part of the so-called trench floor fauna (Menzies and George 1967); however, some shallow-water species have been described from the Canary Islands (5 m), New Zealand (20 m), and from the Mediterranean (Adriatic Sea 60 m). Members of the family are either free-living or permanent residents in tubes (Blake and Petersen 2000, Petersen 2000); the tubes are built of cemented silt grains, and often, they are made inside the shell of dead scaphopod or gastropod mollusks or even inside some tubular foraminiferans (*Bathysiphon* Sars, 1872) (Fig. 7.3.1.3.1 A–F).

The scarcity of available material might explain the fact that there are only a few studies beyond morphology. For this contribution, we have gathered new information based mostly upon the material available in the collections of the Los Angeles Natural History Museum and in the collection of the Zoological Museum of the Moscow State University.

McIntosh (1922), Hartman (1971), and Fauchald and Rouse (1997) pointed out the presence of palps in fauveliopsids, but Riser (1987) and Petersen (2000) showed that there are no head appendages at all. The body of the members of the family is subcylindrical or club shaped, and in the latter, the anterior region usually is the narrower end. Furthermore, the parapodia are displaced dorsally, with their notopodia clearly dorsolateral, while their neuropodia are lateral and they are directed anteriorly.

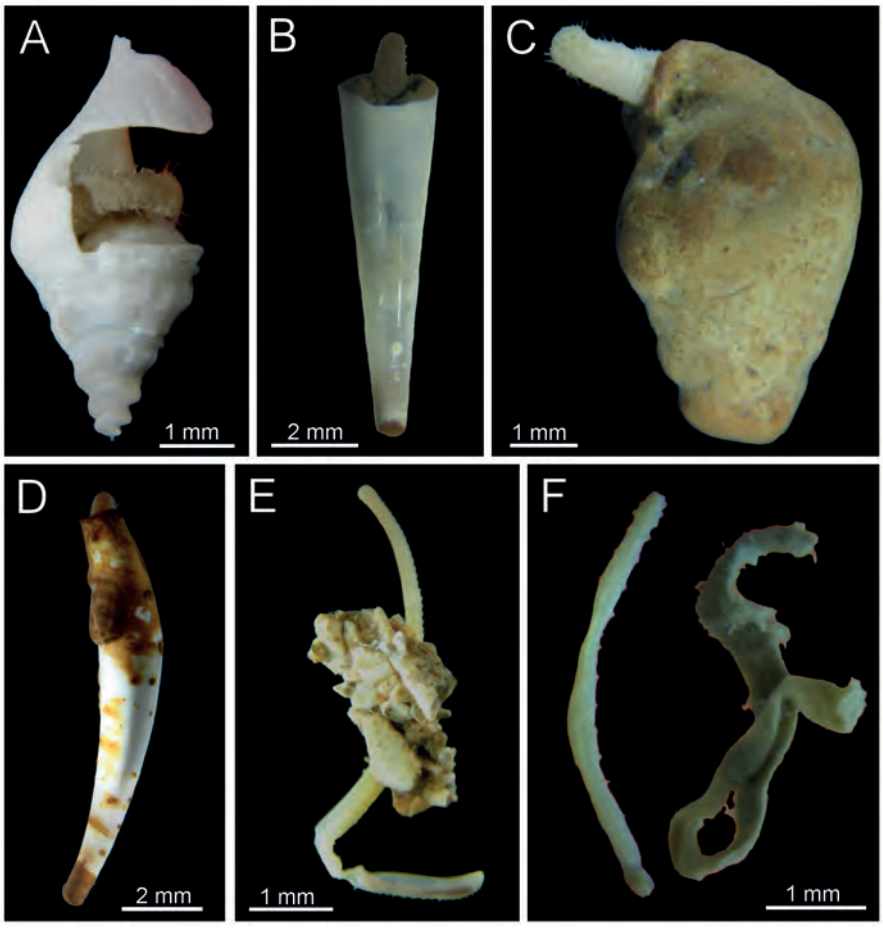


**Fig. 7.3.1.3.1:** Species of fauveliopsids in living conditions, anterior end exposed (specimens housed in the Natural History Museum of Los Angeles County [LACM] Allan Hancock Foundation [AHF]). A, *Fauveliopsis scabra* Hartman & Fauchald, 1971, LACM-AHF Poly 4376, off New England in gastropod shell. B–D, *Fauveliopsis* cf. *glabra*, LACM-AHF Poly 4379, off New England, in scaphopod shells and foram test. E, *Fauveliopsis* cf. *arabica*, LACM-AHF Poly 4377, off Durban, in agglomerated shell fragments. F, *F.* cf. *glabra*, LACM-AHF Poly 4378, off Western Mexico, from sabellid-like tube.

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So the combination of a usually wider region and the parapodial disposition, together with the presence of some anal papillae, has caused some confusion about the body polarity, which was first indicated by Laubier (1972). This confusion stemmed from a similarity to some other tubiculous families exhibiting four more or less widespread features among these groups: (1) the anterior region is wider than the rest of the body; (2) the segments are less defined toward the anterior end; (3) the chaetal bundles are placed toward the anterior region of each chaetiger, being displaced to the median region and later toward the posterior region in median to posterior chaetigers; and (4) the chaetae are directed anteriorly in few anterior chaetigers and toward the posterior region in the rest of the body.

Thus, this typical pattern is obviously inverted in fauveliopsids (Fig. 7.3.1.3.2 A, B). The main reason for this might be that they have evolved for living within tubes, bending their bodies obliquely or ventrally, and by directing their chaetal bundles anteriorly, a fact originally noticed by McIntosh (1922). This combination of features would be advantageous by providing a better anchoring role for both chaetae and parapodia. The dorsal displacement of parapodia might be explained likewise, since living inside empty shells or tests, better seen in those living in gastropod shells, the dorsal surface is facing the wider space available and is not oriented toward the columella.

Furthermore, it has been shown that it is the thinner region that is exposed outside the shells they occupy (Katzmann and Laubier 1974: Fig. 3 C). The confusion was clarified by Riser (1987) and emphasized by Blake and Petersen (2000); the latter standardized the description of several species, but the earlier descriptions should be reevaluated since a potential confusion about body polarity might have happen.

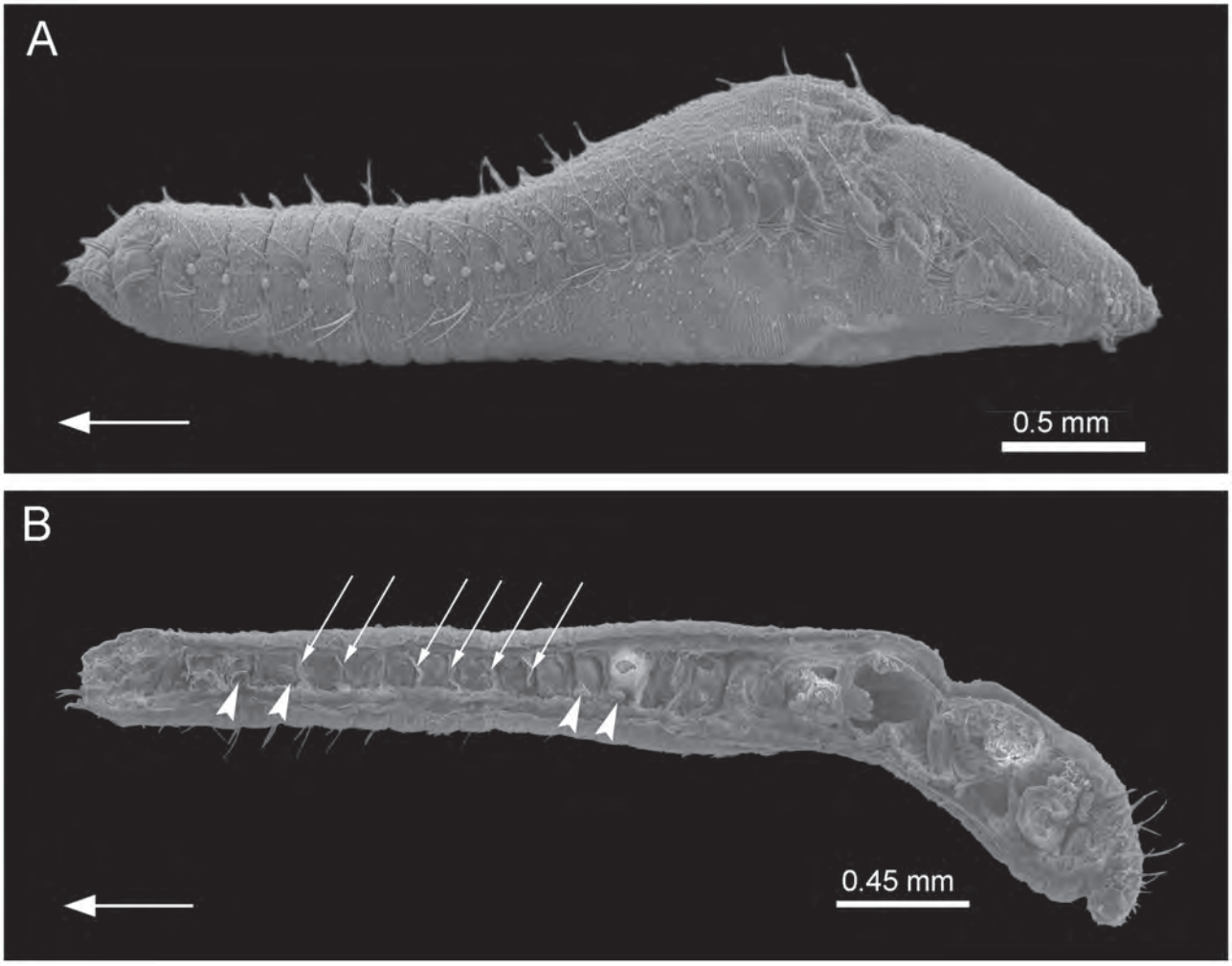


**Fig. 7.3.1.3.2:** Body structure and internal organization of *Fauveliopsis* species; anterior ends point toward the left. A, *Fauveliopsis scabra*, lateral view. B, *Fauveliopsis glabra*, after sagittal section. Complete septae (arrows) and presumably nephridia (arrowheads) are visible.

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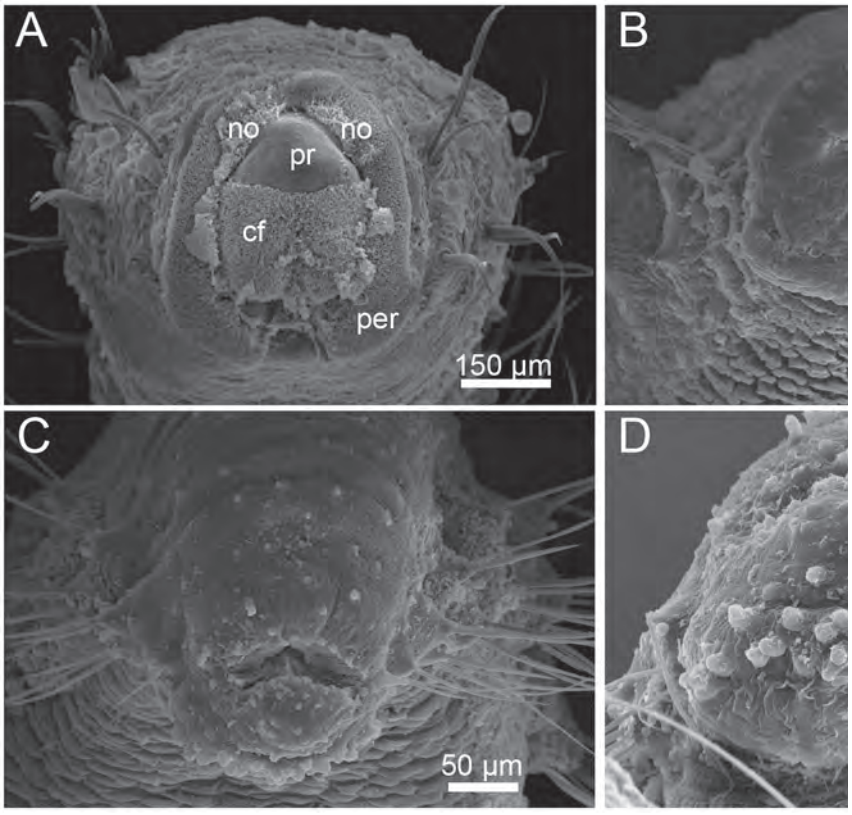


**Fig. 7.3.1.3.3:** Anterior and posterior ends of *Fauveliopsis*. A, *Fauveliopsis scabra*, anterior end, frontal view. B, *Fauveliopsis* cf. *rugosa*, posterior end, frontal view. C–D, *F. scabra*, posterior end in frontal view of two different specimens from the same lot. cf, ciliated field; no, nuchal organ; pr, prostomium; per, peristomium.

## Morphology

### External morphology

The body often is cylindrical, but it may have an anterior or medial expansion or show a posterior expansion, giving the animals a club-shaped outline; usually, both body ends are blunt (Figs. 7.3.1.3.1 E, F, 7.3.1.3.2 A, 7.3.1.3.5 A, B, and 7.3.1.3.7 A, H). The integument is smooth or rugose, especially along the anterior region, whereas the posterior region tends to be smoother. There are small to medium-sized papillae between the parapodial rami and some others can be found over the body surface (Figs. 7.3.1.3.2 A, 7.3.1.3.3 A–D, 7.3.1.3.4 A–C, 7.3.1.3.5 B, D, E, and 7.3.1.3.7 C–G). Based on the parapodial shape and types of chaetae, the body can be divided to two to three regions. The number of chaetigers can be fixed for those species having definite growth or variable in those species having indefinite growth. Their usage to identify species has been indicated several times (Katzmann and Laubier 1974, Riser 1987).

**Prostomium and Peristomium.** The anterior end is eversible and usually withdrawn upon disturbances. Thus, it is rarely exposed, especially in fixed material (Figs. 7.3.1.3.3 A and 7.3.1.3.5 B). This fact, together with obvious earlier misinterpretations of the body polarity, causes several problems in orienting specimens correctly, which were first indicated by Laubier (1972). There are neither pigmented eyes nor appendages on the prostomium and peristomium. Reports of grooved palps being present in Fauveliopsidae are erroneous (see Rouse and Pleijel 2001). However, photoreceptor-like sensory structures, called ocellar tubes, are situated in the brain. However, thus far, they were only described in *Fauveliopsis* cf. *adriatica* (Purschke 2005, 2011). As in sipunculids, these are embedded in epidermal follicles that extend deeply into the brain. The prostomium bears a pair of comparatively large ciliated nuchal organs on its posterior margin and can also bear a ciliated field on the ventro-lateral part (Purschke 1997, Thiel *et al*. 2011: Figs. 3 D–F and 4 D, Purschke 2011: Fig. 1). There are peristomial lateral ciliated fields or complete ciliated rings on the border between prostomium and peristomium.

The parapodia are displaced dorsally, such that the notopodial lobes point dorsolaterally while the neuropodia are lateral (Figs. 7.3.1.3.2 A, 7.3.1.3.5 B, and 7.3.1.3.7 C–F). All parapodia are biramous and have a variable development of chaetal lobes, which are better developed in posterior chaetigers. In each parapodium, there is a interramal papillae which often is globular, resembling a sessile sphere or pyriform with a distinct peduncle (Figs. 7.3.1.3.2 A, 7.3.1.3.4 A–C, 7.3.1.3.5 D, E, and 7.3.1.3.7 C–F). Their shape

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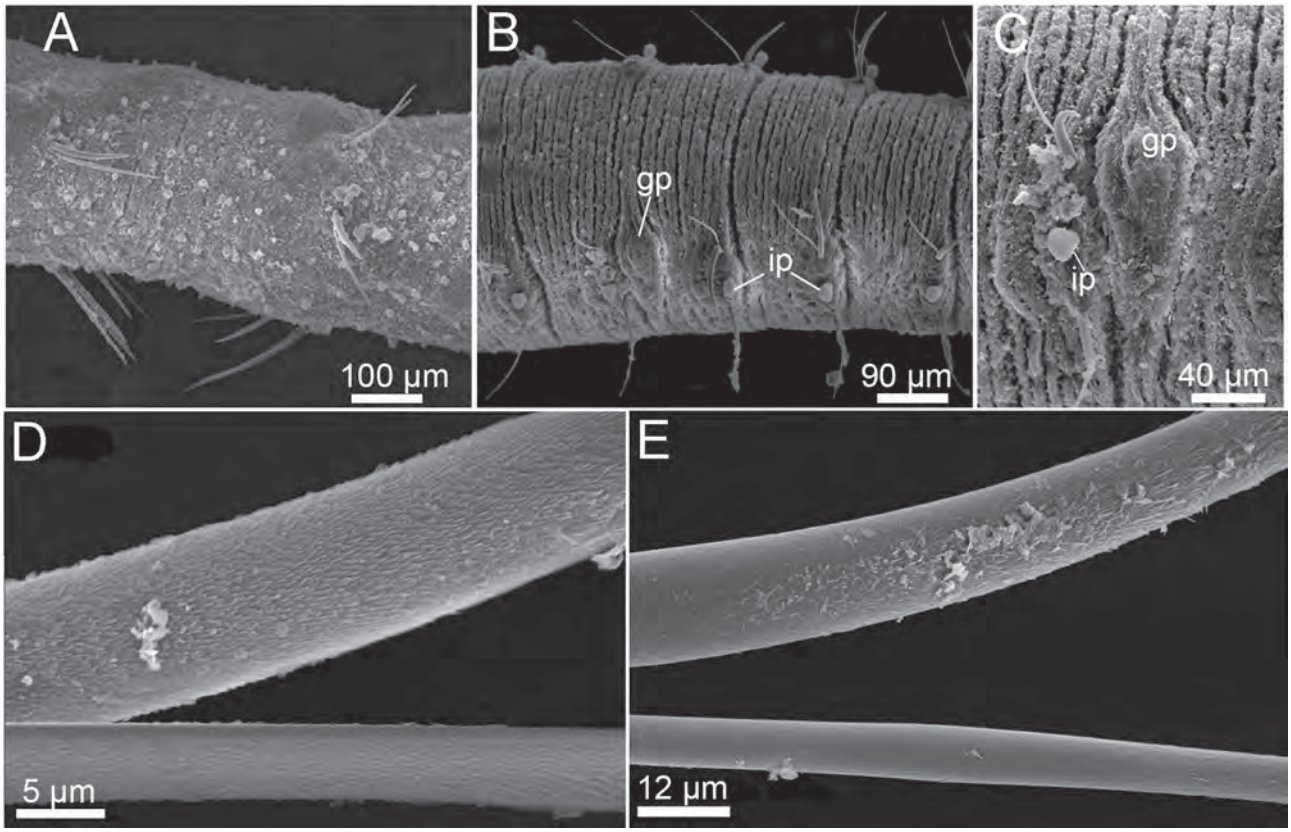


**Fig. 7.3.1.3.4:** Diversity of body wall and genital papillae in *Fauveliopsis* species. A, *Fauveliopsis glabra*, anterior chaetigers in oblique dorsal view. B, *Fauveliopsis* sp., anterior chaetigers, oblique lateral view. C, Close-up of genital papilla (gp) form B. D, E, Details of chaetal surface. D, *F. glabra*, spine and capillary. E, *F. scabra*, spine and capillary. ip, interramal papilla; gp, genital papilla.

might vary along the body and between species, and likewise, their relative position is modified along the body, especially in their proximity to notopodia. It is discussed whether these papillae are homologous with the epidermal papillae and represent an autapomorphy of the group (Glasby 2000, Rouse and Pleijel 2001). Another possibility is that the interamal papillae are lateral organs as present in many sedentary polychaetes (Purschke 2005).

All chaetae are simple, being either capillaries or spines, which could be falcate or sigmoid (Figs. 7.3.1.3.2 A, 7.3.1.3.3 A–D, 7.3.1.3.4 A–E, 7.3.1.3.5 B–E, 7.3.1.3.6 D, and 7.3.1.3.7 B, F). Notochaetal and neurochaetal bundles are quite similar in the same parapodia, although sometimes the neurochaetae are thicker, more abundant, or both, in relation to notochaetae. In some species, the posterior chaetigers have strongly falcate spines, while in some others, spines can have tips with tiny denticles. The relative numbers and their variation along the body have been employed to separate species (Hartmann-Schröder 1983).

Some species possess one single or one pair of lobulate or lobate papillae, which have been regarded as used for reproduction. When present, they are located in the limit among successive chaetigers and above the line of the chaetal lobes (Figs. 7.3.1.3.4 B, C, 7.3.1.3.5 D, E, 7.3.1.3.6 B, and 7.3.1.3.7 A, H). They are usually five to eight times larger than the interramal papillae of adjacent chaetigers and have been linked to testes (Riser 1987), but it is still unknown how the mature oocytes are released. Their presence has still to be documented for the remaining species.

**Pygidium.** The posterior region is often swollen, tapering to a blunt end, or might be bilobed. The pygidium has some small papillae, which might be projected, or consists of a rounded lobe, which is somehow retractable into the previous segment (Figs. 7.3.1.3.3 B–D, 7.3.1.3.5 C, and 7.3.1.3.7 G).

### Anatomy

The anatomy of fauvelopsids is not well known. Riser (1987) described some features for *Laubieriopsis arenicola*, *Fauveliopsis brevis*, and *Fauveliopsis glabra*. Zhadan and Atroshchenko (2010) described the inner organization of *Laubieriopsis* sp. Purschke (2011) gave a detailed description of the anterior end of *F.* cf. *adriatica*, as well as its brain and sensory structures. Thiel *et al*. (2011) described some anatomical features of *Fauveliopsis confusa*.

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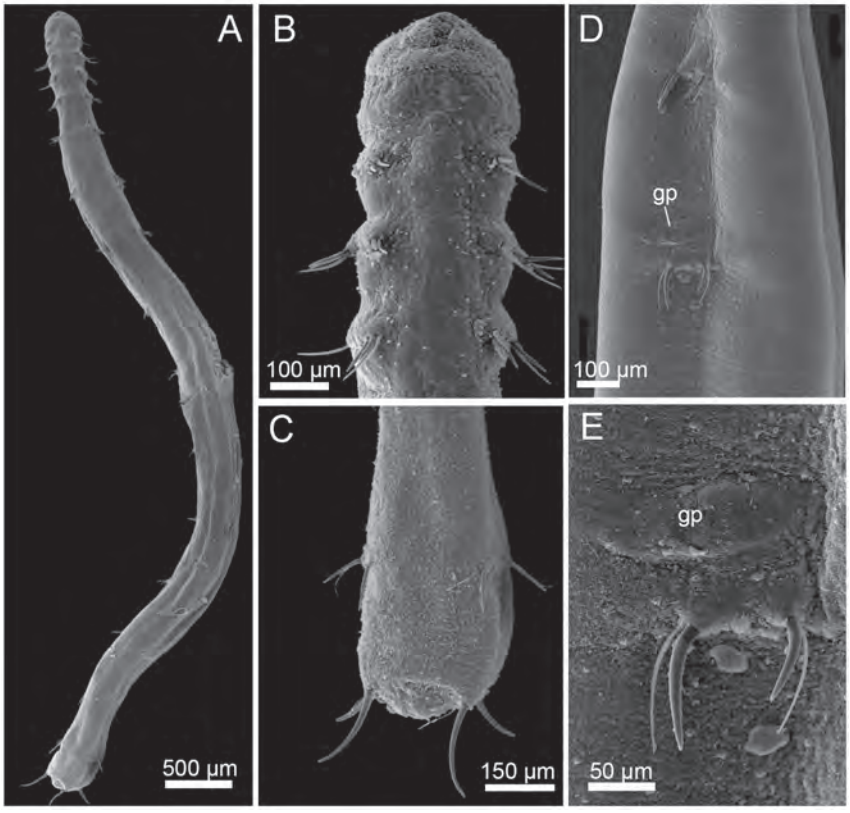


**Fig. 7.3.1.3.5:** External structure of *Laubieriopsis brevis*. A, Entire specimen, dorsal view. B, Same, anterior end, dorsal view. C, Same, posterior end, dorsal view. D, Segment with genital papillae (gp), lateral view. E, Enlargement of D showing the slightly elevated genital papillae (gp), parapodium with interramal papilla.

Representatives of both fauveliopsid genera exhibit a similar internal morphology. The cuticle is thick, consisting of numerous layers of collagen fibers, while the epithelium is two or three times thinner (Fig. 7.3.1.3.6 E). The interramal papillae represent outgrowths of the body wall covered with a thin cuticle. Appendices of epidermal cells penetrate into it, but glandular cells were not found. Two lateral subepidermal glands are present in each segment (Figs. 7.3.1.3.6 C and 7.3.1.3.7 D). There are four longitudinal muscle bands, which are separated by dorsal and ventral mesenteries and are covered by a coelomic epithelium (Fig. 7.3.1.3.6 E). Transversal and circular muscular fibers were not found. Two pairs of dorsal and one pair of ventral retractors of prostomium are strongly developed (Figs. 7.3.1.3.6 F and 7.3.1.3.8 B). Anteriorly, they are attached to the posterior part of the prostomium, and posteriorly, they reach to the body wall of chaetigers II and III. In *F.* cf. *adriatica*, the median retractors attach to the anterior apodeme-like part of the ocellar tubes between the median and lateral lobe of the brain (Purschke 2011). The coelomic cavity is divided by complete dissepiments at the border of each segment (Fig. 7.3.1.3.8 A, E). In the anterior part of the body, the dissepiments are thickened and have a strong muscular wall (Fig. 7.3.1.3.8 A). The gut is connected to the body wall by one dorsal and two ventral mesenteria (Riser 1987). The pharynx has a thick ciliary-glandular epithelium in dorso-lateral parts, but the ventral part is not modified; i.e., a ventral pharyngeal organ was not found (Figs. 7.3.1.3.6 F and 7.3.1.3.8 B). The gut is a straight tube. When the prostomium is inverted, the gut forms transversal folds in its anterior part. A circulatory system is present and represented by dorsal, ventral, and segmental vessels, although the latter are not always discernible (Figs. 7.3.1.3.6 F and 7.3.1.3.8 E). The nephridia are metanephridia opening with a small funnel into the coelomic cavity (Purschke unpublished observation).

**Nervous system.** The ventral nerve cord is well developed, with indistinctly separated ganglia (Figs. 7.3.1.3.6 F and 7.3.1.3.8 A, B, E). Although bulging into the body cavity, the entire nervous system is situated basiepithelially (Purschke 2011; see Fig. 7.3.1.3.6 F). The brain is split into two pairs of large lobes, median and lateral, extending posteriorly to the third chaetiger (Figs. 7.3.1.3.6 F and 7.3.1.3.8 C). The lobes mostly consist of neuronal somata and glial cells. In addition, nonneuronal cells – supportive cells in the nuchal organs and in the ocellar tubes, as well as a few gland cells – also comprise to the lobes. The neuropil is located in the anterior part of the brain and has short outgrowths into each lobe. The dorsal and the ventral roots of the circumesophageal connectives form a wide arc around the mouth. If the prostomium is inverted, they run downward and forward before entering the

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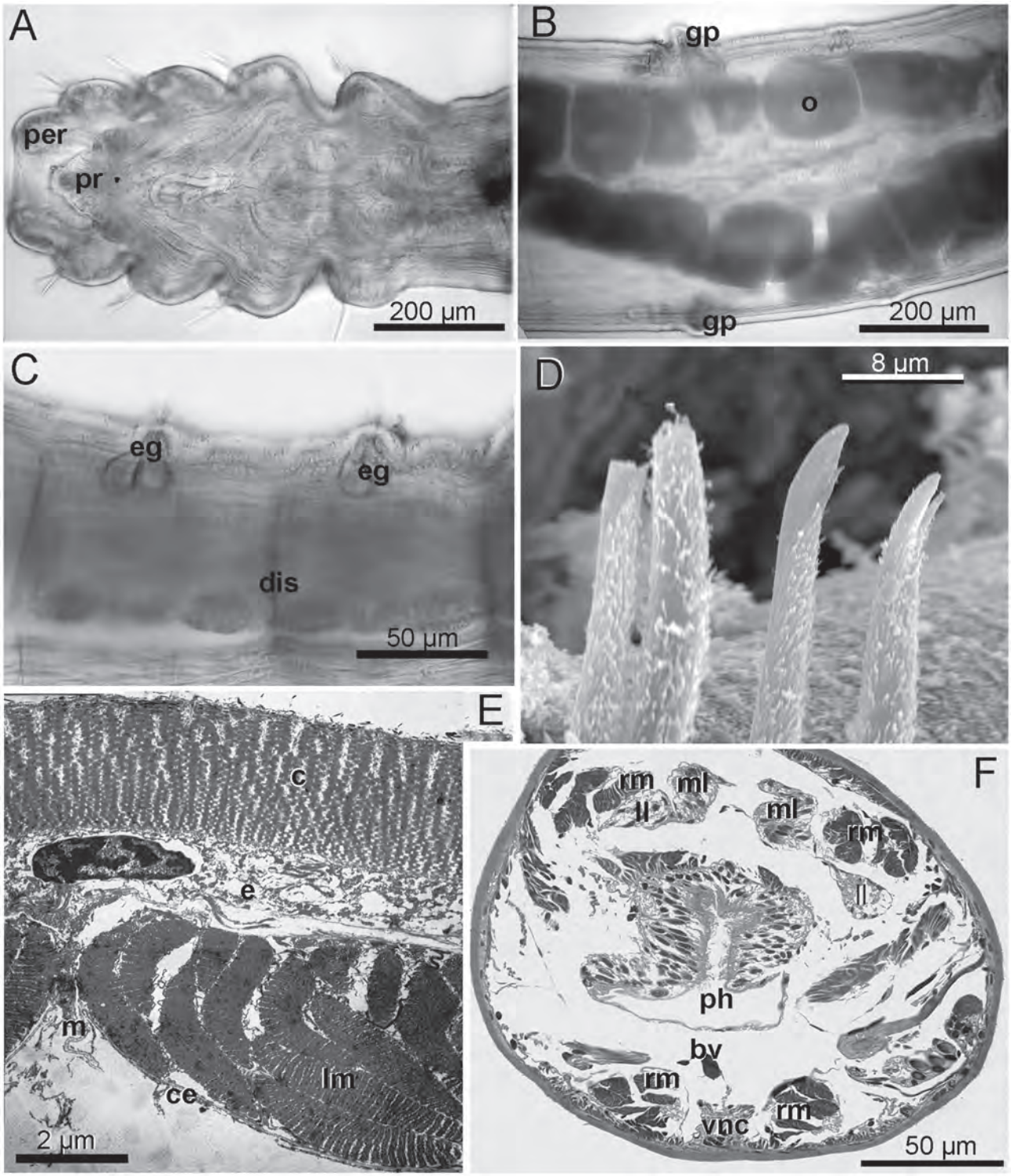


**Fig. 7.3.1.3.6:** *Laubieriopsis norvegica* Zhadan & Atroshchenko, 2012. A–C, glycerine mounts. A, Anterior end with inverted prostomium (pr). B, Chaetigers VII–IX showing paired genital papillae (gp). C, Fragment of middle part of the body showing paired epidermal glands (eg). D, Bidentate neurochaeta of chaetiger 1. E, Transmission electron microscopy, body wall in transverse section showing comparatively strong cuticle (c) above thin epidermal layer (e). F, Transverse section across area of pharynx (ph) with dorsolateral ciliated folds; all four lobes of the brain (ml, ll) and prostomial retractor (rm) visible. bv, blood vessel; c, cuticle; ce, coelomic epithelium; dis, dissepiments; e, epidermis; eg, epidermal gland; gp, genital papilla; ll, latero-posterior lobe of the brain; lm, longitudinal muscle; m, mesenterium; ml, median lobe of the brain; o, oocytes; per, peristomium; ph, pharynx; pr, prostomium; rm, retractor muscles; vnc, ventral nerve cord. From Zhadan and Atroshchenko (2010), modified (©Pleiades Publishing, Inc., 2010).

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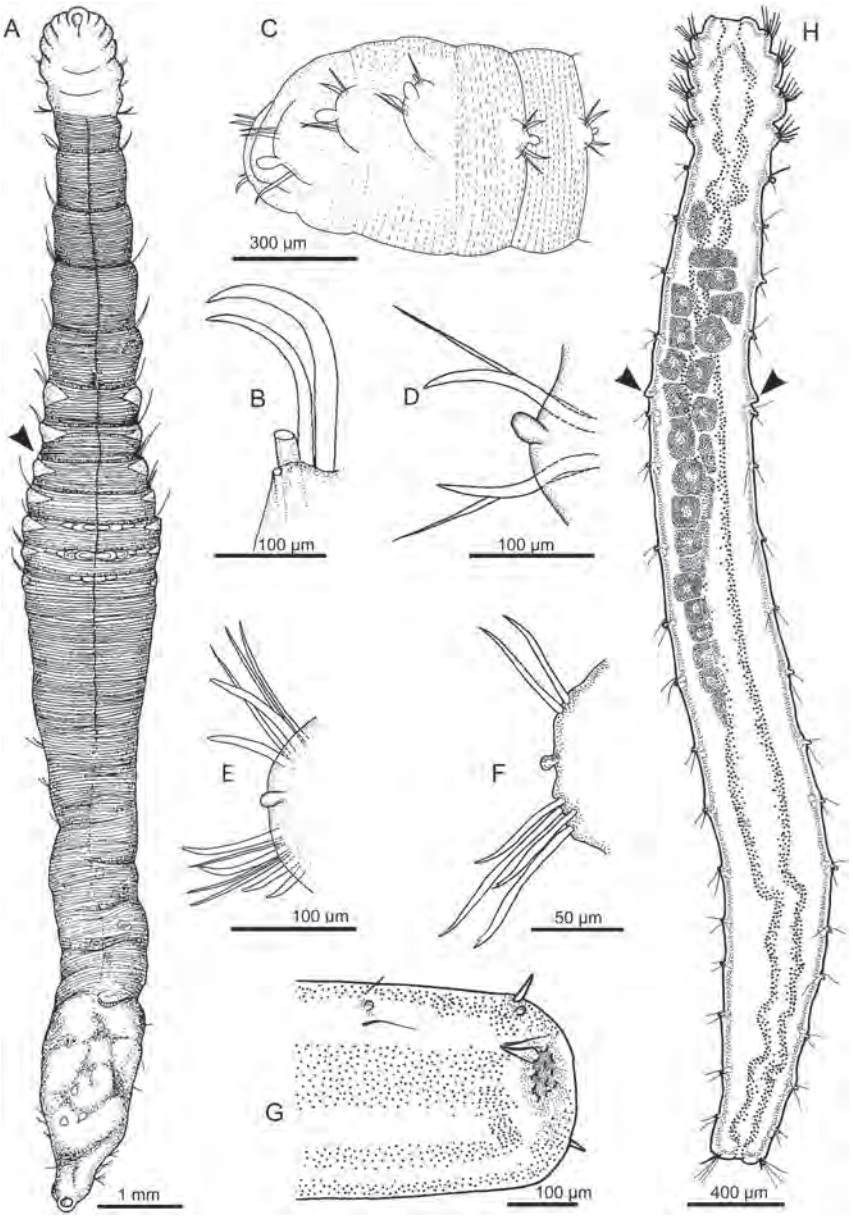


**Fig. 7.3.1.3.7:** A, B, *Fauveliopsis challengeriae*. A, Ventral view of entire specimen, arrowhead marks genital papilla. B, neurochaetae of segment 1. C–E, *Fauveliopsis glabra*. C, anterior part of body, lateral view. D, parapodium of chaetiger 10. E, parapodium of chaetiger 21. F–H, *Laubieriopsis norvegica*. F, parapodium of chaetiger 3. G, posterior part of body, dorso-lateral view. H, Dorsal view of entire specimen, arrowheads mark genital papillae. A, B, From Petersen (2000), modified (©University of Miami–Rosenstiel School of Marine and Atmospheric Science); C–E, redrawn from López (2011); F–H, from Zhadan and Atroshchenko (2012) (©A.E. Zhadan).

subesophageal ganglion. The prostomium is innervated from nerves originating from the dorsal and ventral roots of the circumesophageal connectives. Since this pattern is typical of palp nerve roots, this has been interpreted as being indicative of a loss of palps in the stem lineage of fauveliopsids (Purschke 2011).

All fauveliopsids studied are gonochoristic, have paired or unpaired gonads (which might explain having paired or single genital papillae), and ovisacs or sperm sacs, associated with genital papillae.

**Development.** Larvae and mode of development are unknown. Thiel *et al*. (2011) described juvenile stages of *Laubieriopsis* cf. *brevis*; the smallest consisted of seven to nine chaetigers (Thiel *et al*. 2011: Figs. 2 A and 4 E, F). They have "multiple-toothed chaetae, displaced during development by the chaetae of the adult from anterior to posterior, beginning at the neuropodia, followed at a distance of one to five chaetigers by the notopodia. Rami of middle and posterior region can have up to three chaetae during displacement."

## Biology and ecology

Species of *Fauveliopsis* inhabit either gastropod, scaphopod shells, or foraminiferan tubes and can build their own

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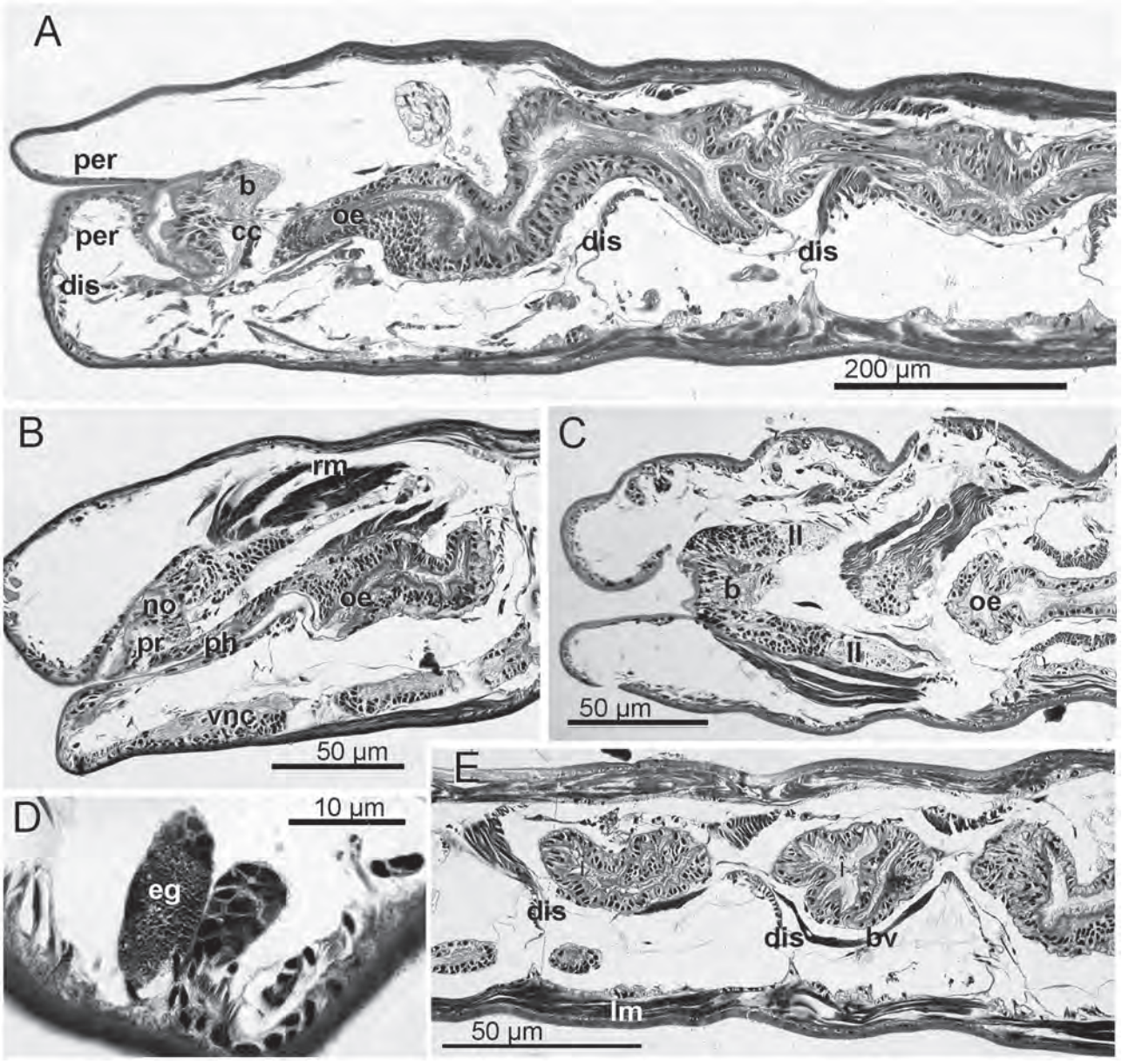


**Fig. 7.3.1.3.8:** *Laubieriopsis norvegica*. A, B, Anterior part, parasagittal sections. A, Brain (b) with circumesophageal connectives (cc), gut and septa (dis). B, Prostomial retractors (rm), nuchal organs (no), note chain of ganglia in the ventral nerve cord (vnc). C, Anterior part, coronal section, brain (b) with left and right lateral lobe (ll) and prostomial retractors. D, Middle part, sagittal section showing paired epidermal glands (eg). E, Middle part, parasagittal section showing gut, dissepiments (dis) and blood vessels (bv). cc, circumesophageal connectives; dis, dissepiments; eg, epidermal glands; ll, latero-posterior lobe of the brain; lm, longitudinal muscles; no, nuchal organs; oe, esophagus; per, peristomium; ph, pharynx; pr, prostomium; rm, retractor muscles; vnc, ventral nerve cord. From Zhadan and Atroshchenko (2010), modified (©Pleiades Publishing, Inc., 2010).

tubes inside the shells. They occur from 5 m to abyssal depths in sandy or muddy substrates. Individuals of *F. glabra* might live in empty scaphopod shells, where the worms seal the smaller opening and accumulate sediment inside. Other species can form rigid tubes by cementing sediment particles together. The thinner and more muscular anterior region is exposed, while the wider part remains within the shell or tube anchoring the body. The worms might be capable of rotating the body within their galleries, as the members of other tube-dwelling families do, but it is remarkable that none of them had the posterior region exposed to the outside. Species of *Lauberiopsis*

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are free-living, inhabiting depths from 22 to 6,835 m, in sandy or muddy sediments; Atlantic and Pacific oceans.

## Phylogeny and taxonomy

### Phylogeny

The phylogenetic affinities of the Fauveliopsidae have been problematic and are still far from being settled. A certain affinity with the Flabelligeridae was concluded by McIntosh (1922:7): "On the whole, *Fauveliopsis* appears to approach the Chloraemidae" (=Flabelligeridae). Even though he already noticed that the simple chaetae were similar to those present in oligochaetes or scalibregmatids, he regarded the anterior end opening as resembling that of some flabelligerids (*Brada*) and the clearly defined segmentation of the anterior region as resembling that of the posterior region of other flabelligerids (*Diplocirrus*). He added that the refraction properties of *Fauveliopsis* chaetae "approach those of this family...in general structure, though not transversely striated." Therefore, a similarity with flabelligerids cannot be sustained on these grounds. The other resemblance to flabelligerids is the retractile anterior end. Retractable part of the body in Fauveliopsidae consists of only prostomium and partly the peristomium (Zhadan and Atroshchenko 2010), and it does not include the first body segments as in Flabelligeridae. Thus, the capability to invert the anterior end most probably is homoplastic in these groups. The other similarity with flabelligerids is having a papillate integument. All fauveliopsids, except for *Fauveliopsis jameoaquensis* Nuñez in Núñez *et al*. (1997), have at least interramal papillae. There are no detailed histological studies of these papillae, but preliminary investigation shows that they are not associated with glandular cells as in flabelligerids. In addition, fauveliopsids lack any kind of palp or tentacle and never possess the cephalic cage typical of flabelligerids. Therefore, no character demonstrates a close relationship between Fauveliopsidae and Flabelligeridae.

Some recent studies of the phylogenetic affinities of the Fauveliopsidae to other polychaete families deserve to be mentioned. Thus, Rouse and Pleijel (2001) treated Fauveliopsidae as part of "Cirratuliformia," also containing Acrocirridae, Cirratulidae, Ctenodrilidae, Flabeligeridae, and *Sternaspis* Otto, 1821. Rouse and Pleijel (2003) found that two fauveliopsid genera form a clade with *Sternaspis*. This clade was part of a larger one that included Acrocirridae, Ctenodrilidae, Flabelligeridae, Flotidae, and Poeobiidae.

The analysis of Rousset *et al*. (2007) applying molecular data did not support the monophyly of Cirratuliformia and found a sister-group relationship between *Sternaspis* and Fauveliopsidae. The same results were found by Struck *et al*. (2007). In a cladistic analysis of Cirratuliformia based on morphological data by Salazar-Vallejo *et al*. (2008), Fauveliopsidae came out as sister group with Cirratulidae and Sternaspidae, and these three groups form a clade with Ctenodrilidae. Zrzavý *et al*. (2009) performed "total-evidence" analyses combining morphological and molecular characters, and their results show that Fauveliopsidae form a clade with either Sternaspidae or Cossuridae or a Paraonidae-Cossuridae group. Andrade *et al*. (2015) analyzed deeply sequenced transcriptomes of annelids and found Fauveliopsis inside Sedentaria, belonging to Cirratuliformia clade and forming a sister group with Sternaspis.

### Taxonomy

#### Genus *Fauveliopsis* McIntosh, 1922

**Type species:** *Fauveliopsis challengeriae* McIntosh, 1922
Fifteen species

**Diagnosis:** Body fusiform, often swollen in the middle region or posteriorly, divided into two or three regions based on chaetation, or division inconspicuous. Variable number of segments. Cuticle rugose, multiannulated or papillated. Chaetae usually directed forward, capillaries and falcate spines.

Members of *Fauveliopsis* species are present worldwide, mostly in peripheral, more eutrophical zones of the oceans. Species are not abundant, but usually they are present in any deep-sea survey or sampling program. However, most species are apparently restricted to certain marine or deep-sea regions. On the other hand, records of *F. brevis* for the Mediterranean Sea (Laubier 1972) indicate that it can be very abundant since in 12 dredgings, about 1,400 specimens were collected.

#### Genus *Laubieriopsis* Petersen, 2000

**Type species:**
*Laubieriopsis brevis* (Hartman, 1965)
Six species

**Diagnosis:** Body cylindrical, divided into two regions based on chaetation. Fixed number of segments. Cuticle smooth, mostly without papillae. Chaetae are capillaries and sigmoid spines, some might be bidentate. Last segment is often bilobed, pygidium is usually retracted inside posterior end.

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## References

Andrade, S.C.S., Novo, M., Kawauchi, G.Y., *et al*. (2015). Articulating "archiannelids": phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution* 32: 2860–2875.

Blake, J.A. & Petersen, M.E. (2000): Family Fauveliopsidae Hartman, 1971. In: Blake, J.A. Hilbig, B. & Scott, P.V. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel. The Annelida 4, Polychaeta: Flabelligeridae to Sternaspidae*. Santa Barbara Museum of Natural History, Santa Barbara: 31–45.

Buzhinskaya, G.N. (1996): Unique morphological features of certain deep-water pelagic polychaetes. *Doklady Biological Sciences* 347: 139–141.

Fauchald, K. & Rouse, G. (1997): Polychaete systematics: past and present. *Zoologica Scripta* 26: 71–138. DOI: 10.1111/j.1463-6409.1997.tb00411.x

Glasby, C.J. (2000). Family Fauveliopsidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. Vol. 4 Part A xii. CSIRO Publishing, Melbourne: 214–215.

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

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

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

Hartman, O. (1974): Polychaetous annelids of the Indian Ocean including an account of species collected by members of the International Indian Ocean Expeditions, 1963–'64 and a catalogue and bibliography of the species from India. *Journal of the Marine Biological Association, India* 16: 191–252.

Hartmann-Schröder, G. (1983): Zur Kenntnis einiger Foraminiferengehäuse bewohnender Polychaeten aus dem Nordostatlantik. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 80: 169–176.

Katzmann, W. & Laubier L. (1974): Le genre *Fauveliopsis* (Polychète Sédentaire) en Méditerranée. *Mikrofauna des Meeresbodens* 50: 529–542.

Laubier, L. (1972): Découverte du genre abyssal *Fauveliopsis* (annélide polychète) en Méditerranée occidentale. *Comptes rendus de l'Academie des Sciences, Paris* 274: 697–700.

López, E. (2011): Occurrence of *Fauveliopsis glabra* (Fauveliopsidae: Annelida: Polychaeta) in a rhodolith bed off the south-eastern coast of Spain (western Mediterranean Sea). *Marine Biodiversity Records* 4: e38. DOI: 10.1017/S1755267211000418.

McIntosh, W.C. (1922): Notes from the Gatty Marine Laboratory, St. Andrews, 44: 1. On new and rare Polychaeta, Gephyrea, etc., from various regions; 2. Recent additions to the British marine Polychaeta (continued). *Annals and Magazine of Natural History, Series 9*, 9: 1–30.

Menzies, R.J. & George R.Y. (1967): A re-evaluation of the concept of hadal or ultra-abyssal fauna. *Deep Sea Research and Oceanographic Abstracts* 14: 703–704.

Núñez, J., Ocaña, O., & Brito, M. C. (1997): Two new species (Polychaeta: Fauveliopsidae and Nerillidae) and other polychaetes from the marine lagoon cave of Jameos del Agua, Lanzarote (Canary Islands). *Bulletin of Marine Science* 60(2): 252–260.

Orensanz, J.M. (1974): Poliquetos de la provincia biogeográfica argentina, 10. Acrocirridae. *Neotropica* 20: 113–118.

Petersen, M.E. (2000): A new genus of Fauveliopsidae (Annelida: Polychaeta), with a review of its species and redescription of some described taxa. *Bulletin of Marine Science* 67: 491–515.

Pettibone, M.H. (1979): Redescription of *Bruunilla natalensis* Hartman (Polychaeta: Polynoidae), originally referred to Fauveliopsidae. *Proceedings of the Biological Society of Washington* 92: 384–388.

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

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

Purschke, G. (2011): Sipunculid-like ocellar tubes in a polychaete, *Fauveliopsis* cf. *adriatica* (Annelida, Fauveliopsidae): implications for eye evolution. *Invertebrate Biology* 130(2): 115–128.

Riser, N.W. (1987): A new interstitial polychaete (Family Fauveliopsidae) from the shallow subtidal of New Zealand with observations on related species. *Bulletin of the Biological Society of Washington* 7: 211–216.

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

Rouse, G.W. & Pleijel, F. (2003): Problems in polychaete systematic. *Hydrobiologia* 496: 175–189.

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

Salazar-Vallejo, S.I. & Zhadan A.E. (2007): Revision of *Buskiella* McIntosh, 1885 (including *Flota* Hartman, 1967), and description of its trifid organ (Polychaeta, Flotidae). *Invertebrate Zoology* 4: 65–82.

Salazar-Vallejo, S.I, Carrera-Parra, L.F. & Fauchald, K. (2008): Phylogenetic affinities of the Flabelligeridae (Annelida, Polychaeta). *Journal of Zoological Systematics and Evolutionary Research* 46: 203–215.

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Struck, T.H., Schuelt, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007): Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7:57 DOI: 10.1186/1471-2148-7-57.

Thiel, D., Purschke, G. & Böggemann, M. (2011): Abyssal Fauveliopsidae (Annelida) from the South East Atlantic. *Journal of Natural History* 45: 15, 923–937.

Zhadan A.E. & Atroshchenko M.M. (2010): The morphology of *Laubieriopsis* sp. (Polychaeta, Fauveliopsidae) and the position of fauveliopsids in the polychaete system. *Biology Bulletin* 37: 9, 876–885.

Zhadan A.E. & Atroshchenko M. M. (2012): A new species of Fauveliopsidae (Annelida) from the North Sea. *Zookeys* 181: 1–10.

Zrzavý J., Říha P., Piálek, L. & Janouškovec J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189. DOI: 10.1186/1471-2148-9-189.

Harlan K. Dean and James A. Blake

### 7.3.1.4 Ctenodrilidae Kennel, 1882

Dedicated to Dr. Mary E. Petersen 1938–2014

## Introduction

Ctenodrilidae are small polychaetes found from the intertidal zone to depths of 4,000 m. There are two subfamilies, the Ctenodrilinae, with short bodies and no branchial filaments, and the Raphidrilinae, with more elongate bodies and branchial filaments dorsal to the notochaetal bundles (Hartmann-Schröder 1971, Petersen and George 1991). Ctenodrilinae includes *Ctenodrilus* Claparède, 1863, with two species, and *Aphropharynx* Wilfert, 1974 with a single species. Raphidrilinae consists of two genera, *Raphidrilus* Monticelli, 1910a and *Raricirrus* Hartman, 1961, each with three described species. Due to the lack of parapodia and the presence of simple chaetae emerging directly from the body wall, Ctenodrilidae are similar to Cirratulidae (see Chapter 7.3.1.5) and also share morphological characters with Parergodrilidae (see Chapter 7.1.3). All ctenodrilids, except *Ctenodrilus*, possess simple capillaries, which may be accompanied by pectinate or coarsely serrate hooks and stout spines.

Fauchald and Jumars (1979) characterized the ctenodrilids as surface deposit feeders; they have often been found associated with organically enriched sediments, perhaps feeding on diatoms and organic detritus. They may be hermaphroditic or gonochoric and may also reproduce asexually. Asexual reproduction by paratomy has been reported in *Ctenodrilus*, and asexual fragmentation followed by regeneration has been noted for some species of the Raphidrilinae. Viviparity by release of seven-chaetiger swimming embryos from the female has been reported in *Ctenodrilus serratus* (Schmidt, 1857) (see Schmidt 1857, Rouse and Pleijel 2001), and larval development in jelly masses has been described in what was identified as *Raphidrilus nemasoma* (see further in the text) from western Canada (Qian and Chia 1989). Additionally, both sexual and asexual dispersive forms (and epitokes) have been reported in the genus *Raricirrus* (see Petersen and George 1991, Dean 1995).

## Morphology

### External morphology

Ctenodrilids are relatively small worms with a cylindrical body not divided into regions, a rounded to conical prostomium, and without projecting parapodial lobes. *Ctenodrilus* and *Aphropharynx* (Ctenodrilinae) are smaller, with 7–12 chaetigers, a reported length of 1.5 to 8 mm, and width of 0.1–3 mm. Species of *Raricirrus* and *Raphidrilus* (Raphidrilinae) are larger, with 4–35 chaetigers, a length of 1–17 mm, and a width of 0.25–0.5 mm.

**Prostomium and peristomium.** The short, conical, or rounded prostomium lacks antennae, palps, and pigmented eyespots. A pair of dorso-lateral nuchal organs is present posteriorly on the prostomium; those of *Raricirrus maculatus* were reported by Petersen and George (1991) as anterolateral patches of cilia, which may have been the result of an eversion of the nuchal organs. The peristomium is a complete ring, sometimes indistinguishable from the prostomium (and perhaps the first chaetiger) in the genera *Aphropharynx* and *Ctenodrilus,* although Salazar-Vallejo and Rincon (1983) and Bastida-Zavala (1994) show a clear separation between these two segments in specimens of *C. serratus* from Mexico. In these two genera, the first chaetigerous segment lies immediately behind the peristomium. In the genus, *Raphidrilus* there are one or two achaetous segments between the peristomium and the first chaetigerous segment, whereas in the genus *Raricirrus* the prostomium, peristomium, and the first chaetiger are united dorsally.

A ciliary field has been reported ventrally on the prostomium on either side of a groove anterior to the mouth (Rouse and Pleijel 2001: Fig. 54.2 b, c) and from the peristomium to the end of the second chaetiger in *C. serratus* (see Wilfert 1973, Westheide 1981, Scharff 1887). *Raricirrus beryli* Petersen & George, 1991 has a pair of ciliated bands extending ventrally posterior to the nuchal organs and uniting on the ventrum to form a single ciliated band on the peristomium and the first few chaetigers (Petersen and George 1991). A ventral ciliated band is absent in *R. maculatus* Hartman, 1961 and *Raricirrus variabilis* Dean, 1995 (Petersen and George 1991, Dean 1995). *Aphropharynx heterochaeta* Wilfert, 1974 possesses a small ciliated field

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restricted to the ventrum of the prostomium anterior to the mouth opening (Wilfert 1974). A ventral ciliated field was reported for *R. nemasoma* by Qian and Chia (1989), but Petersen and George (1991) indicate that their species had a ciliated ventral field, "normal" capillaries, and serrated multidentate chaetae. These are all characters noted for *Raricirrus* but not seen in *Raphidrilus*; thus, Petersen and George (1991) regard Qian & Chia's material as an undescribed species. There are no reported ciliated fields on the ventral side of the body for any of the described species of *Raphidrilus*.

**Body segments.** There is little differentiation of chaetigerous segments along the body, and the noto- and neurochaetae emerge directly from the body wall (Fig. 7.3.1.4.1 A, B). Dorsal branchiae occur postero-dorsal to the notochaetal bundles in Raphidrilinae (*Raphidrilus* and *Raricirrus*); branchiae are absent in Ctenodrilinae (*Ctenodrilus* and *Aphropharynx*). The posterior body is unmodified in the genera *Aphropharynx*, *Ctenodrilus*, and *Raphidrilus* with the pygidium consisting of a simple lobe lacking cirri and with a terminal or dorso-terminal anus. Salazar-Vallejo and Rincon (1983) mentioned a ring of cilia around the anus in specimens of *Ctenodrilus serratus* from Mexico. The last 6–14 chaetigers are widened, shorter, and crowded relative to other chaetigers in species of *Raricirrus* (Fig. 7.3.1.4.1 B). The simple-lobed pygidium lacks cirri and the terminal anus is dorsal. The wide posterior region of *Raricirrus variabilis* has a ventral opening (interpreted as a gonopore) with one and perhaps two pairs of associated large reproductive spines (Dean 1995: Fig. 7.3.1.4.1 C). There is also a pair of enlarged spines present in the wide posterior region of *Raricirrus maculatus*, but no gonopore was noted by Petersen and George (1991). The pygidium is simple, with no associated appendages and a terminal or dorso-terminal anus.

**Chaetae.** Chaetae are entirely serrate capillaries in the genus *Raphidrilus*. Those of *Raricirrus* include capillaries as well as pectinate and coarsely serrate chaetae in the notochaetal and neurochaetal bundles (Fig. 7.3.1.4.2 A–C). In *Ctenodrilus*, all chaetae are stout, multidentate acicular spines (Fig. 7.3.1.4.2 D). The chaetae of *Aphropharynx heterochaeta* include capillaries in a few anterior noto- and neurochaetal bundles and acicular spines bearing several large dentations in the remaining chaetigers. Elongate natatory chaetae occur in epitokous or dispersive forms of *Raricirrus* (Petersen and George 1991, Dean 1995).

**Sensory organs.** The most obvious sensory structures in the Ctenodrilidae are the paired, oval nuchal organs located posteriorly on the prostomium adjacent to the peristomial region. Those of *Raphidrilus beryli* and *Raphidrilus nemasoma* are described as pits surrounded by cilia (Petersen and George, 1991), whereas

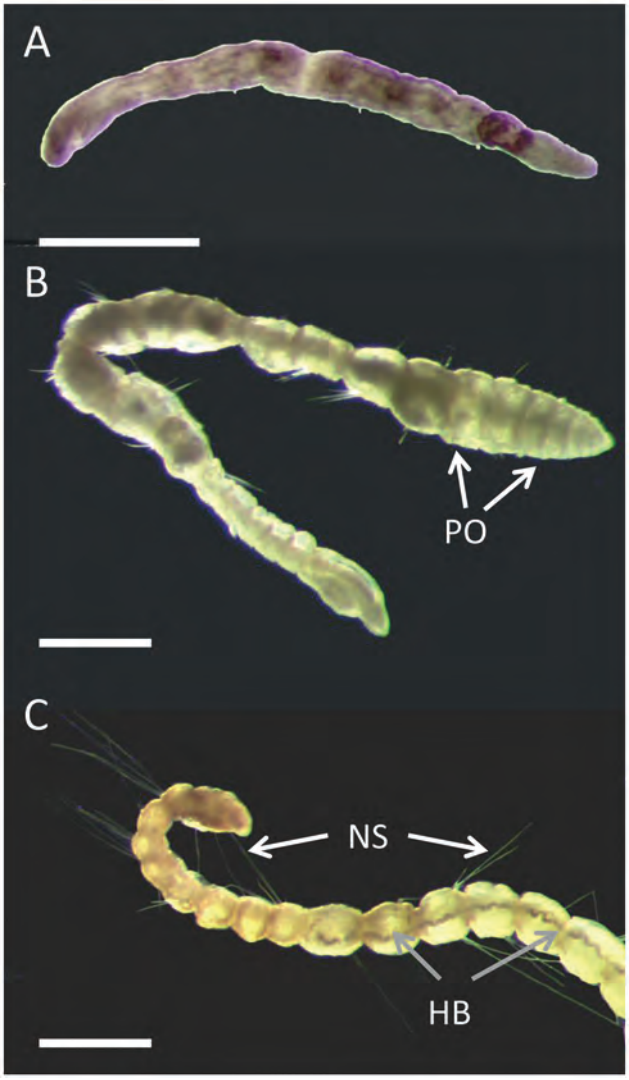


**Fig. 7.3.1.4.1:** A, *Ctenodrilus serratus* from South Africa, lateral view. B, *Raricirrus variabilis* from the Gulf of Mexico, lateral view. C, *R. variabilis* from the Gulf of Mexico, epitoke/dispersal phase. HB, heart body; NC, natatory chaetae. Scale bars = 500 µm.

those of *Raricirrus variabilis* (Dean 1995) and all other species of *Raphidrilus* (see Sokolow 1911, Magalhães *et al.* 2011) are described as ciliated pits. It is possible that these organs may be capable of eversion, thus explaining these differences in structure. Qian and Chia (1989) noted the presence of sensory tufts of cilia on the surface of the prostomium and postero-dorsal to the notochaetae of juveniles of their undescribed species of *Raphidrilus* from British Columbia, Canada. Similar sensory tufts may also be seen on the surface of the prostomium of a species of *Ctenodrilus* from Nahant, MA, USA (Rouse and Pleijel 2001: Fig. 54.2 b, c). Wilfert (1974) also described fine, short "touch hairs (Tasthärchen)" on the prostomium of *Aphropharynx heterochaeta*. Qian and Chia (1989) also reported the presence of pigment spots ("eyes") on

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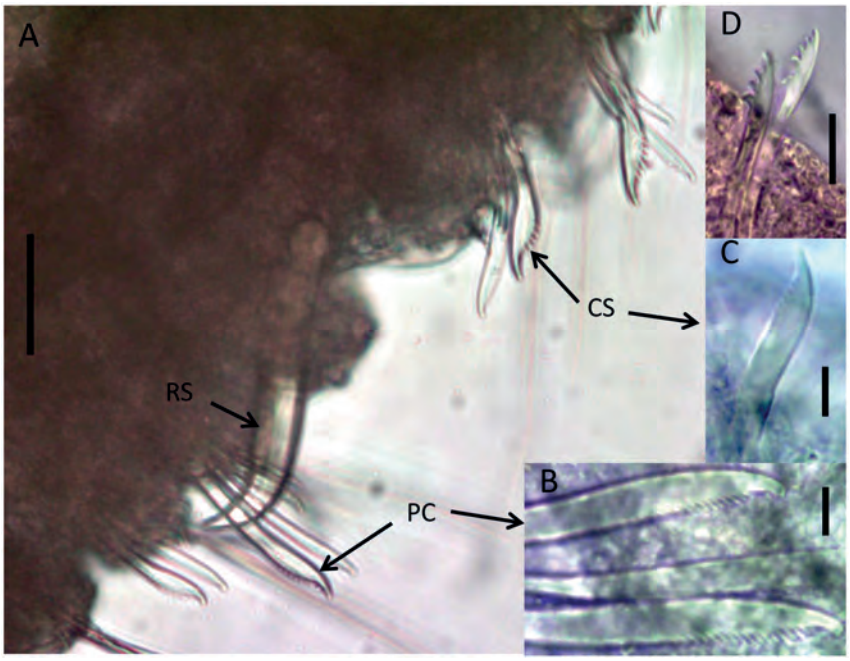


**Fig. 7.3.1.4.2:** A, *Raricirrus variabilis* from Tongue of the Ocean, Virgin Islands, reproductive stylet, ventral view. CS, coarsely serrate chaetae; PC, pectinate chaetae; RS, reproductive stylet. B, *R. variabilis* from the Gulf of Mexico, pectinate chaetiger. C, *R. variabilis* from the Gulf of Mexico, coarsely serrate chaetae. D, *Ctenodrilus serratus* from South Africa, multidentate acicular spines. Scale bars A = 50 µm, B–D = 10 µm.

the rear of the prostomium of their undescribed species of *Raphidrilus*, but such eyespots are unknown in other species of Ctenodrilidae.

### Anatomy

A pair of segmental organs, or nephridia, was reported in *C. serratus* within the first chaetiger and opening on the peristomium (Galvagni 1905, Wilfert 1973). In *R. nemasoma*, the segmental organs occurred in the single achaetous segment and opened anteriorly, perhaps on the peristomium (Monticelli 1910b).

**Blood vascular system.** A closed circulatory system, along with a dorsal heart body, occurs in Ctenodrilidae. In *Ctenodrilus* and *Aphropharynx* the heart body begins in chaetiger 1 and is weakly developed. In the genus *Raphidrilus* the heart body begins in chaetiger 4 (Magalhães *et al.* 2011) and extends for a number of chaetigers from 1 to 5. In *Raricirrus*, there is great variation in the development of the heart body from chaetigers 8 to 9 in *R. maculatus* and *R. beryli* and extending posteriorly for 6–15 chaetigers; in *R. variabilis* the heart body begins in chaetiger 4–6 and extends posteriorly for 4–11 chaetigers in the benthic forms and 8–16 in epitokous forms (Dean 1995; Fig. 7.3.1.4.1 C).

**Coelom.** The coelom of *C. serratus* was found to be only partially covered by peritoneum, with the muscles of the outer body wall and the parapodial muscle bundles uncovered by epithelial cells, but with flat extensions of cytoplasm from the outer muscle cells (Franzen 1980).

**Digestive System.** The gut of ctenodrilids is a straight tube, which is somewhat widened in midbody segments, with an anterior soft pharyngeal structure. Using transmission electron microscopy, Purschke (1988) found that the pharynx of *C. serratus* consists of a bulbous muscle with a tongue-like structure made up of lateral folds. Based upon light microscopy, this type of bulbous muscle system is believed to be homologous to those of other Ctenodrilidae, Terebellidae, Cirratulidae, Orbiniidae, Flabelligeridae, Poecilochaetidae, Spionidae, and Poeobiidae. This type of pharyngeal structure is believed to be used in the scraping of food particles from the substrate (Purschke 1988).

**Nervous system.** Gelder and Palmer (1976) analyzed the nervous system of *C. serratus* and found it to consist of central, stomatogastric, and peripheral segments. The central system consists of a cerebral ganglion (brain), a circumesophageal loop, and two ventral nerve cords. The stomatogastric portion consists of a small stomodeal loop, which sends branches to form a nerve plexus along the gut, and a loop around the eversible pharynx. The peripheral nervous system consists of four pairs of nerves per segment emerging from the ventral nerve cords; these join to a pair of longitudinal epidermal nerve cords dorsally, and there is also a small nephridial plexus. These authors pointed out the similarities of this nervous system with those described for *Cirratulus* and *Dodecaceria* in Cirratulidae as evidence of the affinities between these two families.

### Reproduction and development

Ctenodrilidae exhibit a variety of reproductive strategies, including both asexual and sexual reproduction. Paratomic asexual reproduction by formation of chains of

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differentiated individuals, followed by separation, has been reported for Ctenodrilinae, such as *C. serratus* (see Kennel 1882, Monticelli 1907, Peters 1923, Hartman 1944) and *A. heterochaeta* (see Wilfert 1974). Ben-Eliahu (1976) saw no indication of asexual reproduction in *C. paucidentatus*. In the Raphidrilinae, asexual reproduction by fragmentation, followed by regeneration (architomy), is known for *Raphidrilus nemasoma*, *R. hawaiiensis*, *R. beryli*, and *R. maculatus* (Monticelli 1910a, Petersen and George 1991, Magalhães *et al.* 2011). No evidence of asexual reproduction has been observed in *Raphidrilus* sp. from British Columbia, *R. harperi* from Hawaii, and *R. variabilis* from deep-water off St. Croix (Qian and Chia 1989, Dean 1995, Magalhães *et al.* 2011).

Petersen and George (1991) observed what they termed dispersal forms in *R. maculatus* and *R. beryli*, distinguishing these from morphologically similar sexual epitokes that contain well-developed gametes. These dispersive forms are smaller than the benthic forms, possess elongate capillary chaetae two to four times longer than the body width, and appeared to have been formed by asexual fragmentation. Dean (1995) described two specimens of *R. variabilis* with elongate capillaries as epitokes, but since they contained no gametes, they are more correctly regarded as dispersive stages, although there was no evidence of asexual fragmentation (Fig. 7.3.1.4.1 C). The elongate capillaries of these asexual dispersive forms most likely allow for greater dispersive capabilities.

Sexual reproductive modes in the ctenodrilids include gonochoric forms as well as protandric and simultaneous hermaphrodites. Within Ctenodrilinae, *C. serratus* has generally been reported as reproducing asexually, but Monticelli (1907) first noted female individuals with developing larvae moving freely within the coelom. This viviparous reproduction has also been described by Rouse and Pleijel (2001), who reported male individuals of *C. serratus* from Belize ranging from embryos to the seven-chaetiger stage in the body coelom of females; these seven-chaetiger specimens were released into the water column as ciliated, swimming juveniles. Bastida-Zavala (1994) also noted the occurrence of a simultaneously hermaphroditic individual of *C. serratus* from Pacific Mexico. Sexual reproduction was not observed in *C. paucidentatus* by Ben-Eliahu (1976), nor did Wilfert (1974) observe any evidence of sexual reproduction in his description of *A. heterochaeta*.

Sexual reproduction within the Raphidrilinae is somewhat more complicated than that reported for the Ctenodrilinae. In Monticelli's (1910b) description of *R. nemasoma*, the type species of the genus, he reported both male and female individuals, as well as protandric hermaphrodites, and noted the presence of robust, weakly curved spines on chaetigers 5–9 of the males. The type material has been lost, no specimens could be found in the Gulf of Naples type locality (Petersen and George 1991), and Magalhães *et al.* (2011) found no such spines on any specimens collected from the nearby Adriatic Sea. Magalhães *et al.* (2011) also found no such reproductive spines on *R. harperi* or *R. hawaiiensis* and none were mentioned in the undescribed species of *Raphidrilus* of Qian and Chia (1989). Therefore, sexual dimorphism as implied by Monticelli (1910b) for *Raphidrilus* has not been confirmed in subsequent investigations.

Monticelli (1910b), and later Sokolow (1911), described viviparity in *R. nemasoma*, noting the presence of segmented larvae within the maternal coelom and the subsequent release of juveniles from the body cavity. Magalhães *et al.* (2011) also found achaetous worm-like organisms within the body cavity of specimens of *R. harperi* and *R. hawaiiensis*, but no sexually mature specimens of these ctenodrilid species were seen, and it is possible that these organisms were actually intracoelomic gregarine parasites. The undescribed species of *Raphidrilus* of Qian and Chia (1989) was found to lay gelatinous egg masses that reached the blastula stage after about 48 hours and the trochophore stage by day 3. After about 11 days, three to four chaetiger young emerged from the egg mass and developed into juveniles about 2 weeks after emergence.

Reproduction is also varied in the three known species of *Raricirrus*. Petersen and George (1991) reviewed sexual reproduction in *R. maculatus* and *R. beryli* and reported mature male and female forms in both species. Some, but not all, specimens of *R. maculatus* with gametes had large hooked spines on one or two anterior segments of the enlarged posterior body region and coarsely serrated noto- and neurochaetae in subsequent posterior body segments. They also found fragments containing eggs in their material and saw sperm platelets in a specimen from California, but these lacked the elongate chaetae of epitokes so are considered dispersive forms. No female epitokes were found in *R. beryli* (Petersen and George, 1991), but they did find a few male epitokes similar in size to the benthic form with elongate (1.5× body width) "natatory" chaetae. Dean (1995) found simultaneous hermaphroditic individuals of *R. variabilis* from deep-sea wood islands with hooked spines on the first one or two segments of the widened posterior end and coarsely serrated chaetae in subsequent posterior segments similarly to the arrangement reported for *R. maculatus* (Fig. 7.3.1.4.1 C). Additionally, *R. variabilis* had a ventral, medial pore located anteriorly in the broad posterior region and a reproductive stylet associated with a sac containing what appeared to be sperm, five to nine chaetigers anterior to this gonopore. Epitokes with a wider body and a greater

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number of chaetigers than the benthic form were also present and possessed elongate capillaries and oocytes.

Irvine *et al*. (1997) recovered homeobox gene fragments from the chaetopterid polychaete *Chaetopterus variopedatus*, which has three highly differentiated body regions, and from *C. serratus*, which has little variability in body segments. These homeobox genes have been shown to act in the shifts in morphology along the anterior-posterior axis of various metazoans. Their results indicate that these worms share the same complement of homeobox genes despite their differences in morphology. This perhaps indicates that it is the regulation of Hox gene expression that may explain the differences in segmental diversity between the two polychaete taxa.

## Biology and ecology

### Distribution

Ctenodrilids range from the intertidal to the deep sea; many species appear to be opportunistic and often associated with organically enriched sediments. *Raricirrus beryli* was originally described from upper slope sediments near oil rigs at depths of 200–500 m in the North Sea (Petersen and George 1991), later on the Norwegian continental shelf (Ugland *et al*. 2008), and more recently as a colonizer on organically enriched sediments in experiments near mud volcanoes in the Bay of Cádiz (Cunha *et al*. 2013). *Raricirrus variabilis* is known from an experimental wood island placed at 4,000 m off St. Croix in the Caribbean Sea and more recently from soft continental slope sediments, ca. 800 m, in the Gulf of Mexico near an operating oil and gas platform off Louisiana (Blake unpublished data; Fig. 7.3.1.4.1 B, C). *Raricirrus maculatus* is known from organically enriched sediments off the California (USA) coast. *Raricirrus jennae* was collected from sunken wood in the deep sea off California and from hydrothermal sites on East Scotia Ridge in the southern Ocean (Magalhães *et al*., 2017). *Aphropharynx heterochaeta* has only been collected from a museum aquarium in Germany, and *C. serratus* has often been collected from aquaria and running seawater tables of marine laboratories (Wilfert 1973, Hartmann-Schröder 1996). *Ctenodrilus serratus* has also been reported to occur as a commensal on sea urchins (Fauchald and Jumars 1979, Bastida-Zavala 1994). The undescribed species of *Raphidrilus* of Qian and Chia (1989) was collected from decaying *Zostera* roots on Vancouver Island, Canada. *Ctenodrilus paucidentatus* Ben-Eliahu, 1976 has been reported only from the Gulf of Aqaba (Gulf of Elat), Israel (Ben-Eliahu 1976). *Ctenodrilus pacificus* Magalhães *et al*., 2016 was described from a lagoon on Oahu, Hawaii in the Pacific Ocean. *Raphidrilus nemasoma* is known from the Italian Mediterranean and Adriatic Seas; *Raphidrilus harperi* Magalhães *et al*., 2011, from Florida; and *Raphidrilus hawaiiensis* Magalhães *et al*., 2011, from Hawaii, USA (Magalhães *et al*. 2011).

*Ctenodrilus serratus* has been considered a cosmopolitan species (Salazar-Vallejo and Rincon 1983), thought to perhaps be the result of its abilities for asexual reproduction. Westheide *et al*. (2003) analyzed internal transcribed spacers (ITSs) and 5.8S DNA and found that there were no significant molecular differences between populations from northern Europe and the eastern United States, perhaps indicating a significant transatlantic exchange of genetic material. These authors did note some differences in ITS sequences in a population from Bermuda perhaps due to the geographic isolation of that site.

### Dateline

Ctenodrilids were characterized as motile herbivores and surface deposit feeders by Fauchald and Jumars (1979), and Jumars *et al*. (2015) updated this by classifying ctenodrilids as highly selective feeders on microbial films and rich organic debris. Wilfert (1973) maintained laboratory populations of *C. serratus* feeding on the diatom *Dunaliella* sp., and his observations indicated that they used their lower lip (and perhaps tongue-like organ) to feed on benthic diatoms and detritus in the field (Wilfert 1973). Purschke (1988) described the pharyngeal apparatus of *C. serratus* as consisting of a muscular bulb with associated glandular cells and an overlying laterally attached tongue-like organ. Feeding is believed to occur by extrusion of the tongue-like organ and bulb followed by intake of detritus or algal cells. Moore (1991) analyzed the gut contents of *R. beryli* in the North Sea and found the median grain size of ingested material to be greater than that of the surrounding sediments, indicating that they were feeding selectively on sediment grains and suggested that they were utilizing the associated organic material on these particles. On the basis of Moore's observations, Jumars *et al*. (2015) suspected that *R. beryli* was highly selective for organic coatings, possibly diatoms found on grains of sediment at the sediment-water interface. Petersen *et al*. (2012) collected specimens of *R. beryli* from a whale fall in the Kosterfjord, Sweden, and found sulfur-oxidizing chemosynthetic bacteria, similar to those found in bathymodiolin mussels from hydrothermal vents and cold seeps in the surface mucous layer of the worms. The association between these bacteria and the ctenodrilid is unclear, but it is possible that there is a

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symbiotic association between these organisms in highly organic habitats.

### Environmental aspects

Most of the ctenodrilids are associated with sediments having high organic content (Petersen and George 1991, Dean 1995, Magalhães *et al*. 2011). *Ctenodrilus serratus* has been used as a laboratory test organism for metals, petrochemicals, and polluted sediments and indicated that this species was relatively more tolerant of chromium, cadmium, and zinc in terms of the suppression of reproduction. Moore (1991) (Reish and Gerlinger 1997) found dense populations of *R. beryli* present in sediments contaminated by hydrocarbons in the North Sea and suggested that this species could be used as a pollution indicator. Ugland *et al*. (2008) later included this species as an indicator species in an environmental stress index for the oilfields of the Norwegian continental shelf. The heart body (Fig. 7.3.1.4.1 C) has been thought to perhaps be a site of blood cell production. However, Vovelle *et al*. (1994) analyzed the heart body of specimens of *R. beryli* from the North Sea and found levels of iron (among other metals) correlated with proximity to offshore oil platforms. Perhaps, the heart body may be involved in the detoxification of pollutants, such as iron, rather than hematopoiesis, thus explaining its ability to thrive in these polluted environments.

## Phylogeny and taxonomy

### Phylogeny and dateline Morphological studies

The first ctenodrilid was described by Schmidt (1857) as *Parthenope serrata* Schmidt, 1857, later placed in the genus *Ctenodrilus* by Claparède (1863), who considered the species to be in Oligochaeta. Kennel (1882) more fully described *Ctenodrilus pardalis* Claparède, 1863 (later placed in synonymy with *C. serratus*) and established the family Ctenodrilidae but was unclear as to its affinities. Mesnil and Caullery (1897) and Caullery and Mesnil (1898) reviewed *C. serratus* (Schmidt, 1857) and *Ctenodrilus monostylos* Zeppelin, 1883 (later transferred to the genus *Zeppelina*) and compared them to specimens of the cirratulid genus *Dodecaceria*. Caullery and Mesnil (1898) pointed out that the lack of tentacular cirri was a negative character, likely the result of regression, and therefore could not be used as a family-defining character and they referred *Ctenodrilus* to the Cirratulidae.

Monticelli (1910a) described *R. nemasoma* Monticelli, 1910a and included it within Ctenodrilidae, separate from Cirratulidae. *Raphidrilus* was characterized as possessing filiform branchiae dorsal to the notochaetal bundles and having only one type of chaeta (simple, elongate, or spinous) in each bundle. Nevertheless, later workers (Fauvel 1927, Day 1967) included the ctenodrilids as a subfamily of Cirratulidae. Hartman (1944) reported and described *C. serratus* from the California coast and regarded the family Ctenodrilidae as distinct from the Cirratulidae based on ciliation of the prostomium and ventrum of the first segment, the reduced number of body segments, the lack of tentacular cirri, and simple chaetal fascicles. Hartman (1961) later described *R. maculatus* Hartman, 1961 and considered it to be in Cirratulidae despite its lack of tentacular cirri and the branchiae being limited to a few anterior chaetigers. Its larger number of chaetigers (about 22) and the presence of branchiae precluded her from including it in Ctenodrilidae with *Ctenodrilus*. While Ctenodrilidae and Cirratulidae are very similar morphologically, it has been difficult to unite them into a single family given that the dorsal tentacles of Cirratulidae are lacking in ctenodrilids.

Dales (1963) recognized Ctenodrilidae as a separate family and included both Ctenodrilidae and Cirratulidae within Cirratulida. Hartmann-Schröder (1971) also considered Ctenodrilidae to be a separate family and included it in Drilomorpha, a group that also included Cirratulidae, Arenicolidae, Capitellidae, and perhaps Maldanidae and Sternaspidae. Fauchald (1977), and later Hartmann-Schröder (1996), placed Ctenodrilidae within an order separate from Cirratulidae, Ctenodrilida, along with Parergodrilidae, but with no explanation. The small body form and the lack of parapodia and anterior appendages in Parergodrilidae are similar to those of *Ctenodrilus*, but the single pair of chaetal bundles on each segment and the presence of furcate chaetae or stout spines are not present in *Ctenodrilus*.

Rouse and Fauchald (1997) were among the first to apply cladistic analysis to understanding the relationships among polychaete families. In coding the characters for Ctenodrilidae, they used simple dorsal branchiae and dentate hooks as the plesiomorphic character states of a *Raricirrus*/*Raphidrilus*-like ctenodrilid. Both of these character states are absent in *Ctenodrilus*. In the authors' unweighted presence/absence analysis, Ctenodrilidae were grouped with Aeolosomatidae, Parerogodrilidae, and Potamodrilidae while in the weighted presence/absence analysis, they were grouped with Acrocirridae, Cirratulidae, Fauveliopsidae, Flabelligeridae, Poeobiidae, and Sternaspidae. Using a multistate data matrix, the position of Ctenodrilidae was unresolved. Rouse and Fauchald (1997) established a new classification for the polychaetes based on a cladistic analysis of a restricted

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number of families, which did not include Ctenodrilidae. Ctenodrilidae were included in Canalipalpata in the clade Terebellida, along with Acrocirridae, Flabelligeridae, Cirratulidae, Alvinellidae, Ampharetidae, Pectinariidae, Terebellidae, and Trichobranchidae, despite their lacking grooved palps or tentacles, a synapomorphy of the Canalipalpata.

In a later more focused look at polychaete systematics, Rouse and Pleijel (2003) used Cirratuliformia (various families that had been associated with Cirratulidae) as an example of paraphyly in polychaetes. Their morphologically based strict consensus cladogram resulted in no clear relationships between Ctenodrilidae, Cirratulidae, and other families, and Ctenodrilidae, Cirratulidae, Fauveliopsidae, Flabelligeridae were not considered monophyletic. They proposed that, perhaps, Acrocirridae, Ctenodrilidae, Fauveliopsidae, Flabelligeridae, Flotidae, Poeobiidae, and Sternaspidae could all be included within the single family Cirratulidae. They included both *Ctenodrilus* and *Raphidrilus* in their analyses and these two genera were not found within the same clade nor were any of the three species of Cirratulidae. However, only 2 of the 15 characters utilized in this analysis were appropriate for discerning the relationships between the members of Ctenodrilidae and Cirratulidae: (1) branchial occurrence/distribution and (2) the presence/absence of tentacles. While differentiating these two families from other taxa included in the analysis between Cirratulidae and Ctenodrilidae was not the main focus of this study, the relationships between and within these two families were not addressed by their analysis.

Salazar-Vallejo *et al*. (2008) included Cirratulidae and Ctenodrilidae as outgroups in their analysis of phylogenetic affinities of Flabelligeridae. While not the focus of the analysis, Ctenodrilidae, Cirratulidae, and Fauveliopsidae formed a clade based mainly upon the presence of simple falcate hooks and a smooth epidermis. *Ctenodrilus* and *Raricirrus* showed close affinities to each other based upon the presence of monoserially denticulate neurochaetae. They differed in this analysis only by the median body segments being scored as indistinct in *Ctenodrilus* and distinct in *Raricirrus*. The absence of branchiae in *Ctenodrilus* was not a character state in the analysis. The emphasis of this study was the phylogenetic affinities of Flabelligeridae, and only 8 of the 36 characters included in the analysis were pertinent to the relationships between members of the out group.

**Dateline.** As with morphological relationships between Ctenodrilidae and other polychaete families, molecular efforts have also often been inconclusive. Bleidorn *et al*. (2003) examined 18S rDNA sequences in their analysis of relationships between polychaetes and found that *C. serratus* had a close affinity with three genera of Cirratulidae, with its closest affinity being with two species of *Dodecaceria*. A Bayesian analysis of the consensus tree also showed a supported sister-group relationship between this clade and three species of Scalibregmatidae. In the Struck and Purschke (2005) analysis of relationships between the Potamodrilidae and the Aeolosomatidae based on 18S rDNA, a close relationship was found between *C. serratus* and the Cirratulidae, especially with species of *Dodecaceria*. While unsupported by bootstrap values, the Cirratulidae/Ctenodrilidae clade was most closely associated with Opheliidae. Rousset *et al*. (2007) added sequences from the D1 region of 28S rDNA, Histone 3, and mitochondrial 16S rDNA to the 18S rDNA sequences and again noted a well-supported relationship with *C. serratus* and the six species of Cirratulids included in the study with closest kinship to the genus *Dodecaceria*. A strict consensus tree of the complete data set aligned Ctenodrilidae and Cirratulidae with Capitellidae and the Echiuran genus *Bonellia*, but jackknife values showed no support for these associations. Struck *et al*. (2008) assessed both saturation and homoplasy in 18S and 28S rDNA sequences in order to exclude saturated nucleotide positions from their analysis. Whether excluding all possibly saturated sites or ambiguously aligned positions, *C. serratus* showed close affinities to the single species of cirratulid included in their analysis, *Cirratulus spectabilis* (Kinberg, 1866), while associations with Flabelligeridae and Poeobiidae, included in the *Cirriformia*, were unsupported. Zrzavý *et al*. (2009) used both morphological data and six molecular partitions and found that *C. serratus* was associated with the only cirratulid included in the analysis, "Cirratulidae." An association of these two species with *Aberranta* and *Saccocirrus* lacked bootstrap/Bremer support. In a further study Magalhães *et al*. (2017) reported *Raricirrus beryli* and *Raricirrus pacifica* to be a sister group to the *Ctenodrilus/Dodecaceria* clade based upon 16S and Cytochrome Oxidase I (COI) analyses.

In all the above studies an association between the Ctenodrilidae and the Cirratulidae is apparent. Osborn and Rouse (2010) analyzed the molecular phylogeny of Acrocirridae and Flabelligeridae using 18S, 28S, 16S, COI, and Cytochrome B sequences and used six species of Cirratulidae and *C. serratus* as outgroups for the analyses. Using 18S and 28s rDNA sequences and morphological data, *C. serratus* was clearly included within Cirratulidae and strongly associated with the cirratulid genera *Dodecaceria* and *Aphelochaeta*. Weidhase *et al*. (2015) analyzed the COI sequence of *C. serratus* and found it to be closely related to, if not nested within, the *Dodecaceria*. In addition, they found *Raricirrus beryli* to

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be a sister taxon to a clade of the multitentaculate genera *Cirratulus, Cirriformia* and *Timarete*.

**Dateline: Conclusions**

Morphologically based attempts to resolve the relationships of the Ctenodrilidae to other polychaetes have been inconclusive. Associated families have included such taxa as Arenicolidae, Capitellidae, Maldanidae, Sternaspidae, and Parergodrilidae, but the most frequently associated group to Ctenodrilidae is Cirratulidae. Morphological cladistic analyses that have included Ctenodrilidae are few, and often, they have been included only as outgroups. A major problem is the lack of dorsal tentacles in Ctenodrilidae, thus making it difficult to justify their inclusion in Cirratulidae.

Molecular studies of ctenodrilid affinities are also few, and results have been variable. Unsupported affinities have been indicated between Ctenodrilidae and Flabelligeridae, Capitellidae, Potamodrilidae, Aeolosomatidae, Poeobiidae, Polygordiidae, Saccocirridae, and *Aberranta*, among others. In all cases, however, there is a strongly supported relationship between *C. serratus* and members of Cirratulidae, especially with the genus *Dodecaceria*. George and Petersen (1991), however, suggested that *Dodecaceria* appeared to be more closely related to Ctenodrilidae than Cirratulidae. The analysis by Osborn and Rouse (2010) included several genera of Cirratulidae and indicated an affinity not only between *Ctenodrilus* and *Dodecaceria* but also with the genus *Aphelochaeta*. Weidhase *et al*. (2015) suggest that members of the Ctenodrilidae may be the product of progenetic evolution with the loss of dorsal tentacles being a juvenile characteristic. There is strong support for the inclusion of *C. serratus* in the Cirratulidae, and perhaps *Raricirrus beryli* as well but a clearly defined taxonomic group which includes both the Ctenodrilidae and Cirratulidae has yet to be characterized.

**Taxomony**

Schmidt (1857) described the first ctenodrilid as *Parthenope serrata* from the Mediterranean Sea. Claparède (1863) recognized that *Parthenope* was preoccupied and renamed the homonym *Ctenodrilus* for *C. serratus* (Schmidt 1857), a small bodied species lacking parapodia, tentacules, and branchiae but with multidentate hooks. Kennel (1882) more fully described *C. pardalis* Claparède, 1863 (later placed in synonymy with *C. serratus*) and established the family Ctenodrilidae to include *Ctenodrilus* and another genus and species proposed by Vaillant (1890), *Zeppelina monostyla* (Zeppelin, 1883). The genus *Zeppelina* differed from *Ctenodrilus* by the presence of what was believed to be an unpaired medio-dorsal tentacule, but later descriptions of species in this genus included those with paired lateral tentacules. George and Petersen (1991) reviewed the genus *Zeppelina* and found that in seven of the eight then recognized species, including the type species *Z. monostyla*, this tentacule was actually one of a pair of tentacules similar to those that occur in the cirratulid genus *Dodecaceria* (the eighth species was a specimen of the ctenodrilid *R. nemasoma*) and the genus *Zeppelina* was therefore abandoned and effectively synonymized with *Dodecaceria*. A second species of *Ctenodrilus*, *C. paucidentatus*, was described by Ben-Eliahu (1976) from the Gulf of Elat (Gulf of Aqaba), Israel, differing from *C. serratus* by only slight differences in chaetal morphology. Westheide *et al*. (2003) pointed out that the number of subdistal teeth on the chaetae of *C. serratus* was highly variable, even in a single individual, suggesting that *C. paucidentatus* might not be a valid species. Another species, *Ctenodrilus parvulus* Scharff, 1887, continues to appear in the literature, but it is clearly not a ctenodrilid and is most likely a regenerating posterior fragment of a *Dodecaceria,* similar to that described by Gibson and Clark (1976) for *Dodecaceria caulleryi* Dehorne, 1933 (later synonymized with *Dodecaceria concharum* Örsted, 1843 by George and Petersen 1991). In fact, Galvagni (1905) reported the presence of paired tentacules in specimens identified as *C. parvulus* and indicated that this species was synonymous with *Z. monostyla* (Zeppelin, 1883) (which was later identified as a species of *Dodecaceria* by George and Petersen (1991)). More recently, Magalhães *et al*. (2016) attempted to recognize C. parvulus as a valid species but the asexual reproduction of this species described by Scharff (1887) is similar to that described for *Dodecaceria pulchra* by Gibson (1977). Additionally, the suggestion by Magalhães *et al*. (2016) that Galvagni (1905) must have mistakenly been looking at a mixture of two species is unsubstantiated speculation and must be discounted. A third recognized species of *Ctenodrilus, C. pacificus*, was described by Maghalães *et al* (2016) from shallow subtidal waters on Oahu, Hawaii. The genus *Aphropharynx*, with the single species *A. heterochaeta,* was collected from a museum aquarium in Germany and described by Wilfert (1974). This genus is similar to *Ctenodrilus* but differs in the presence of capillary chaetae anteriorly and finely toothed chaetae in addition to coarse multidentate chaetae in subsequent chaetigers.

Monticelli (1910a, b) described *Raphidrilus nemasoma* Monticelli, 1910 from the Gulf of Naples and referred it to the family Ctenodrilidae and at the same time established the subfamily Heterodrilinae. This subfamily included *Zeppelina* and *Raphidrilus,* both with a more elongate body form (15–18 chaetigers) than those of *Ctenodrilus* and with branchiae or tentacules. *Raphidrilus* was

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characterized as possessing filiform branchiae dorsal to the notochaetal bundles and having only one type of chaeta, simple, elongate, or spinous, in each chaetal bundle. Heterodrilinae, however, is an invalid name as there is no polychaete genus from which to derive the family level name; Hartmann-Schröder (1971) renamed the subfamily as the Raphidrilinae, in which she included *R. nemasoma* and the later to be abandoned genus *Zeppelina* (George and Petersen 1991). The Raphidrilinae were longer bodied (>15 segments) and possessed branchiae and capillary chaetae, as well as serrate chaetae and spines. Magalhães *et al*. (2011) described two new species of *Raphidrilus*, *R. harperi* Magalhães, Bailey-Brock & Davenport, 2011, from Venice, FL (USA), and *R. hawaiiensis* Magalhães, Bailey-Brock & Davenport, 2011, from shallow water in Hawaii. Petersen and George (1991) had earlier emended the subfamily Raphidrilinae to include species with pectinate and coarsely serrate chaetae, thus incorporating the genus *Raricirrus*, described by Hartman (1961) for *R. maculatus* collected off the coast of California. At the time, Hartman (1961) considered *Raricirrus* to belong to the Cirratulidae despite its lack of tentacules and limited number of anterior branchiae; the greater number of chaetigers (about 22) and the presence of branchiae precluded her, at the time, from including it in the Ctenodrilidae with *Ctenodrilus*. Petersen and George (1991) redescribed *R. maculatus* and described a new species from the North Sea, *R. beryli* Petersen & George, 1991. Dean (1995) later described *R. variabilis* from experimental wood islands deployed off the Bahamas at 4,000 m depth. The most recent species of *Raricirrus* to be described is *R. jennae* from Monterey Bay California in 3100 m (Magalhães *et al*. 2017).

### Current taxonomy

### Ctenodrilidae Kennel, 1882

**Type genus:** *Ctenodrilus* Claparède, 1863

**Diagnosis:** Small polychaetes with few to many distinct segments. Prostomium and peristomium lacking appendages, tentacular cirri absent. Partially eversible pharynx simple with a ventral muscular bulb. Ciliated nuchal organs present. Simple branchiae present or absent. All chaetigers biramous, parapodial lobes lacking with chaetae emerging directly from body wall. Chaetae simple, include capillaries, pectinate, and coarsely serrate forms; reproductive spines in some species. Dioecious or hermaphroditic as well as both sexual and asexual forms present.

### Ctenodrilinae Kennel, 1882

**Diagnosis:** Short-bodied Ctenodrilidae with 7–12 segments as adults, branchiae lacking. Chaetae include simple capillaries and coarsely serrate spines.

#### *Ctenodrilus* Kennel, 1882

**Diagnosis:** Short-bodied forms with only coarsely serrate noto- and neurochaetae, branchiae lacking.

**Type species:** *Ctenodrilus serratus* (Schmidt, 1857)

**Four species:**

*Ctenodrilus pacificus Magalhães et al*. 2016; shallow subtidal lagoon, Oahu, Hawaii.

*Ctenodrilus paucidentatus* Ben-Eliahu, 1976; intertidal vermetid reef, Gulf of Elat, Israel.

*Ctenodrilus serratus* (Schmidt, 1857); considered cosmopolitan, intertidal to shallow subtidal waters, seawater aquaria.

*Ctenodrilus parvulus* Scharff, 1887 nomen dubium (see above); collected from a seawater aquarium in England.

#### *Aphropharynx* Wilfert, 1974

**Diagnosis:** Short-bodied forms with simple capillary and finely serrate chaetae anteriorly, coarsely serrate chaetae posteriorly, branchiae lacking.

**Type species:** *Aphropharynx heterochaeta* Wilfert, 1974 (only species, monotypic); collected from a seawater aquarium in Düsseldorf, Germany.

### Raphidrilinae Hartmann-Schröder, 1971

**Type genus:** *Raphidrilus* Monticelli, 1910.

**Diagnosis:** Ctenodrilidae with up to 40 chaetigers as adults, with simple branchiae on most segments. Chaetae include capillaries, simple pectinate, coarsely serrate forms, and spines.

#### *Raphidrilus* Monticelli, 1910a

**Type species:** *Raphidrilus nemasoma* Monticelli, 1910a

**Diagnosis:** Peristomium distinct from prostomium dorsally and ventrally, first one or two segments achaetous. Nuchal organs ciliated pits. Heart body from chaetiger 4. Serrate capillaries throughout. Reproduction sexual and asexual.

**Four species:**

*Raphidrilus harperi* Magalhães, Bailey-Brock & Davenport, 2011; shallow subtidal sand and shell hash, Venice, FL.

*Raphidrilus hawaiiensis* Magalhães, Bailey–Brock & Davenport, 2011; shallow subtidal algal beds, off Oahu Island, Hawaii.

*Raphidrilus nemasoma* Monticelli, 1910b; shallow subtidal sediments, Mediterranean Sea.

*Raphidrilus* sp. (=*R. nemasoma* of Qian and Chia (1989). Undescribed species (fide Petersen and George 1991); lower intertidal sandy beach, Vancouver Island, British Columbia, Canada.

#### *Raricirrus* Hartman, 1961

**Type species:** *Raricirrus maculatus* Hartman, 1961

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**Diagnosis:** Peristomium not distinct from prostomium dorsally, achaetous segments lacking. Nuchal organs ciliated pits or flat areas surrounded by fields of cilia. Last six to nine segments shorter than preceding ones, forming distinct posterior region; with enlarged reproductive spines in some species. Heart body present beginning from segment 4–10. Notochaetae smooth to serrate capillaries, natatory capillaries, and coarsely serrate forms; neurochaetae falcate and finely pectinate, coarsely serrate forms posteriorly; simple curved reproductive spines present in one or two posterior chaetigers in some species. Reproduction sexual and asexual.

**Four species:**

*Raricirrus beryli* Petersen & George, 1991; organically enriched sediments, 60–300 m, North Sea, off Norway.

*Raricirrus jennae Magalhães,* Linse & Wiklund, 2017. Monterey Bay, California, 3100 m; Scotia Ridge, Southern Ocean, 2100–2600 m.

*Raricirrus maculatus* Hartman, 1961; organically enriched sediments 46–300 m, off California.

*Raricirrus variabilis* Dean, 1995; experimental wood islands, deep water, 4,000 m, off Bahamas.

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**References**

Bastida-Zavala, J.R. (1994): Hermafroditismo simultáneo y extensíon de ámbito de *Ctenodrilus serratus* (Polychaeta: Ctenodrilidae) en Baja California Sur, Mexico. *Revista de Biologia Tropical* 42(3): 737–741.

Ben-Eliahu, M.N. (1976): Errant polychaete cryptofauna (excluding Syllidae and Nereidae) from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat. *Israel Journal of Zoology* 25: 156–177.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003). New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogentics and Evolution* 29: 279–288.

Caullery, M. & Mesnil, F. (1898): Les formes épitoques et l'évolution des cirratuliens. *Annales de l'Université de Lyon* 39: 1–200.

Claparède, É. (1863): *Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt*. Wilhelm Engelmann, Leipzig.

Cunha, M.R., Matos, F.L., Génio, L., Hilário, A., Moura, C.J., Ravara, A. & Pfannkuche, O. (2013). Macrofaunal assemblages from mud volcanoes in the Gulf of Cadiz: abundance, biodiversity and diversity partitioning across spatial scales. *Biogeosciences* 10: 2553–2568.

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

Day, J.H. (1967): *A Monograph on the Polychaeta of Southern Africa. Part 2. Sedentaria*. British Museum (Natural History), London. Publication 656: 459–878.

Dean, H.K. (1995): A new species of *Raricirris* (Polychaeta: Ctenodrilidae) from wood collected in the Tongue of the Ocean, Virgin Islands. *Proceedings of the Biological Society of Washington* 108: 169–179.

Fauchald, K. (1977): The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series, Science Series* 28: 1–190.

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

Fauvel, P. (1927): Polychètes Sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. *Fauna de France* 16: 1–494.

Franzen, M.E. (1980): Ultrastructure of coelomic organization in annelids I. Archiannelids and other small polychaetes. *Zoomorphologie* 95: 235–249.

Galvagni, E. (1905): Histologie des Genus *Ctenodrilus* Clap. *Arbeiten aus den Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest* 15: 47–80.

Gelder, S.R. & Palmer, R. (1976): The nervous system of the marine polychaete *Ctenodrilus serratus* and its importance in the taxonomic position of the Ctenodrilidae. *Transactions of the American Microscopal Society* 95: 156–164.

George, J.D. & Petersen, M.E. (1991): The validity of the genus *Zeppelina* Vaillant (Polychaeta: Ctenodrilidae). *Ophelia, Supplement* 5: 89–100.

Gibson, P.H. & Clarke, R.B. (1976): Reproduction of *Dodecaceria caulleryi* (Polychaeta: Cirratulidae). *Journal of the Marine Biological Association of the United Kingdom* 56: 649–674.

Hartman, O. (1944): Polychaetous annelids. Part 6. Paraonidae, Magelonidae, Longosomidae, Ctenodrilidae, and Sabellariidae. *Allan Hancock Pacific Expeditions* 10: 311–389.

Hartman, O. (1961): Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* 25: 1–226.

Hartmann-Schröder, G. (1971): Annelida, Borstenwürmer, Polychaeta. In: Dahl, M. & Peus, F. (eds.) *Die Tierwelt Deutschlands 58,* Gustav Fischer, Jena: 1–594.

Hartmann-Schröder, G. (1996): Annelida, Borstenwürmer, Polychaeta. In: Dahl, M. & Peus, F. (eds.) *Die Tierwelt Deutschlands 58.* 2nd ed. Gustav Fischer, Jena: 1–648.

Irvine, S.Q., Warinner, S.A., Hunter, J.D. & Marindale, M.Q. (1997): A survey of homeobox genes in *Chaetopterus variopedatus* and analysis of polychaete homeodomains. *Molecular Phylogenetics and Evolution* 7(3): 331–345.

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

Kennel, J.V. (1882): Über *Ctenodrilus pardalis* Clpd. Ein Beitrag zur Kenntnis der Anatomie und Knospung der Anneliden.

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*Arbeiten aus dem Zoologisch-Zootomischen Institut Würzburg* 5: 373–429.
Magalhães, W.F., Bailey-Brock, J.H. & Davenport, J.S. (2011): On the genus *Raphidrilus* Monticelli, 1910 (Polychaeta: Ctenodrilidae) with description of two new species. *Zootaxa* 2804: 1–14.
Magalhães, W.F., Linse, K. & Wiklund, H. (2017): A new species of *Raricirrus* from deep-water sunken wood off California. *Zootaxa* 4353: 51–68.
Magalhães, W.F., Weidhase, M, Schultze, A & Bailey-Brock, J.H. (2016): Taxonomic remarks on the genus *Ctenodrilus* (Annelida: Cirratulidae) including description of a new species from the Pacific Ocean. *Zootaxa* 4103 (4): 325–343.
Mesnil, F. & Caullery, M. (1897): Sur la position systématique de genre *Ctenodrilus* Clap.; ses affinités avec les Cirratuliens. *Comptes Rendus hebdomadaire des Séances de l'Académie des Sciences* 125: 542–544.
Monticelli, F.S. (1907): Sessialita e gestazione nello *Ctenodrilus serratus* O. Schm. *Atti del congresso dei Naturalisti italiani (Settembre 1906), Milano* 1907: 524–526.
Monticelli, F.S. (1910a): Di un nuovo Ctenodilidae del Golfo de Napoli; Nota preliminare riassuntiva del socio ordinario. *Rendiconto dell'Accademia delle Scienze Fisiche e Matematiche (Sezione della Societá Reale de Napoli) serie 3* 16(3/4): 61–64.
Monticelli, F.S. (1910b): *Raphidrilus nemasoma* Montic. Nuovo Ctenodrilide del Golfo di Napoli (Revisione de'Ctenodrilidi). *Archivio Zoologico* 4: 401–436.
Moore, D.C. (1991): *Raricirrus beryli* Petersen and George (Ctenodrilidae): A new polychaete indicator species for hydrocarbon-polluted sediments. *Ophelia Supplement* 5: 477–486.
Osborn, K.J. & Rouse, G.W. (2010): Phylogenetics of Acrocirridae and Flabelligeridae (Cirratuliformia, Annelida). *Zoologica Scripta* 40: 204–219.
Peters, N. (1923): Über das Verhältnis des natürlichen zur künstlichen Teilung bei *Ctenodrilus serratus* (O. Schmidt). *Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere* 40: 293–350.
Petersen, J.M., Wentrup, C., Verna, C., Knittel, K. & Dubilier, N. (2012): Origins and evolutionary flexibility of chemosynthetic symbionts from deep-sea animals. *Biological Bulletin* 223: 123–137.
Petersen, M.E. & George, J.D. (1991): A new species of *Raricirrus* from Northern Europe, with notes on its biology and a discussion of the affinities of the genus (Polychaeta: Ctenodrilidae.). *Ophelia Supplement* 5: 185–208.
Purschke, G. (1988): Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida) V. The pharynges of the Ctenodrilidae and Orbiniidae. *Zoomorphology* 108: 119–135.
Qian, P.Y. & Chia, F.S. (1989): Sexual reproduction and larval development of *Raphidrilus nemasoma* Monticelli, 1910 (Polychaeta: Ctenodrilidae). *Canadian Journal of Zoology* 67: 2345–2351.
Reish, D.J. & Gerlinger, T.V. (1997): A review of the toxicological studies with polychaetous annelids. *Bulletin of Marine Science* 60(2): 584–607.
Rouse, G. & Pleijel, F. (2001): *Polychaetes.* Oxford University Press, Oxford, England.
Rouse, G.W. & Fauchald, K. (1997): Cladistics and Polychaetes. *Zoologica Scripta* 26(2): 139–204.
Rouse, G.W. & Pleijel, F. (2003): Problems in polychaete systematics. *Hydrobiologia* 496: 175–189.
Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 23: 41–63.
Salazar-Vallejo, S. & Rincon, O. (1983): *Ctenodrilus serratus* (Schmidt), first record for Mexico of the family Ctenodrilidae (Annelida: Polychaeta) with biogeographic considerations. *Ciencias Marina* 9: 97–107.
Salazar-Vallejo, S.I., Carrera-Parra, L.F. & Fauchald, K. (2008): Phylogenetic affinities of the Flabelligeridae (Annelida, Polychaeta). *Journal of Zoological Systematics and Evolutionary Research* 46(3): 203–215.
Scharff, R. (1887): On *Ctenodrilus parvulus*, nov. spec. *Quarterly Journal of Microscopical Science* 27: 591–604.
Schmidt, O. (1857): Zur Kenntnis der Turbellaria, Rhabdocoela und einiger anderer Wuermer des Mittelmeeres. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Klasse* 23: 347–366.
Sokolow, I. (1911): Über eine neue Ctenodrilusart und ihre Vermehrung. *Zeitschrift für wissenschaftliche Zoologie, Leipzig* 97: 546–603.
Struck, T.H., Nesnidal, M.P., Purschke, G. & Halanych, K.M. (2008): Detecting possibly saturated positions in 18S and 28S sequences and their influence on phylogenetic reconstruction of Annelida (Lophotrochozoa). *Molecular Phylogenetics and Evolution* 48: 628–645.
Struck, T.H. & Purschke, G. (2005): The sister group relationship of Aeolosomatidae and Potamodrilidae (Annelida: ''Polychaeta'') a molecular phylogenetic approach based on 18S rDNA and cytochrome oxidase I. *Zoologischer Anzeiger* 243: 281–293.
Ugland, K.I., Bjørgesæter, A., Bakke, T., Fredheim, B. & Gray, J.S. (2008): Assessment of environmental stress with a biological index based on opportunistic species. *Journal of Experimental Marine Biology and Ecology* 366: 169–174.
Vaillant, M.L. (1890): Lumbriciniens, Hirudiniens, Bdellomorphes, Térétulariens et Planarians. *Histoire naturelle des Annelés marins et d'eau douce* 3(2): 452–458.
Vovelle, J., Petersen, M.E., Grasset, M. & Beaunier, P. (1994): Bioaccumulation du fer dans le corps cardiaque de *Raricirrus beryli* Petersen and George (Polychaeta: Ctenodrilidae). *Mémoires du Muséum Nationale d'Historie Naturelle, Paris* 162: 73–80.
Weidhase, M., Bleidorn, C. & Simon, C.A. (2015): On the taxonomy and phylogeny of *Ctenodrilus* (Annelida: Cirratulidae) with a first report from South Africa. *Marine Biodiversity* 46 (1): 243–252.
Westheide, W. (1981): Interstitial fauna of Galapagos XXVI. Questidae, Cirratulidae, Acrocirridae, Ctenodrilidae (Polychaeta). *Mikrofauna des Meeresbodens* 82: 1–24.
Westheide, W., Haß-Cordes, E., Krabusch, M. & Müller, M.C.M. (2003): *Ctenodrilus serratus* (Polychaeta: Ctenodrilidae) is a truly amphi-Atlantic meiofaunal species – evidence from molecular data. *Marine Biology* 142: 637–642.
Wilfert, M. (1973): Ein Beitrag zur Morphologie, Biologie und systematsichen Stellung des Polychaeten *Ctenodrilus serratus*. *Helgoländer wissenschaftliche Meeresuntersuchungen* 25(2–3): 332–346.
Wilfert, M. (1974): *Aphropharynx heterochaeta* nov. gen. nov. spec., ein neuer Polychaet aus der Familie Ctenodrilidae Kennel 1882. *Cahiers de Biologie Marine* 15: 495–504.
Zrzavý, J., Říha,, P., Piálek, L. & Janouškovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189: 1–14.

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James A. Blake and Wagner Magalhães

## 7.3.1.5 Cirratulidae Ryckholt, 1851

### Introduction

Cirratulids are deposit-feeding polychaetes that burrow or crawl through sediment, although species of at least one genus, *Dodecaceria*, are able to bore into or construct calcareous structures. In organically enriched sediment in estuaries, cirratulids often reach high population densities. They typically bury their bodies just below the surface with their long branchiae and tentacles visible at the surface. Cirratulids have a frilly appearance because of the numerous branchiae along the length of their bodies (Fig. 7.3.1.5.1 A, B).

The Cirratulidae formerly included several taxa that have since been removed to separate families (e.g., Ctenodrilidae, Cossuridae, and Acrocirridae). At present, there are three major groups of Cirratulidae with 11 genera recognized:

1. The multitentaculate species typically have a wedge-shaped head and numerous dorsal tentacles that occur in two groups on the anterior part of the body (Figs. 7.3.1.5.1 A, B and 7.3.1.5.2 A–C); most species have capillaries and spines; *Protocirrineris* species have only capillaries. The multitentaculate species are more common in intertidal and nearshore habitats and are rarely encountered in deep water. There are five genera, *Cirratulus*, *Cirriformia*, *Fauvelicirratulus*, *Protocirrineris*, and *Timarete*, currently assigned to this category.
2. The bitentaculate sediment dwelling species have a narrow head consisting of a distinct prostomium and peristomium and with a pair of long dorsal tentacles usually arising from the posterior margin of the peristomium (Figs. 7.3.1.5.1 C–E and 7.3.1.5.2 D–E); branchiae are present along most of the body. The bitentaculate species occur from the intertidal to abyssal depths. There are five genera, *Aphelochaeta*, *Caulleriella*, *Chaetozone*, *Kirkegaardia*, and *Tharyx*, currently assigned to this category.
3. The bitentaculate shell or rocks boring species belong to a single genus, *Dodecaceria*. These cirratulids are able to bore or otherwise occupy burrows in calcareous substrates; the paired tentacles are lateral rather than dorsal and their branchiae are limited to a few anterior segments (Figs. 7.3.1.5.1 F and 7.3.1.5.2 F). Although widespread, most species of *Dodecaceria* are limited to nearshore habitats.

The Cirratulidae as currently defined, include approximately 278 species. However, the diversity of cirratulids has been greatly underestimated. The rate of new species descriptions has increased markedly in recent years as numerous new taxa have been identified in offshore surveys. For example, of 170 known species of bitentaculate sediment dwelling cirratulids, 100 or more than half were described in just the past 25 years and many more species await description.

In addition to systematics and morphological studies, recent research has focused on their reproductive biology that includes asexual reproduction and/or regeneration (Petersen 1999). In offshore benthic habitats, cirratulids are typically among the most diverse and abundant groups of polychaetes.

In the sections that follow, we describe the morphology of adult and larval cirratulids, their biology and behavior, phylogenetic relationships, taxonomy, and current classification.

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List of Abbreviations used with the figures: akT, akrotroch; apC, apical cilia; br, branchiae; dCrest, dorsal crest; dG, dorsal groove; dpR, dorsal peristomial ridge; dR, dorsal ridge; dT, dorsal tentacle; dtR, dorsal thoracic ridge; eyS, eyespot; gsT, gastrotroch; hB, heart body; ne, nephridia; neT, neurotroch; nuO, nuchal organ; per, peristomium; pr, prostomium; prT, prototroch; pyg, pygidium; tent, tentacle; teT, telotroch; tF, tentacular filament; vG, ventral groove.

### Morphology

#### External morphology

**Body shape and size.** The body of cirratulids consists of numerous segments with weakly developed parapodia, but with distinct noto- and neuropodial bundles of chaetae. The bodies are typically elongated, cylindrical in cross-section, tapering anteriorly and posteriorly (Figs. 7.3.1.5.1 A–E and 7.3.1.5.2 A–D). The anterior or thoracic region is often expanded with narrow segments; the middle or abdominal segments are longer and sometimes beaded or moniliform (Fig. 7.3.1.5.1 D); the last few prepygidial segments are sometimes expanded (Fig. 7.3.1.5.1 D). Some species of *Kirkegaardia* have parapodia of the thoracic region elevated over the dorsum, producing a mid-dorsal thoracic groove (Blake 2016). The mudball worms of the genus *Kirkegaardia* have an enlarged prechaetigerous and thoracic region that

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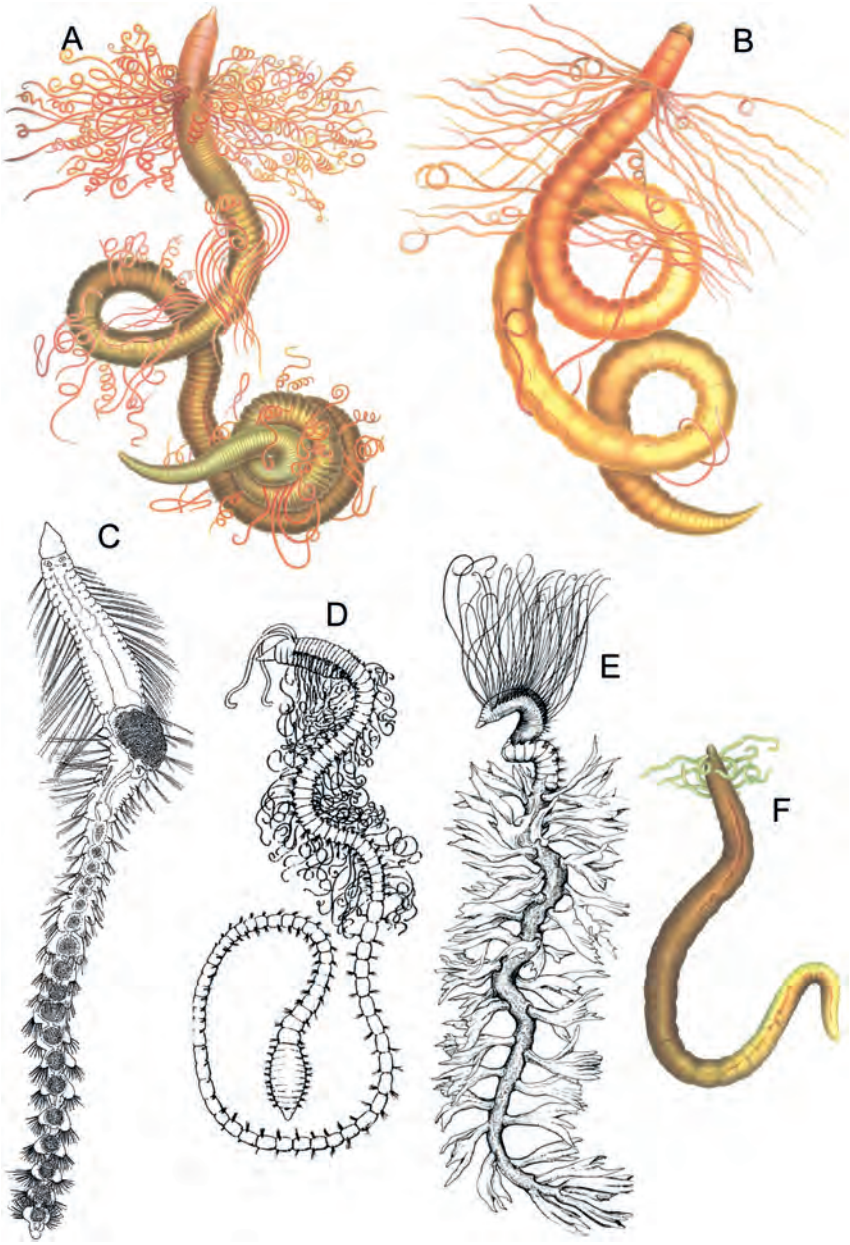


**Fig. 7.3.1.5.1:** Different kinds of Cirratulidae. A, *Cirriformia tentaculata*. B, *Cirratulus cirratus*. C, *Chaetozone brunnea*. D, *Aphelochaeta monilaris*. E, *Kirkegaardia tesselata*. F, *Dodecaceria concharum*. A, B, F, After McIntosh (1915); C, after Blake (2006); D–E, after Hartman (1960).

together provides a bulbous anterior end that might be used to block the tube opening or perhaps open cracks in the mud during burrowing; the rest of their body is narrow and twisted and conforms to the shape of their burrows (Blake 2016). Some *Chaetozone* species have the posterior abdominal region greatly modified into cinctures (Figs. 7.3.1.5.1 C and 7.3.1.5.3 G), with thin intersegmental and wide segmental regions (Chambers 2000, Blake 2015a). Two species of *Chaetozone*, *Chaetozone brunnea* and *Chaetozone ronaldi*, have been described with enlarged segments at the junction of the thorax and abdomen (Fig. 7.3.1.5.1 C), providing a distinct shape (Blake 2006, Magalhães and Bailey-Brock 2013a). Woodham and Chambers (1994) described an enlarged, hump-backed shape for the thoracic region of *Chaetozone gibber*. However, most cirratulids do not have such distinctive shapes to the bodies.

Some species of multitentaculate cirratulids are large, with robust bodies and numerous segments. For example, *Cirriformia spirabrancha*, a rocky intertidal species from California, attains lengths of 200 mm with 300–400 segments (Blake 1996). Most cirratulids, however, are less than 25 mm in overall length and have more fragile bodies.

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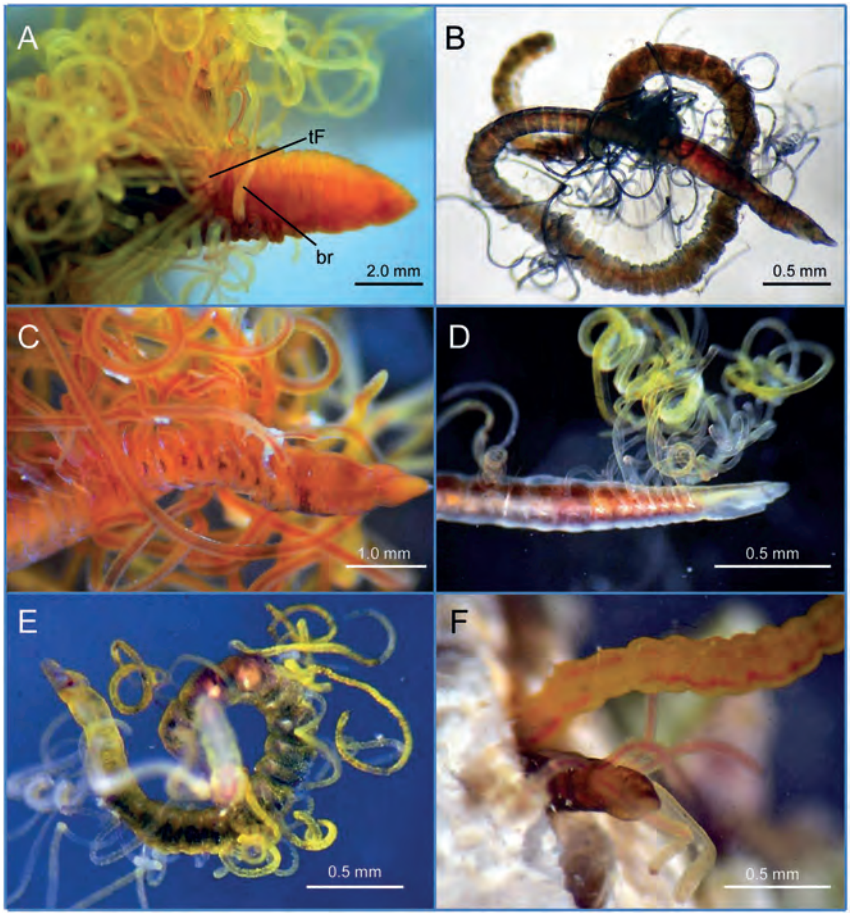


**Fig. 7.3.1.5.2:** Photographs of living cirratulid species. A, *Cirriformia crassicollis*. B, *Protocirrineris mascaratus*. C, *Timarete hawaiensis*. D, *Aphelochaeta honouliuli*. E, *Caulleriella bioculata*. F, *Dodecaceria laddi*. All original.

**Color.** Distinct body pigmentation on cirratulids is not common or well described but is important when present. In life, the branchiae are typically red against a light or tan body; deep-water cirratulids have been observed with an overall blue-green color that in preservative fades to tan to brown. For example, the *Chaetozone brunnea* described by Blake (2006) from deep water off California from preserved specimens was reported to have brown pigment, most evident in anterior segments. In life, however, this pigment was found to be blue-green (Blake 2015a). Both *Chaetozone pigmentata* and *Chaetozone bathyala* described by Blake (2015a) from preserved specimens had brown to black pigment on their bodies; in the first species, the pigment was concentrated in small speckles; in the second, the pigment was diffuse but concentrated in anterior segments. Some species of *Tharyx* have lateral peristomial pigment spots that help identify species when present (Blake 1996, Blake and Göransson 2015). Blake (1996) reported preserved specimens of *Timarete perbranchiata* with gray to bluish black bodies with dusky pigment on the dorsal sides of notopodia and ventral sides of neuropodia throughout, forming paired segmental series along the body; the numerous tentacular filaments were crossed with dark bands; branchiae were white to tan or yellow. Live specimens of *Caulleriella bioculata* were observed with green speckles throughout the body, including branchiae (Figs. 7.3.1.5.2 E and 7.3.1.5.6 C); *Protocirrineris mascaratus* has black pigments (Fig. 7.3.1.5.2 B); and *Timarete hawaiensis* (Fig. 7.3.1.5.2 C), *Timarete caribous*, and *Timarete ceciliae* have body, tentacular, and branchial filaments that are bright orange (Magalhães *et al*. 2014). *Timarete punctata* is well known for its distinct pigmentation on body, tentacular, and branchial filaments. Preserved lectotypes were redescribed by Çinar (2007) as having body with irregular black spots dorsally and ventrally, tentacular filaments with few black lateral stripes, and branchiae also bearing irregular black spots.

**Anterior segments.** The shape and configuration of the prechaetigerous region of cirratulids differs widely between species of the multi- and bitentaculate genera and certain features are of taxonomic importance.

**Prostomium.** The prostomium of multitentaculates is typically broad and wedge shaped (Figs. 7.3.1.5.1 B and 7.3.1.5.2 A), whereas bitentaculates usually have a

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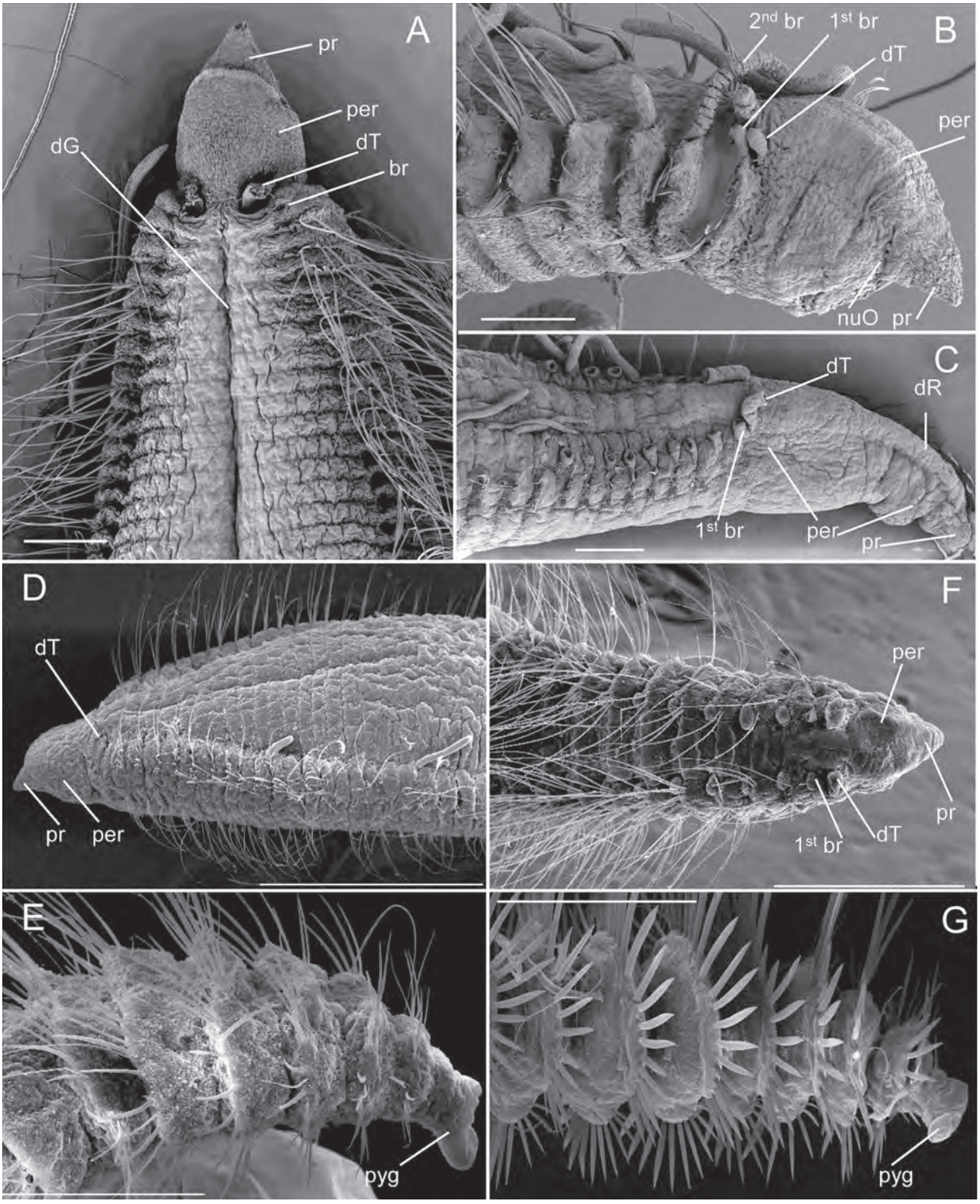


**Fig. 7.3.1.5.3:** External morphology of species of *Aphelochaeta, Kirkegaardia*, and *Chaetozone*. A, *Aphelochaeta* sp. (Gulf of Mexico), anterior end, dorsal view. B. *Kirkegaardia baptisteae*, anterior end, right lateral view. C. *Kirkegaardia hampsoni*, anterior end, right lateral view. D, E, *Chaetozone spinosa*: D, anterior end, left lateral view; E, posterior end with pygidium, left lateral view. F, G, *Chaetozone palaea*: F, anterior end, dorsal view; G, posterior end, ventrolateral view. All original. Scale bars: A, C, 200 µm; 50 µm; D, F, G, 1 mm; E, 400 µm.

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narrower, elongate prostomium. Multiple eyespots are present and conspicuous in two prominent rows in most species of *Cirratulus* (Fig. 7.3.1.5.6 D). Individual eyespots of *Cirratulus* have a distinct clear lens surrounded by either red or black pigment (Blake 1996). In other cirratulids, such as *Chaetozone*, eyespots, when present, are small and paired and have been reported as reddish or black in color. Paired black eyespots are distinctive in *Chaetozone corona* (Blake 1996, 2015a), *C. bioculata* (Fig. 7.3.1.5.6 C), and *Caulleriella apicula* (Blake 1996) and very enlarged in *Caulleriella magnaoculata* (Hartmann-Schröder 1962). However, some reports of such eyespots may actually represent pigmented nuchal organs (Blake 2015a).

All cirratulids have a pair of ciliated nuchal organs visible on the dorso-lateral margins of the prostomium (Fig. 7.3.1.5.3 B). Details of the external morphology of cirratulid nuchal organs have rarely been described. However, for most species of bi- and multitentaculate species, these are visible as small ciliated oval or slit-like openings (Fig. 7.3.1.5.6 A, B) (Doner and Blake 2006), the interior of which is sometimes pigmented and mistaken for eyes. Gibson (1997) compared the size and shape of nuchal organs in four species of *Dodecaceria*. In *Dodecaceria concharum* (as *Dodecaceria fimbriata*) and *Dodecaceria pulchra*, they were small and oval; in *Dodecaceria ater* (as *D. concharum*), they were narrow and elongate; in *Dodecaceria joubini*, they were long and serpentine, extending posteriorly over the peristomium.

**Peristomium, dorsal tentacles, and tentacular filaments.** The peristomial segment is achaetous and may be smooth (Fig. 7.3.1.5.3 A, D) or have several transverse furrows or segmental lines that produce annulations (Fig. 7.3.1.5.3 B, C), but these are not true segments. Day (1967) notes that although the peristomium of cirratulids often exhibits external annulations, dissection shows it to be one segment rather than a fusion of several. The peristomium of *Kirkegaardia heterochaeta* is relatively smooth in external appearance, but Laubier (1966) noticed thin superficial lines that, when he studied with thin sections, suggested the presence of two annular rings. Blake (2016) was unable to see these on the same species from the type locality even when specimens were stained with Shirlastain A. The number and nature of the peristomial annulations are important taxonomic characters and serve to distinguish between closely related species. In some species, the dorsal surface of the peristomium may extend posteriorly, overlying the anterior chaetigers; in *Chaetozone bansei*, this extends posteriorly for four to seven segments, also carrying the dorsal tentacles posteriorly (Blake 1996); a similar but not as long posterior extension also occurs in *Chaetozone careyi* (Blake 2015a). The number of peristomial annuli and their relative lengths have been especially helpful to separate species of *Aphelochaeta*, due to the scarcity of additional distinguishing characters. While most species have three subequal annulations, they could have from one to four and of different lengths (Doner and Blake 2009).

Dorsal tentacles are paired in the bitentaculate genera (Fig. 7.3.1.5.3 A–D and F) and in groups of numerous tentacular filaments in the multitentaculate genera (Fig. 7.3.1.5.2 A). The tentacular filaments and dorsal tentacles are always grooved, whereas the segmental branchiae are always cylindrical.

The paired dorsal tentacles of bitentaculate cirratulids typically arise from the posterior part of the peristomial segment, or sometimes these structures are shifted posteriorly for three or more segments as part of a posterior extension of the peristomium as in the two species of *Chaetozone* noted previously. The location of these tentacles and their position relative to the first and second pairs of branchiae are of taxonomic importance. The tentacles of *Dodecaceria* species arise laterally from the peristomium. The groups of tentacular filaments of multitentacular cirratulids arise from anterior thoracic segments instead of the peristomium (Fig. 7.3.1.5.2 A). The arrangement and placement of these tentacles are important at the generic level. The tentacular filaments are arranged in longitudinal rows in *Protocirrineris* species or in transverse or oblique rows in the other four genera. In *Cirratulus* species, the tentacular filaments arise from a single anterior segment together with the first branchiae. In *Cirriformia* species, the tentacular filaments arise between chaetigers 2 and 7 and encompass one to three anterior chaetigers. In *Timarete* species, the tentacular filaments arise from two or more anterior chaetigers posterior to chaetiger 1.

**Segmentation and parapodia.** Parapodia of cirratulids are biramous, with the lobes rudimentary and indistinct. Anterior or thoracic segments are typically narrow, widened, and crowded, transitioning to longer abdominal segments that may be long and moniliform. Far posterior segments usually become narrower and crowded again.

The bodies of many cirratulids have distinct grooves, usually on the venter. The presence of these, their location along the body, and the degree of development are of taxonomic importance. Dorsal grooves are also present in some genera such *Chaetozone*. *Chaetozone careyi* has both dorsal and ventral grooves (Blake 2015a). In some *Kirkegaardia* species, the parapodia are shifted toward the dorsal midline, forming a mid-dorsal channel (Blake 2016).

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**Posterior segmentation and the pygidium.** The posterior end of the body typically exhibits crowded segments that may be inflated in some species of *Aphelochaeta* (Fig. 7.3.1.5.1 D) (Blake 1996). These posterior segments may be cylindrical in cross-section, ventrally flattened, or with dorsal and/or ventral grooves. Details of these segments are important taxonomic characters. The pygidium of cirratulids terminates in a simple rounded or pointed lobe, a ventral subanal disk (Fig. 7.3.1.5.3 E, G), or long terminal cirrus.

**Branchiae.** Branchiae in most bitentaculate species are usually present as a single pair per segment with the first pair usually prechaetigerous; this pair, however, like the dorsal tentacles, may sometimes arise more posteriorly. Branchiae normally occur throughout the body but are limited to a few anterior chaetigers in *Dodecaceria*. Branchiae are usually located just dorsal to the notochaetae (Fig. 7.3.1.5.3 A–B, D, and F), although in *Kirkegaardia dorsobranchialis* and several related species, they are shifted toward a groove along the dorsal midline (Fig. 7.3.1.5.3 C).

Some multitentaculate species of *Timarete* and *Fauvelicirratulus* have multiple sets of branchiae arising from the notopodial lobes, and these may shift from a lateral position just dorsal to the notochaetae to a more dorsal position high up on the body. The notopodial lobes in *Fauvelicirratulus dollfusi* are enlarged to accommodate up to 18 branchial filaments on each segment (Çinar and Petersen 2011). When multiple sets of branchiae occur per segment, these, when combined with the numerous tentacular filaments, provide such worms with so many filaments that they obscure other relevant morphology and often need to be removed in order to further study the worms.

**Chaetae.** The chaetae arise directly from small tori and include capillaries, bifid or multidentate hooks, acicular spines, and finely tapering spines. In species of *Chaetozone*, the posterior segments are modified forming high membranes providing an accordion-like appearance with the acicular spines arrayed in broad spreading fascicles, called cinctures, that encircle most of the lateral, ventral, and dorsal sides of individual segments, giving the posterior end the appearance of a pin cushion (Figs. 7.3.1.5.1 C and 7.3.1.5.3 E, G). The development and arrangement of these spines in posterior segments are diagnostic at the species level. Spines of *Chaetozone* come in different forms but are mostly heavy, weakly curved, and with blunt to weakly pointed tips (Figs. 7.3.1.5.3 G and 7.3.1.5.4 J–K and N). One group of *Chaetozone* species has spines where the tip tapers, becoming a fine point that curves ventrally and fuses with the shaft (Fig. 7.3.1.5.4 K and inset). *Chaetozone hartmanae* from California and *Chaetozone dimorphoseta* from Australia have short serrations on the convex side of the curved spines of the neuropodia (Hutchings and Murray 1984, Blake 1996).

All multitentaculate genera (except *Protocirrineris*) have noto- and neuropodial acicular spines. The arrangement, segmental origin, number, and color of these chaetae are important taxonomic characteristics. The shape and size of notopodial acicular spines may differ from those of neuropodial spines. *Timarete perbranchiata* and *T. caribous* have neuropodial chaetae of posterior abdominal segments limited to a single, large, curved, dark spine (Blake 1996, Çinar 2009, Magalhães *et al.* 2014). Çinar and Petersen (2011) described *Fauvelicirratulus dollfusi* lacking short acicular spines and having long, straight, tapering spines appearing from noto- and neuropodia of chaetiger 12. These long spines are as long as capillaries and placed superiorly on notopodia and inferiorly on neuropodia (Çinar and Petersen, 2011).

The type of chaetae present may be a generic-level character, and the distribution and micromorphology of the chaetae are important species-level characters. Although the exact segment or range of segments where one type of chaeta occurs is usually considered a species-level character, this trait is often growth related, and care needs to be taken to ensure that specimens are mature. It is also important that some posteriorly complete specimens be available to confirm the presence or absence of spines in far posterior segments, as well as the place where these begin in a specimen of known size and number of segments. Capillary chaetae are smooth or with emergent fibrils sometimes seen with scanning electron microscopy (SEM) (Fig. 7.3.1.5.4 G). Other capillaries have a distinctly serrated or sawtooth edge that is important in recognizing species of the genus *Kirkegaardia*. Details of these chaetae are also important in separating one species from another (Fig. 7.3.1.5.4 B–E).

Bidentate hooks are characteristic of the bitentaculate genus *Caulleriella* but also occur with posterior spines in a few species of *Chaetozone* (Blake 1996, Doner and Blake 2006). As part of this review, SEMs of bidentate hooks of an undescribed species of *Caulleriella* from deep-water off New England were observed to have the apical "tooth" formed as a broad hood that is variously developed (Fig. 7.3.1.5.4 L–M). The main fang of these same hooks also has a distinct hole or opening on the tip (Fig. 7.3.1.5.4 L). Both the nature of this type of apical tooth and the opening on the tip of the spine have not been previously reported

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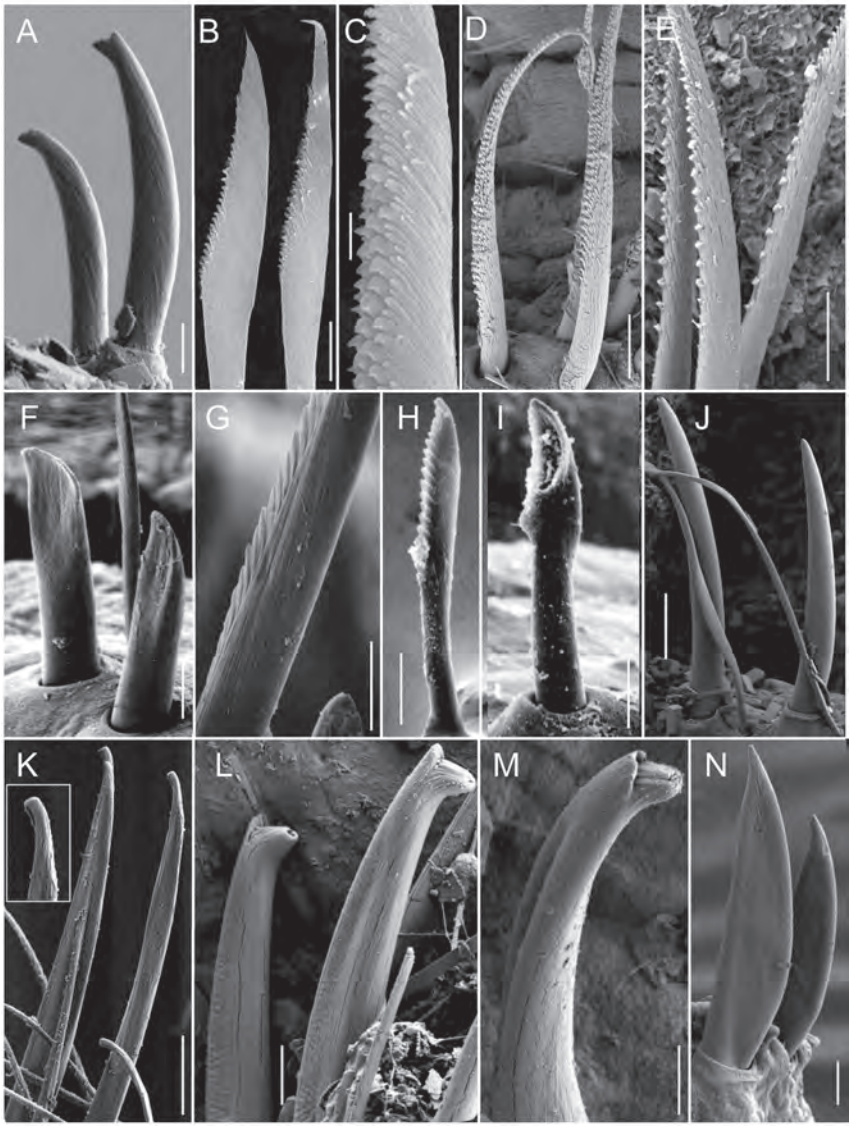


**Fig. 7.3.1.5.4:** External morphology of some cirratulid chaetae. A, *Tharyx* sp. B (Boston Harbor), posterior neuropodial hooks. B, C, *Kirkegaardia olgahartmanae*: B, denticulated neurochaetae; C, same, detail of denticles. D, *Kirkegaardia brigitteae*: denticulate neurochaetae from anterior abdominal segment. E, *Kirkegaardia* sp. (Gulf of Mexico), denticulated neurochaetae. F, G, *Dodecaceria ater* (Plymouth, UK): F, chisel-shaped acicular spines and capillary from posterior notopodium; G, detail of serrated edge of same capillary. H, I, *Dodecaceria concharum* (Denmark): H, serrated acicular spine from regenerating anterior end; I, spoon-shaped acicular spine from original segments of a regenerating specimen. J, *Chaetozone* sp. (U.S. Atlantic continental slope), posterior neuropodial spines and capillaries. K, *Chaetozone* sp. 6 (Gulf of Mexico), posterior neuropodial acicular spines with apically curved tip adhering to shaft (inset not to scale). L, M, *Caulleriella* sp. (U.S. Atlantic continental slope). M, neuropodial acicular spines with hood-like apical "tooth"; N, *Chaetozone* sp. (U.S. Atlantic continental slope), neuropodial acicular spines. Scale bars: A, E, 2 µm; B, D, I, K, N, 10 µm; C, G, H, L, M, 5 µm; F, J, 20 µm. A, E, J–N, Originals; F–H, original scanning electron microscopy images, M.E. Petersen; B–D after Blake (2016).

for cirratulid chaetae. Bidentate hooks are also reported in postlarvae of two species of *Cirriformia*, but these hooks are entirely replaced by capillaries and spines in adults (Wilson 1936, Blake 1975).

Species with knob-tipped or sub-bidentate hooks (Fig. 7.3.1.5.4 A) instead of distinctly bidentate hooks are characteristic of the genus *Tharyx* (see Blake 1991). In addition, juveniles of multitentaculate cirratulids of the genus *Cirriformia* have been found to have bidentate chaetae prior to the appearance of spines (Wilson 1936, Blake 1975, Magalhães *et al*. 2014).

Species of *Dodecaceria* have stout, acicular spines with chisel-shaped (Fig. 7.3.1.5.4 F) or spoon-shaped (Fig. 7.3.1.5.4 I) tips. In juvenile or regenerating individuals of *Dodecaceria*, serrated hooks (Fig. 7.3.1.5.4 H) similar to those of *Ctenodrilus* (see George and Petersen 1991) may be present. Sigmoid hooks with distally attached aristae have been described for *Chaetozone flagellifera* (see Gallardo 1968, Magalhães and Bailey-Brock 2015) and *Chaetozone retierei* (see Lechapt 1994).

**External details of the integument.** Staining reactions with methyl green or methylene blue have been used in recent years to supplement traditional morphology. These stains dye subdermal glands that are arranged in various locations along the body. Several species of *Aphelochaeta*, *Chaetozone*, and *Kirkegaardia*, for example, have a characteristic ventral staining in bands of posterior thoracic segments (Fig. 7.3.1.5.5 A–D) (Doner and Blake 2009, Blake 2016). Species of *Chaetozone* and other genera often exhibit distinct staining patterns on the prostomium and peristomium (Fig. 7.3.1.5.5 D–F). The nature and function

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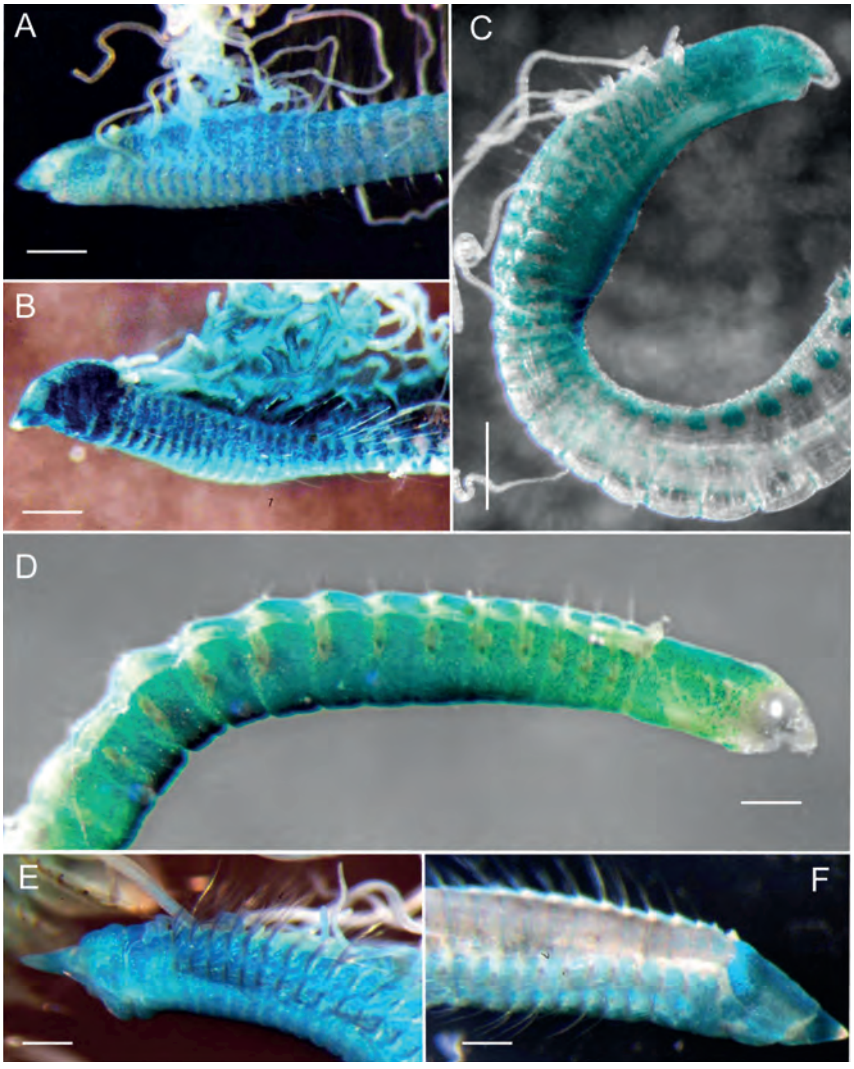


**Fig. 7.3.1.5.5:** Methyl green staining patterns in some Cirratulidae. A, *Aphelochaeta guttata*. B, *Aphelochaeta* sp. (off California). C, *Kirkegaardia hampsoni*. D, *Kirkegaardia carinata*. E, *Chaetozone malmgreni*. F, *Chaetozone bathyala*. Scale bars: A–E, 200 µm; F, 500 µm. A, After Doner and Blake (2009); B, original; C, D, after Blake (2016); E–F, after Blake (2015).

of the glands that stain, however, are not known, and many species have no staining reaction at all. Bitentaculate species generally have more distinctive staining patterns than do the multitentaculates, and species that are pigmented when preserved generally exhibit only weak staining reactions or none at all.

Staining patterns often differ among species and provide a means to differentiate several similar species lumped in single collections. When used to process large collections, species-specific staining patterns often permit even anterior fragments to be recognized. To date, however, staining patterns have not been commonly used in keys or applied to taxonomic analyses. In applying methyl green, however, some caution needs to be taken because it appears that the condition of the specimens and how well they were preserved may modify stain uptake. For this reason, specimens from several samples should be compared wherever possible to obtain the widest range of staining results.

**Anatomy**

Structural studies about cirratulid anatomy have been available since Claparède (1868) and Meyer (1887), who observed live specimens or sectioned individuals for histological studies. More recent studies have used modern techniques to investigate the architecture of neural systems during regeneration of anterior and posterior ends (e.g., Weidhase *et al.* 2014a, 2015).

**Epidermis.** The integument of cirratulids as in many polychaetes contains a monolayered epithelium with supportive, ciliary, secretory, and sensory cells (Storch 1988). Epidermal cells in *Timarete luxuriosa* are composed of columnar epithelial elements that rest on a basement membrane and are covered by a thin cuticle (Baskin 1976). Mastrodonato *et al.* (2006) provided histochemical and ultrastructural analysis of the mucus cells in the epidermis of *Timarete filigera*. They found a pseudostratified epidermis rich in melanin and with secretory and

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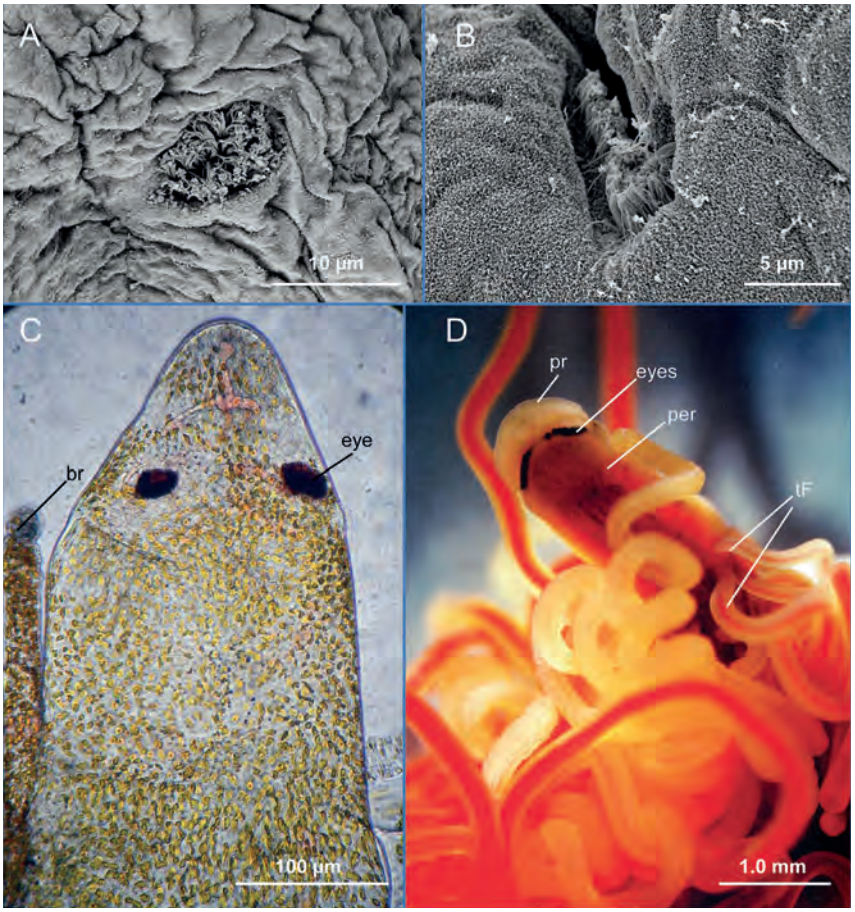


**Fig. 7.3.1.5.6:** Sense organs in cirratulids. A, Nuchal organ of *Aphelochaeta* sp. (Gulf of Mexico). B, Nuchal organ of *Cirriformia* sp. C, Single paired eyespots of *Caulleriella bioculata*. D, Eyespots organized in two rows on *Cirratulus cirratus* (SW England, UK). A–C, Original; D, original photograph by the late Mary E. Petersen.

nonsecretory cells. The epidermis produces a collagenous cuticle that covers the body wall and mucous cells were present in the dorsal and ventral regions, with no differences in their structure and content (Mastrodonato *et al.* 2006). The authors identified three types of cells that were all 20–25 µm tall and represented different stages of secretory activity.

**Musculature.** The muscular system in cirratulids is composed of mainly longitudinal and circular fibers (Lanzavecchia *et al.* 1988). Detailed observations were made in *Cirratulus* (Weidhase *et al.* 2014a) and *Timarete* (Weidhase *et al.* 2015) species. Both have a body wall musculature composed of an outer circular and an inner longitudinal layer (Weidhase *et al.* 2014a, 2015). The longitudinal layer in *T.* cf. *punctata* has two dorsal and two ventral strands; the dorsal longitudinal strands form a plate encircling the dorsal half of body, whereas the ventral ones are more compact and reach up to the notochaeta and are penetrated by neurochaetae, appearing partially bipartite (Weidhase *et al.* 2015). The authors found that the circular musculature was most prominent at the level of the chaetae, and additional musculature was also found associated with the parapodia, around the intestine and at the posterior side of the mouth opening.

**Sensory organs.** Cirratulids have a pair of ciliated nuchal organs present on the dorsolateral region of the prostomium, and some species may have paired eyespots. The presence of nuchal organs may be obscured by a fold of the epidermis if the specimens are not fixed and preserved adequately, but all species that have been examined with SEMs have a pair of ciliated nuchal organs (Fig. 7.3.1.5.6 A, B) (also see Blake 2006, Dean and Blake 2007, Magalhães and Bailey-Brock 2013a). Nuchal organs are usually composed of ciliated supporting cells, bipolar primary sensory cells with cilia, unmodified epidermal cells, and retractor muscle cells (Storch and Schlötzer-Schrehardt 1988). Brauer (2014) investigated the ultrastructure of the nuchal organs in adults and some pelagic larvae and juveniles of *Aphelochaeta marioni*, *Dodecaceria concharum*, and *Cirriformia tentaculata*. The author found that a retractor muscle can move the organ deep inside the tissue, resulting in only narrow furrows being observed. Two types of cells were observed in all three species: multiciliated supporting cells that form a stable unit and monociliated

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sensory cells. A considerably thicker cuticle above the sensory areas was found in all species, and the author discusses that this unique feature could be an apomorphy of cirratulids.

Eyespots have been observed in some bitentaculate cirratulid genera such as *Chaetozone* and *Caulleriella* (Fig. 7.3.1.5.6 C) but are more prominent in *Cirratulus* species, where they are numerous and grouped into two transverse rows (Fig. 7.3.1.5.6 D). These light-sensitive organs were investigated in *Cirriformia tentaculata* and *Dodecaceria concharum* by Brauer (2014). The eyespots are composed of one pigment cell and two receptor cells. The two sensory dendrites pass around the pigmented supporting cell ventrally and give rise to numerous microvilli and one cilium each (Brauer 2014). The microvilli are then extended into the optic cavity that is opened toward the cuticle and covered with cuticular material. Brauer (2014) pointed out the similarities of the eyespots in *Cirriformia* with those in flabelligerids.

**Nervous system.** The architecture of the nervous system has recently been studied in adult individuals of *Cirratulus* (see Weidhase *et al.* 2014a) and *Timarete* (see Weidhase *et al.* 2015). Cirratulids possess a rope-ladder-like nervous system with a prominent anterior brain and a ventral nerve cord having distinct segmental nerves (Weidhase *et al.* 2014a, 2015). The brain of *T.* cf. *punctata* is located in the prostomium and anteriorly orientated and linked to the ventral cord via two circumesophageal connectives (Weidhase *et al.* 2015). In *Cirratulus* cf. *cirratus*, a group of about 15 serotonergic neurons are present dorsal to the brain and a meshwork of immunoreactivity is present posterior to the mouth opening (Weidhase *et al.* 2014a). The ventral nerve cord in *T.* cf. *punctata* was found to be divided into two main strands, each composed of several neurite bundles, and one pair of ganglia was present in the peristomium and each chaetiger (Weidhase *et al.* 2015). The pair of palps in *D. concharum* and the multiple tentacles in *C. tentaculata* are innervated directly from the brain (Brauer 2014). In *C. tentaculata,* each tentacular filament is innervated individually (Brauer 2014).

**Digestive system.** The alimentary canal of cirratulids is a simple tubular gut typically with two compartments, a foregut and hindgut (Penry and Jumars 1990); a gular membrane is absent (Meyer 1887). The gut can sometimes have helical coiling in the posterior half of the body in order to accommodate a gut longer than the body (Jumars *et al.* 2015). Jenner (1932) described the anatomy of the anterior part of the digestive system of *Dodecaceria concharum* and *Cirriformia tentaculata* and considered the stomodaeum to be divided into a dorsal region that extends to the ventral surface of the prostomium and a ventral region, composed of a pharyngeal diverticulum with a thick cuticle and strong musculature. This ventral muscular region was also observed by Orrhage (1964) for *Dodecaceria* and *Chaetozone* and by Michel (1978) for *Cirriformia tentaculata* and described as a ventral pharynx. Michel (1978) provided detailed anatomical, histological, and histochemical information of the buccal region of *C. tentaculata*. The epithelium of the ventral pharynx includes numerous mucous glandular cells producing a mixed sulphated and carboxylated mucus. The author suggested that *C. tentaculata* could be using the partly eversible ventral pharynx as a "mucous tongue."

Blake (2006) described an enlarged and darkly pigmented stomach region in *Chaetozone brunnea* from around chaetigers 20–24, followed by an intestine region containing spherical fecal pellets (Fig. 7.3.1.5.1 C). A similar enlarged stomach region was found in *Chaetozone ronaldi* from chaetigers 12–15 (Magalhães and Bailey-Brock 2013a), and another undescribed species of *Chaetozone* having a similar enlarged stomach is known from the Southern Ocean (Blake unpublished). Penry and Jumars (1990) investigated the gut volume of four cirratulids having simple tubular guts: *Aphelochaeta* sp. (as *Tharyx multifilis*), *Kirkegaardia luticastella* (as *Tharyx*), *Cirratulus* sp. (as *C. cirratus*), and *Chaetozone* cf. *setosa*. Species with simple tubular guts as with these four species often occur in sediments with high organic enrichment and require less through time to process their food resource (Penry and Jumars 1990).

**Excretory system and nephridia.** Cirratulids have a pair of metanephridia (or mixonephridia *sensu* Goodrich 1945) situated anteriorly and usually extending for just a few segments (Fig. 7.3.1.5.7 A, D) (Smith 1992) and numerous posterior metanephridia in the genital region (gonoducts) composed almost entirely of large coelomostome (Goodrich 1945). Anterior metanephridia have been described in *Cirratulus filiformis* as a single pair of ciliated tubes that are bent and extend through segments 1–5 with internal and external openings (Keferstein 1862). Langerhans (1884) showed the pair of metanephridia in *Cirratulus glandularis* (as *Archidice glandularis*) as occupying chaetigers 1 and 2 and green in color. In *Protocirrineris chrysoderma*, the opening is at the first chaetiger by an oval aperture on the inner side of neuropodia (Claparède 1868). In *Cirratulus cirratus*, the nephrostome opens into the cavity of the buccal segment situated on the anterior end of the first septum (Cunningham 1887). The proximal part of the tube passes backward from the nephrostome, and it reaches the second septum, then it passes upward to the dorsal body wall, where it opens into the wider distal part of the tube, which opens to the exterior beneath the neuropodium

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of chaetiger 2 (Cunningham 1887). The author described the posterior metanephridia as smaller, simpler with a typical nephrostome (an elongated funnel with its aperture directed forwards), appearing from chaetiger 12 and present throughout.

**Blood vascular system.** Cirratulids, as many other polychaetes, have a complete circulatory system with a dorsal longitudinal vessel, a highly muscularized dorsal vessel (with heart-body), a ventral longitudinal vessel, a sinus associated to the gut, perineural vessels, segmental vessels, and a ganglionic blood sinus (Gardiner 1992). The heart body is the anterior region of the dorsal vessel, forming an enlarged, loose, spongy intravasal tissue (Kennedy and Dales 1958). It was first mentioned in Claparède (1868) and later also found in several terebellimorphs and flabelligerids (Kennedy and Dales 1958). The heart-body of cirratulids was studied in detail for *Cirriformia tentaculata* (as *Audouinia tentaculata*; Picton 1899, Kennedy and Dales 1958), *C. setosa* (Meyer 1887), *C. cirratus* (Cunningham 1887, Kennedy and Dales 1958), *Timarete filigera* (as *Audouinia filigera*; Picton 1899), and *Protocirrineris chrysoderma* (as *Cirratulus chrysoderma*; Picton 1899).

The hematopoietic function of the heart-body was confirmed in several cirratulids (Meyer 1887). Compared to other polychaetes, the heart-body in cirratulids is probably the most extensive in number of segments and can reach the anterior abdominal region (Fig. 7.3.1.5.7 A–C). Kennedy and Dales (1958) suggested its close relationship with the branchiae, so the extent of the heart-body would be throughout the region in which the dorsal vessel supplied vessels for respiratory function. Therefore, the heart-body in cirratulids would have a mechanical function; the contraction of the vessel wall would obliterate the heart cavity at systole passing its content to the branchiae (Picton 1899). Kennedy and Dales (1958) provided histochemical and histological analyses in the heart-body of *C. tentaculata* and *C. cirratus*. Coproporphyrin III and protohaematin were found in the heart-body of *C. cirratus*, whereas in *C. tentaculata*, it contained Coproporphyrin I and III. Coproporphyrin III was the predominant pigment also found in terebellimorphs and flabelligerids (Kennedy and Dales 1958).

The segmental origin and extent of the heart-body have proved to be relevant for generic and specific distinctions within the closely related ctenodrilids, and it should be further investigated for cirratulid genera. For example, in the genus *Ctenodrilus,* the heart-body extends from chaetigers 1 to 3 (Magalhães *et al*. 2016); in *Raphidrilus*, from chaetigers 3 to 7 (Magalhães *et al*. 2011); and in *Raricirrus*, from as early as chaetiger 4 and present in up to 10 segments (Petersen and George 1991, Dean 1995). It was observed from chaetiger 7 in *D. concharum* (Marcel 1963), from chaetiger 6 and extending to up to chaetiger 20 in *Aphelochaeta honouliuli*, from chaetiger 6 in *Protocirrineris* sp., from chaetiger 5 in *P. mascaratus* (Fig. 7.3.1.5.7 A), from chaetiger 12 and present for about 40 chaetigers in *T. hawaiensis*, and from chaetiger 6 and present for over 60 chaetigers in *Cirriformia crassicollis*.

Marcel (1963) provided a detailed description and illustrations of the vascular system of *D. concharum*. The dorsal vessel of this species is divided into two superposed vessels from chaetiger 7. The most superficial vessel, named by the author as the main dorsal vessel, contains the heart-body. At the middle of each segment, these two dorsal vessels are connected by an anastomosis that travels through the mesentery in the vicinity of the digestive tract. The ventral vessel branches off latero-ventrally into a genital vessel and a second vessel that penetrates into the posterior segment, where it enters the parietal network. The main dorsal vessel emits two branchial vessels for the first pair of gills and then divides into two blind branches, which reach into the palps.

Histological analysis of the blood vessels of *C. cirratus* was provided in Dyrssen (1912). The following layers were found in the wall of the dorsal vessel and the outer wall of the gut sinus: peritoneal epithelium, muscle fibers, and a skeleton coat in which are embedded a few flat nuclei. Cirratulids possess erythrocruorin (extracellular hemoglobins) with a usually high affinity for oxygen (Swaney and Klotz 1971, Dales and Warren 1980), but Warren *et al*. (1981) found different erythrocruorin oxygen affinity strategies employed for *Cirratulus* and *Cirriformia* species.

**Respiration.** Cirratulids respire using their long filiform branchiae. Afferent and efferent vessels are present and are strongly contractile and surrounded by a coelomic epithelium (Dales and Warren 1980). In *Cirriformia tentaculata*, the branchial vessels are separated by an epithelium 40–50 µm thick, but superficial capillary network may also aid respiratory exchange across the body wall (Dales and Warren 1980). Worthington (1989) recorded the appearance or disappearance and the number of branchiae protruding the sediment surface during aerated and anaerobic conditions in *Cirriformia* sp. The author observed seven individuals and counted 15–20 filaments above the sediment surface before the air supply was cut off, and that increased to 70–80 branchiae 3 minutes after turning off the air supply. Pardo and Amaral (2004) observed that a Brazilian population identified as *Timarete filigera* would typically extend up to four branchial filaments for aeration. Uptake of oxygen across the body wall may be relevant when the body of the worm lies in

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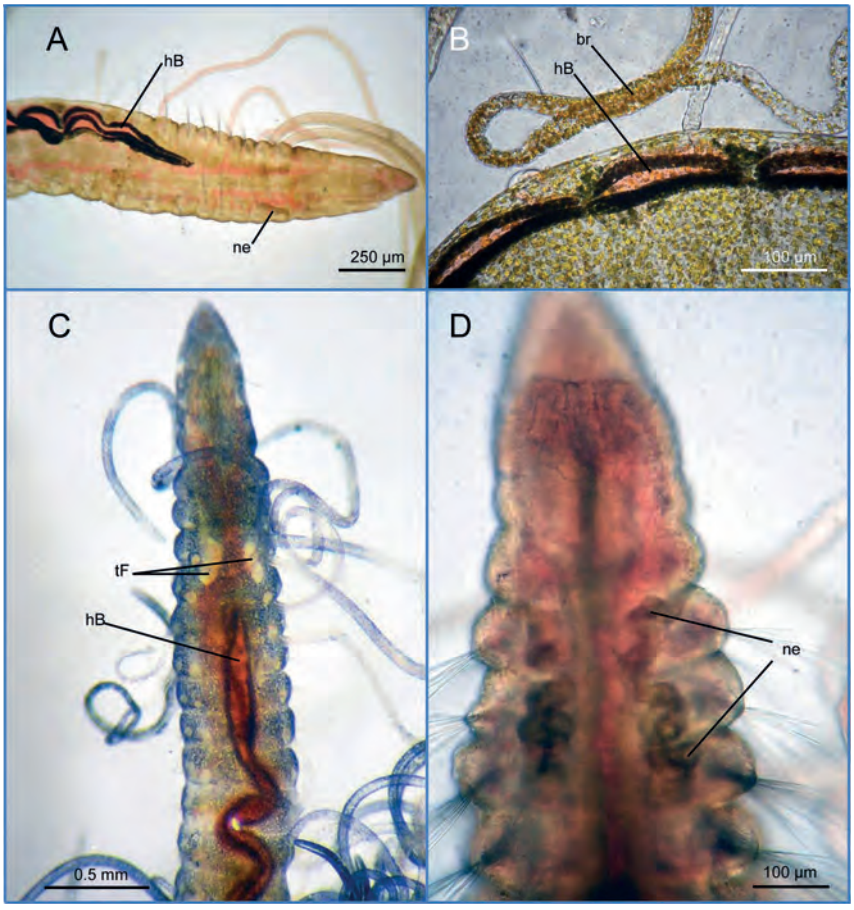


**Fig. 7.3.1.5.7:** Vascular and excretory systems in cirratulids. A, *Aphelochaeta honouliuli* showing anterior pair of nephridia (ne) and heart-body (hB). B, Heart-body in midsegments of *Caulleriella bioculata*. C, Heart-body in *Protocirrineris mascaratus* and insertion scar of tentacular filaments (tF). D, Ventral view of *A. honouliuli* showing anterior pair of nephridia ranging from chaetigers 1–3. All original.

well-oxygenated sediment (Dales and Warren 1980), and George (1968) observed worms on the surface of the sediment at periods of low tide. Warren (1981) and Bestwick *et al.* (1989) investigated the anaerobic energy metabolism of *C. tentaculata* in intertidal sediments. This species is often found in hydrogen-sulphide-rich environments, and when values of oxygen are below 30%, they accumulate both alanine and succinate. In addition to increasing the production of alanine during 5-hour periods of reduced oxygen, the worms would also reduce significantly the blood pH (Warren 1981).

## Reproduction and development

Reproductive processes in cirratulids involve both asexual and sexual components, with the asexual processes highly developed in some species. The topic has been reviewed by Caullery and Mesnil (1898), Schroeder and Hermans (1975), and Petersen (1999). As will be seen in the sections that follow, asexual reproduction often alternates with production of sexual epitokes, providing life history patterns that are sometimes complex and serve to complicate systematics. For example, an entire genus, *Zeppelina*, with eight species was found to be based totally on regenerating specimens of the cirratulid genera *Dodecaceria* and *Monticellina* (now *Kirkegaardia*) and the ctenodrilid genus *Raphidrilus* (George and Petersen 1991).

### Reproduction

**Sexual reproduction.** Sexual dimorphism is rare in cirratulids, according to Petersen (1999), who noted widespread evidence of hermaphroditism for species of *Aphelochaeta*, *Caulleriella*, *Cirratulus*, and *Chaetozone*. Studies on the reproductive cycles and population dynamics of cirratulids are relatively few, and documentation of sexual condition is not sufficient to draw overall conclusions about cirratulids. However, brooding and viviparity are relatively common; broadcast spawning and production of planktic larvae are relatively rare; when present, planktic larvae are always lecithotrophic.

George (1964a,b) conducted a series of investigations on the biology of *C. tentaculata* from Southampton, UK. The species was found to have a prolonged breeding season between March and September, with several mass spawnings during that time. The fewest individuals were

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recorded in April, followed by a rapid increase in density during May. The density of the populations varied from year to year. Growth of the worms was correlated with seasonal variation in temperature. A growth rate of 8 mm per year was calculated. The distribution of the worms over the mudflats was strongly correlated with wave action or water movement.

Olive (1970) followed the reproduction of *C. cirratus* in Cullercoats Bay (UK) over a 2-year period. He determined that the species reproduces continuously throughout the year, with the majority of females always at various stages of oogenesis. Adult males always contained mature sperm. His data suggest that females live to spawn up to five times during their lives and grow an average of 2 cm between spawnings.

Gibbs (1971) was able to follow the annual populations of *Chaetozone caputesocis* (as *Caulleriella*), *Aphelochaeta* sp. (as *T. marioni*), *C. tentaculata*, and *C. cirratus* from Plymouth, UK. The main spawning seasons were as follows—(1) *Chaetozone caputesocis*: August–October, with egg diameters of 110 μm, but with the highest densities achieved in June (22,000 individuals $m^{-2}$). (2) *Aphelochaeta* sp.: October–November, with egg diameters of 200–220 μm and with highest densities in winter months (100,000 individuals $m^{-2}$). (3) *C. tentaculata*: late June to early July, with egg diameters of ca. 117 μm. (4) *Cirratulus cirratus* did not exhibit an annual cycle, in agreement with Olive (1970); egg diameters were 135–150 μm all year.

Farke (1979) reported on the reproduction of *T. killariensis* (as *T. marioni fide* Petersen 1999) from the intertidal of the German Bight. Reproduction occurred in spring and early summer.

The population cycle of *Chaetozone zetlandica* (as *Caulleriella caputesocis fide* Petersen 1999) from Southampton, UK, was studied by Oyenekan (1987). He was able to confirm that the species did not breed until the second year, and individuals were monotelic (i.e., breeding only once in its lifetime). Breeding apparently occurred yearround in the population, peaking between May and September. Mature eggs measured 120–160 μm in diameter.

Christie (1984), as part of his description of *Chaetozone vivipara* (as *Tharyx vivipara*) from the Tyne Estuary, UK, observed coelomic contents at various times of the year and determined that the species was a simultaneous hermaphrodite, with gametogenesis initiated in July. Sperm with an elongated head (aberrant) and mature oocytes (100–120 μm) were present in the coelom by February, at which time fertilized eggs and early embryos were also present. Release of the embryos from the body apparently occurred after April because by July, adults again had early gametes in the coelom.

Christie (1985) studied the reproductive cycles of three populations that he identified as *C. setosa*. Morphological and reproductive differences were observed between the populations, but he did not attempt to separate them at the species level. One population spawned in March–April, the other two spawned in November–December.

Lechapt (1983a), working in the Rance area near Dinard on the French side of the English Channel, observed populations of *Chaetozone* sp. (as *C. setosa*) over a 20-month period. He found that reproduction occurred from June to August, but at no time were more than 40% of the population sexually mature. Lechapt's data suggest that the worms live for 2 years, but die after sexual reproduction. In a second paper, Lechapt (1983b) presented meristic data of juveniles and adults to document the morphology of his local species of *Chaetozone*.

Reproduction of *D. concharum* (as *Dodecaceria caulleryi*) was reported by Gibson and Clark (1976) and Gibson (1981). This species reproduces asexually by fragmentation (i.e., worms are divided into a variable number of fragments, each consisting of several segments, *sensu* Petersen 1999) and schizometamery (i.e., larger middle segment of an individual break off singly and is able to regenerate a new individual, *sensu* Petersen 1999) and sexually with epitokes that are broadcast spawners. These authors determined that the species was capable of living for up to six years, reproducing by schizogenesis, and finally reproducing and spawning sexually as epitokes, after which they die. Further details of *Dodecaceria* reproduction are presented in subsequent sections.

Studies of cirratulid reproductive cycles in offshore sediments on the continental shelf are rare. As part of the 3-year monitoring program (1981–1983) on Georges Bank off Massachusetts, Blake and Baptiste (1985) developed data on the reproduction and life history of several abundant polychaete species, including the cirratulids *Aphelochaeta* sp. A (as *Tharyx* sp. A), *K. baptisteae* (as *Tharyx annulosa*), and *T. acutus*. Samples were collected quarterly (February, May, July, and November). *Aphelochaeta* sp. A was studied at a mixed sand/mud station (ca. 84 m). The highest percentage of males (9.3%) and females (14.0%) was in July and the lowest in November (0–3.2%) and February (0–1.1%). Size frequency data indicated a late summer and early fall recruitment with the highest number of juveniles (<25 chaetigers) present in November (24.5%) and February (27.4%). *Kirkegaardia baptisteae* was studied at two stations: a muddy site at 70 m and a sand/mud site at 84 m. At the mud station, the species *K. baptisteae* produced gametes in the winter and spawned in the spring. Males were found in November (19.2%) and

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February (27.9%), and females, in July (22.2%), November (42.3%), and February (32.6%). No gametes were observed May. The highest percentage of juveniles (6.6%) was observed in July. Age/size data for *T. acutus* at the 84 m site with mixed and mud indicated that recruitment occurred in July and November. This recruitment produced a cohort that included 10–45 chaetiger individuals, which were followed through May and somewhat less distinctly through May of the following year. Results suggest a 2-year life cycle where worms do not produce progeny until a 24-month interval has passed. The highest percentages of males and females were in spring and summer months, which agrees with summer and fall recruitment.

### Gametogenesis

**Oogenesis.** Mature cirratulids studied to date have relatively large eggs, typically 110–180 µm, which indicates direct or lecithotrophic development. Petersen (1999) reported an undescribed Danish species of *Aphelochaeta* with unusually large eggs of 400–450 µm.

Olive (1970, 1971) described details of the reproductive biology and gametogenesis of *C. cirratus* from British waters; these results agree with those of Gibbs (1971) (see previous discussion). The species reproduces throughout the year. After spawning, females began to develop another set of oocytes within 30 days. Ovaries of *C. cirratus* occurred two per segment posterior to the twelfth. The worms grew about 2 cm between spawnings.

In *C. cirratus*, oocytes developed in ovaries that consisted of plates of cells on the anterior septa of each vertical mesentery in each fertile segment (starting behind segment 12). Coelomic oocytes grew slowly, taking 1–2 years for complete development. There were two ovaries per segment throughout the fertile region. Olive (1971) described five stages in oocyte differentiation while in the ovaries: stem cells, oogonia, premeiotic oocytes, early oocytes, and terminal oocytes that are released into the coelom. Vitellogenesis takes place in the coelom, where the oocytes grow from about 20 to 150 µm in diameter. Mature eggs ranged from 130 to 150 µm in diameter. Olive's results suggested that the species was long-lived, with females surviving to spawn two to five times. Upon spawning, the eggs were usually in metaphase I of meiosis and fertilized upon release if in the presence of a male. Olive (1973) determined that prior to spawning, the release of new oocytes into the coelom was inhibited. Spawning or artificial removal of coelomic oocytes stimulates a renewed discharge of oocytes from the ovaries to the coelom.

Gibbs (1971) also studied gametogenesis in *Chaetozone caputesocis* (as *Caulleriella*), *Aphelochaeta* sp. (as *T. marioni*), and *C. tentaculata*. He found that the eggs of *Aphelochaeta* sp. and *C. tentaculata*, like *C. cirratus,* matured to metaphase I in the coelom prior to spawning. Only eggs in this condition could be fertilized. Fertile eggs were not identified in *Chaetozone caputesocis*.

Oogenesis for two sympatric species of *Dodecaceria* in the UK was described by Gibson (1981). The first species, *D. ater* (as *D. concharum*), was parthenogenic and atokous and the eggs began development without fertilization within the coelom of the female. The second species, *D. concharum* (as *D. caulleryi*), produced both male and female epitokes, where the anterior tentacles atrophied and disappeared during epitoke formation (Caullery and Mesnil 1898). Oogenesis was identical for the two species. Gonads were paired, and in most of the middle body, segments were attached to the posterior face of each septum. Gametes proliferated from cells adjacent to the septum; these grew and were liberated into the coelom, where they accumulated, matured, and were eventually spawned. Gibson (1981) determined that both species had six chromosomes in the newly proliferated oocytes in metaphase I. Due to an all-female population and parthenogenic development, *D. ater* (as *D. caulleryi*) retained the haploid number as an adult. In contrast, *D. concharum* (as *D. caulleryi*) had the diploid number of 12 chromosomes as an adult.

**Spermatogenesis.** As part of his study of the reproductive cycles of *Chaetozone caputesocis* (as *Caulleriella*), *Aphelochaeta* sp. (as *T. marioni*), *C. tentaculata*, and *C. cirratus*, Gibbs (1971) determined that all four species had similar patterns of spermiogenesis. The mature sperm were of the short-headed, primitive type, with those of *Aphelochaeta* sp. having a more elongate and bullet-shaped nucleus than the other species. Gibbs noted that Dales (1951) had earlier reported a short-headed sperm in a different population attributed to the same species. The elongate sperm of *A. marioni* (as *Heterocirrus marioni*) were figured in the original description by Saint-Joseph (1894). Given the vagaries of species of *Aphelochaeta*, it is likely that several European species are present among those referred to *Tharyx* or *A. marioni* (all as *Aphelochaeta* sp. here).

As part of his studies on the oogenesis of *C. cirratus*, Olive (1971) also described spermatogenesis. Males, like females, had paired gonads in each fertile segment. The gonad released rosettes of cells into the coelom, where development continued. Stem cells have a spherical nucleus and a small nucleolus. Individual packets of primary and secondary spermatocytes in the coelom undergo meiosis. Following completion of meiosis, spherical spermatids were formed that were about 3 µm in diameter; small mitochondria were visible. The sperm tail

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was formed while the spermatids were still in packets. The spermatozoa separated and became active while still in the coelomic cavity and were shed through coelomoducts into the seawater.

Gibson (1981) was able to follow spermatogenesis in *D. concharum* (as *D. caulleryi*), the epitokous species. The proliferation of gametes and release of presumptive spermatocytes into the coelom were the same as for females. The incipient spermatocytes were, however, smaller than comparable oocytes and formed into rings and, eventually, platelets.

## Life cycles

**Spawning and egg laying.** Most species that have been studied spawn their eggs directly into sediment or seawater, where development takes place, either directly or, if in the plankton, as lecithotrophic larvae with a short planktic duration; planktotrophic larvae have never been observed in cirratulids. Epitoky is known where sexually mature adults develop long, natatory chaetae and swim in the plankton (Stephenson 1950b).

Egg masses of various forms have been reported for species of *Cirratulus*. Cunningham and Ramage (1888), Stephenson (1950a), and Olive (1970) described egg masses of *C. cirratus* from the UK as soft, sticky structures that were soon covered with silt. Specimens of *C. cirratus* collected in SW England were observed by M.E. Petersen (unpublished data) to deposit large elongate cylindrical egg masses among gravel and cobbles. The adult worms and egg masses were photographed and are depicted in Fig. 7.3.1.5.8 A–C. Both egg masses with fertilized eggs (Fig. 7.3.1.5.8 B) and others with larvae being hatched (Fig. 7.3.1.5.8 C) were observed. Okuda (1946) described an elongate fusiform egg mass for *Cirratulus* sp. (as *C. cirratus*) from Japan (Fig. 7.3.1.5.8 E). Fauvel (1916) described brooding in *Cirratulus jucundus* from the Falkland Islands, where juveniles with up to 12 chaetigers were found among tentacles and branchiae on the dorsal surface. In a similar manner, Khlebovich (1958) observed eggs and trochophores of *Cirratulus* sp. from the Kuril Islands attached to tentacular cirri and branchiae of females. An unusual form of brood protection has been described for *Cirratulus wladislavi*, an Arctic species, by Buzhinskaja (1992). The worms shed clumps of branchiae and tentacular filaments as a mass that surrounds the fertilized eggs (Fig. 7.3.1.5.8 D), where development proceeds until benthic juveniles emerge and crawl away.

**Larval development.** There have been relatively few complete studies on the larval development of cirratulids. Patterns of development in the few species studied to date indicate that development is either lecithotrophic, direct, or viviparous. Planktotrophic larvae have never been reported for cirratulids. Six species of multitentaculate cirratulids in the genera *Cirratulus* and *Cirriformia* have been studied to varying degrees. However, it is likely that multiple species are present under single names. For example, the development of *C. cirratus* is described by Okuda (1946) and Stephenson (1950a), but Okuda's species from Japan is unlikely to be the same as the one from the UK. In addition, widespread reports of development for *T. marioni* likely include multiple species of *Aphelochaeta* or *Tharyx*, species unknown. For these reasons, some larval accounts reviewed here will be treated at the genus level with differences in the accounts from different geographic areas noted.

### A) Larvae of multitentaculate genera

Okuda (1946) provided a detailed and complete description of the brooding and development of *Cirratulus* sp. (as *C. cirratus*) from Japan. This species spawns an elongate fusiform egg mass attached to rocks on sediment in tide pools by a stalk on either end (Fig. 7.3.1.5.8 E). Eggs are about 100 µm in diameter. Encapsulated larvae develop as classic trochophores with apical cilia, prototroch, telotroch, plus an akrotroch. These larvae swim actively when released from the egg mass and there appears to be a short planktic phase prior to settlement and metamorphosis, but there is no evidence that the larvae feed in the plankton. The segmented larvae rapidly lose their cilia and settle to the bottom, where they glide slowly along the bottom, metamorphosing into juveniles with about six chaetigers.

The larval development of *Cirratulus cirratus* was described by Stephenson (1950a) with supplemental observations by Olive (1970). Briefly, the encapsulated eggs are 150 µm in diameter when deposited. A fertilization membrane about 30 µm thick lifts off the surface a few hours after the eggs are laid; according to Stephenson (1950a), some eggs were not fertilized. The developing larvae begin to elongate and develop cilia, including a broad prototroch and telotroch, together with a patch of short apical cilia and a short neurotroch; a pair of eyespots is also present. These early larvae emerge from the egg mass about 6 days after the eggs were laid and begin to swim slowly, returning to the sediment where they briefly attach. A 1-day-old larva is shown in Fig. 7.3.1.5.8 F. Over the next 2 days, the larvae elongate and become more transparent, presumably due to their yolk reserves being consumed (Fig. 7.3.1.5.8 G). A week after hatching, a second pair of eyespots develops, cilia are being lost, and worms continue to elongate (Fig. 7.3.1.5.8 H–I). These larvae are essentially benthic forms that creep

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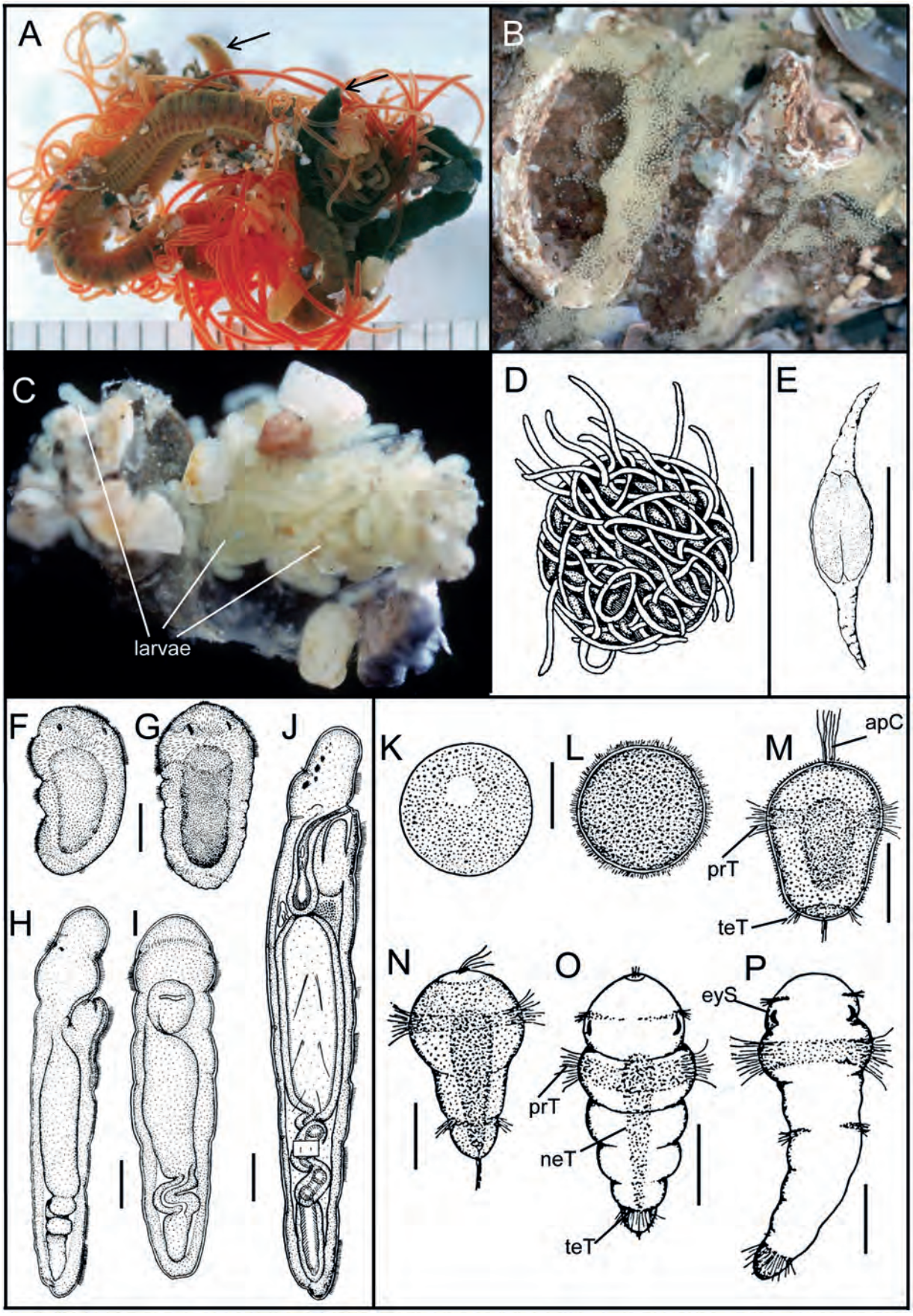


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over the substratum but can swim with ciliary action if disturbed. Development is slow over the next week or so, at which time the first chaetae develop, and they begin feeding on particulate material in the culture dishes (Fig. 7.3.1.5.8 J). Although the early larvae of *C. cirratus* are capable of swimming, this is weak, and essentially, the development is direct, with no defined planktic phase. Readers are referred to Stephenson (1950a) for details of the morphological changes during development. Curtis (1977) suggested that the development of *C. cirratus* in Greenland was direct because the egg diameter was 150 µm. However, these eggs fall into the same size range of the species in Britain as reported by Stephenson (1950a) and Olive (1970, 1971). It is unlikely however, that specimens from the UK and Greenland represent the same species.

Buzhinskaja (1992) described the direct development of *Cirratulus wladislavi* from the Kommandor Islands in the Bering Sea. The worms discharge fertilized eggs into a mass of branchiae and tentacular filaments that are shed during spawning (Fig. 7.3.1.5.8 D). The larval development was observed in the laboratory to continue within the mass of living tentacular/branchial filaments for 17 days, at which time larvae emerged as benthic crawling stages having four to five chaetigers. According to illustrations by Buzhinskaja (1992), the encapsulated larvae developed a prototroch, metatroch, and neurotroch that probably assisted in movements within the egg mass. Larval development, however, is direct, with no evidence of a swimming stage.

The larval development of *C. grandis* was briefly reported by Scott (1911) and Costello *et al.* (1957) from Woods Hole, MA. The worms were reproductively mature in July and August, but mature females were available as early as April (Bumpus 1898, Mead 1898, Costello *et al.* 1957). According to Scott (1911), the worms pawned naturally only sat night and with fertilized eggs present in the morning. Cleavage was unequal, with the second cleavage resulting in three cells. Cleavage proceeded until a gastrula was formed. A trochophore with apical cilia and a poorly developed prototroch developed after 24 hours, but the larva was only weakly able to leave the bottom; a three-segmented benthic larva subsequently developed (Costello *et al.* 1957). The larvae glide over the bottom using a ventral band of cilia, presumably a neurotroch. Development was direct with, no planktic phase.

The larval development of *Cirriformia tentaculata* from the UK, near Plymouth, described by Wilson (1936) (as *A. tentaculata*) was the first report of development of any cirratulid from fertilized eggs through larval development, metamorphosis, and development of juvenile morphology. Ripe males and females were collected in late June. Fertilized eggs were obtained by allowing females to spawn naturally in the laboratory and then adding sperm stripped from ripe males. Unfertilized eggs measured 112 µm in the longest dimension and were somewhat oblong in shape. Development was rapid with the development of a swimming trochophore (135 µm long) with well-developed apical cilia, prototroch, and telotroch 24 hours after fertilization. These larvae were covered with a thick egg membrane through which the cilia protruded. After 3–4 days, the trunk of these swimming larvae had elongated, with evidence of at least two segments; a broad neurotroch was present along the ventral surface, and a narrow akrotroch developed anterior to the broad prototroch (245 µm long). In addition, gastrotrochs were present on the first body segment. These swimming larvae continued to elongate but showed no evidence of feeding, being entirely lecithotrophic. Metamorphosis began after 8 days and consisted of loss of most cilia, development of five distinct segments, but no chaetae; food particles were observed in the stomach and intestine (ca. 335 µm long). After about 12–13 days, chaetae were observed protruding from segments 4 and 5 posterior to the head (365 µm long). The first branchial filament was observed after five chaetigers had developed and arose from the posterior end of the achaetous peristomial region. Some juveniles were observed up to 3 months after fertilization. Among the chaetae were bidentate hooks; these are not present in adults of this species. George (1963, 1964a, 1967) conducted extensive studies on the life history of *C. tentaculata* and, among other things, determined that both free-swimming lecithotrophic larvae and demersal (direct) developing larvae were present simultaneously

◂ **Fig. 7.3.1.5.8:** Reproduction and development of some Cirratulids. A–C, *Cirratulus cirratus*: A, adult female, left, light colored and male, right, dark colored (SW England, UK); B, egg mass spawned by the same female as in A; C, egg mass with late larvae and others emergent from same collection as A and B. D, *Cirratulus wladislavi*, egg mass (Kommandor Islands). E, *Cirratulus* sp. (as *C. cirratus*), egg mass (Japan). F–I, larvae of *C. cirratus* reared in the laboratory from egg masses collected at Cullercoats (UK): F, recently hatched posttrochophore, dorsolateral view; G, 3-day larva, dorsal view; H–I, 5-day benthic crawling stage, in lateral (H) and dorsal views (I); 4-chaetiger juvenile, 20 days after hatching in lateral view. K–P, developmental stages of *Dodecaceria fewkesi* (British Columbia): K, fertilized egg; L, ciliated blastula; M, trochophore larva; N, larva with 1 segment; O, larva with two segments; P, larva with four chaetigerous segments. Scale bars: A, scale spaces 1 mm each; B, C, not to scale; D, 2 mm; E, 10 mm; F–J, 50 µm; K–P, 50 µm. A–C, Photographs by the late Mary E. Petersen (unpublished); D, after Buzhinskaja (1992); E, after Okuda (1946); F–J, after Stephenson (1950a); K–P, after Berkeley and Berkeley (1954).

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in several populations. In some instances, both types of larvae were present in a single spawning. This is an example of poecilogony.

Blake (1975) described the larval development of *Cirriformia moorei* (as *C. spirabrancha*) from Tomales Bay, California. Mature eggs (126–128 μm) and sperm were present in June and July. Ripe females were induced to spawn in the laboratory similar to Wilson (1936), and sperm removed from ripe males were used to fertilize the eggs. Fertilized eggs have a thick refractile membrane, which persists as a larval cuticle throughout development; Wilson (1936) found the same type of membrane in larvae of *C. tentaculata*. The larval behavior and morphology of *C. moorei* are nearly identical to that of *C. tentaculata*. A swimming trochophore with apical cilia, prototroch, and telotroch developed after 20 hours (Fig. 7.3.1.5.9 A). After 2 days, the larva had elongated and formed one body segment on the trunk (Fig. 7.3.1.5.9 B). After 4 days, the larvae (310 μm long) had three body segments (akrotroch, prototroch, and telotroch), a gastrotroch on segment 1, and a long neurotroch extending from the mouth to near the posterior end (Fig. 7.3.1.5.9 C, D). In addition, a pair of yellow eyespots, two small nuchal slits, and a ventral patch of cilia developed anterior to the mouth between the akrotroch and prototroch. By day 7, the larvae began to lose cilia and settled to the bottom. These early juveniles had five body segments (350 μm) (Fig. 7.3.1.5.9 E, F); the neurotroch and ventral patch of cilia anterior to the mouth remained. The larvae began to feed on algae provided to the cultures, and they moved slowly over the bottom, likely assisted by the neurotroch. By 13 days, the juveniles were long (1.0 mm long), thin, and with about seven segments, two of which had chaetae (Fig. 7.3.1.5.9 G), all bidentate hooks. A seven-chaetiger juvenile (1.25 mm long) had two achaetous segments preceding the first chaetiger; the first branchial filament was present on the second achaetous segment anterior to chaetiger 1 (Fig. 7.3.1.5.9 H). This is the same arrangement reported by Wilson (1936) for *C. tentaculata*. Both noto- and neurochaetae were bidentate hooks. This differed from *C. tentaculata*, where Wilson (1936) observed both simple spines and bidentate hooks. A 16-chaetiger juvenile (2.0 mm long) had four branchial filaments (Fig. 7.3.1.5.9 I). Neuropodial of chaetigers 1–3 had both capillaries and bidentate hooks; the neuropodia of chaetigers 4–7 had only hooks. Notopodial of chaetigers 1–7 had both bidentate hooks (Fig. 7.3.1.5.9 J) and capillaries.

The presence of bidentate hooks and branchiae anterior to chaetiger 1 in the juveniles of both *C. tentaculata* and *C. moorei* differs from adults, where chaetae are a mixture of capillaries and unidentate spines. Branchiae occur from chaetiger 1 in adults of both species. However, in descriptions of larvae and juveniles of *Cirratulus* sp. by Okuda (1946) and *C. cirratus* by Stephenson (1950a), bidentate hooks were not present in juveniles, instead only capillaries and simple spines were present. Magalhães *et al.* (2014) found bidentate hooks in juveniles of their new species, *Cirriformia chicoi* from Brazil, and suggested that the occurrence of bidentate hooks in juveniles may be universal among multitentaculates. However, to date, bidentate hooks have been found in only juveniles *Cirriformia*.

**B) Larvae of bitentaculate sediment dwelling genera**

*Tharyx marioni* is a name that has been and is still being applied to what most likely represents several different species of *Aphelochaeta*. Two papers have appeared describing the early development under this name: Dales (1951) from the Thames Estuary, UK, and Cazaux (1972) from Arcachon Bay on the Atlantic coast of France.

Dales (1951) reported on the spawning and early hatching stages of a species we term *Aphelochaeta* sp. Spawning worms were present in April. Unfertilized eggs were approximately 200 μm in diameter. Eggs and sperm were naturally spawned, and Dales assumed that they were deposited directly into the sediment where he collected them. The fertilized eggs produce a conspicuous jelly layer that surrounds the developing larva like a capsule. The developing embryo rotates within this capsule. The surface of this membrane is coated with a growth of diatoms. After 2–3 days, cilia appear on the embryo extending through the fertilization membrane. After 28 days, early larvae similar to trochophores emerged from the capsules. These early larvae, with ciliary bands that approximated a prototroch, telotroch, and neurotroch, were elongate with a pointed anterior end, but segmentation was not evident and there were no chaetae at this stage. These larvae, although ciliated, were sluggish, highly contractile, and appeared to be entirely benthic.

Cazaux (1972) described what he identified as *T. marioni* and considered it to be same species that Dales (1951) had reported. Unlike Dales (1951), however, Cazaux (1972) was able to culture his larvae until benthic juvenile stages were developed. The entire development was

▸ **Fig. 7.3.1.5.9:** Larval development of *Cirriformia moorei*. A, trochophore (20 hours). B, One-segment larva (2 days), dorsal view. C, Three-segment larva (4 days), ventral view. D, Same, dorsal view. E, Five-segment juvenile (7 days), ventral view. F, same, dorsal view. G, Juvenile with two chaetigers (13 days), dorsal view. H, Juvenile with seven chaetigers (40 days), dorsal view. I, Juvenile with 16 chaetigers (61 days), dorsal view. J, Bifid hook. Scale bars: A–G, I, 100 μm; H, 50 μm; J, not to scale. After Blake (1975).

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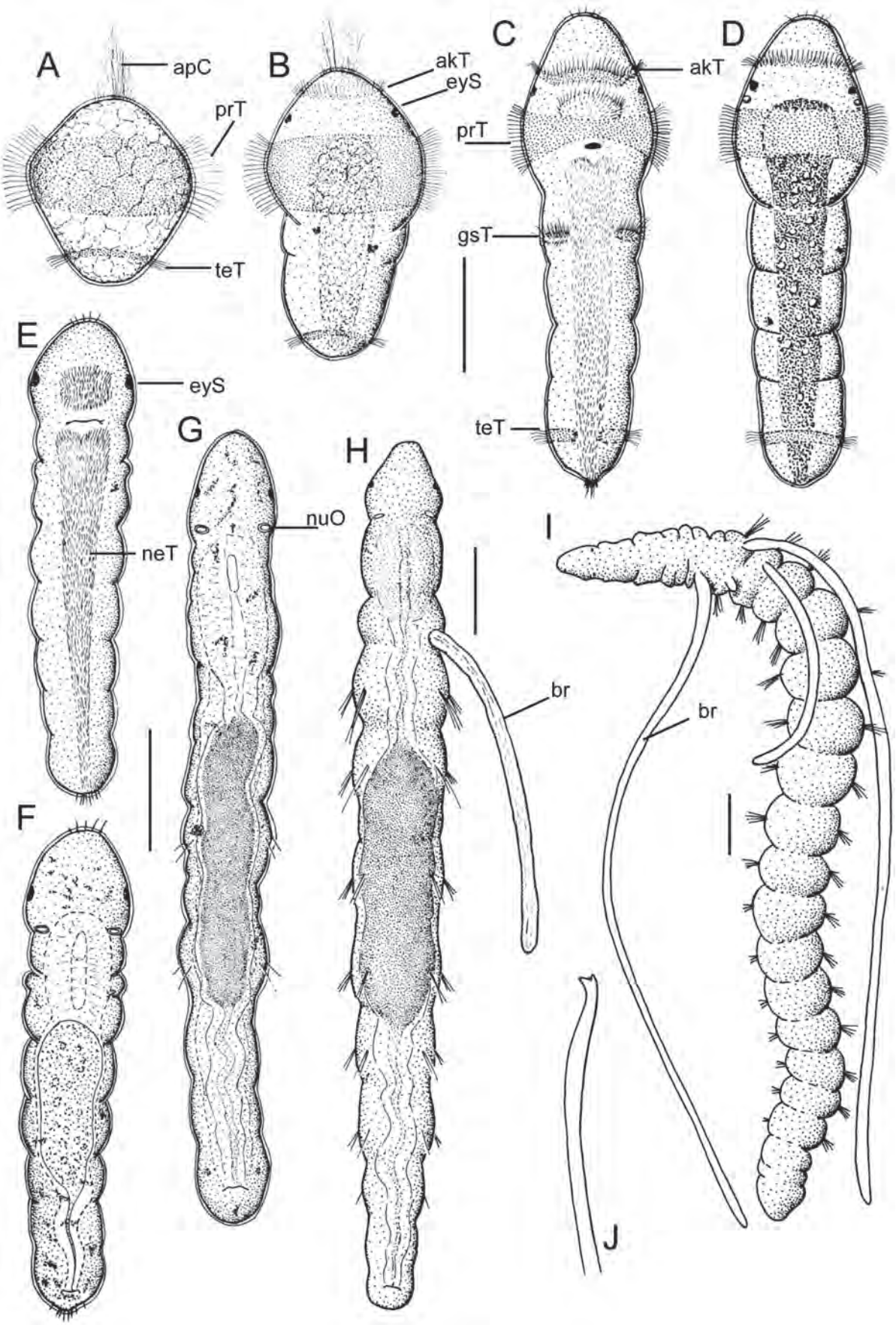


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direct, with no planktic stage. Like reports by Dales (1951), the early larvae developed inside a capsule or shell within which the early larvae began to move within after 2–3 days. They hatched after about 10 days. An early benthic larva was 190 µm long and had a neurotroch along the venter and a broad prototroch, akrotroch, and scattered apical cilia on the head. There was no telotroch. There was one segment between the head and posterior end. Five days after hatching, the larvae (400 µm long) had developed two body segments following the prostomium, the second of which had a single branchia. After nine days (460 µm long), six segments, including three with chaetae, were present. Two achaetous segments separated the prostomium from the chaetigerous segments, which each had two to three capillaries. A single branchia arose on the second achaetous segment. After 1 month, the larvae (600 µm long) had nine segments, with six chaetigers. The neurotroch persisted, but the ciliary bands had disappeared. These larvae were entirely benthic and incapable of swimming. The anterior region included the prostomium and peristomium, followed by two segments. Two branchiae were present from the first chaetiger. Six weeks after hatching, 14 segments, including 11 with chaetae, were present (1350 µm long). Branchiae were present on the first three chaetigers. The intestine was distended by its brown content; the digestive tract included a pharynx, long stomach, and digestive tract that exited through the anus. The body of the young worm was tan in color; the integument was transparent. The juvenile fed by ingesting diatoms available in the culture containers.

Petersen (1999) briefly described the development of an undescribed hermaphroditic Danish species of *Aphelochaeta* from algal holdfasts in rocky habitats with unusually large eggs (400 µm) that were few in number (10–12 eggs) and deposited singly within tubes of the adult worm. The development was direct, with the juveniles remaining in the tubes until 10 or more chaetigers had developed.

Some observations and figures on the early larvae of *Caulleriella parva* from sediments of the Kattegat, Denmark, were provided by Petersen (1999). The species appears to be hermaphroditic and with direct development. Cilia were present but were few and not organized into distinct bands. Development proceeded to a three-segment stage. No tentacles or branchiae were present, but chaetae were beginning to appear.

The only observations on the development of a species of *Chaetozone* are for *C. vivipara* (as *T. vivipara*) by Christie (1984) from the UK. This species is a simultaneous hermaphrodite. Mature and fertilized eggs (100–120 µm) were present in the coelom in February. Early embryos developed in the coelom (100 × 150 µm). The development continued in the coelom until juveniles with three to four chaetigers and a pair of dorsal tentacles had developed. The stage at which juveniles were released and the mode of release from the parent is not known.

Blake (1991) reported that *Tharyx acutus* was also viviparous in winter months. The species is common in shallow water sediments throughout the northeastern USA.

Farke (1979) provided some details on the development of *T. killariensis* (as *T. marioni fide* Petersen, 1999) from the southeastern North Sea, Germany. The eggs were spawned into sediment, were encapsulated, and were similar to those reported for *Aphelochaeta* sp. by Dales (1951) and Cazaux (1972) (see previous discussion). Early larvae with cilia developed in the capsules, whereupon they began moving. After 10 days, the larvae hatched from the capsules. These larvae were entirely benthic and somewhat oval in shape. Three days after hatching, they had elongated, and after 4 days, four segments were evident and the first tentacle was present on the second segment. Twenty-one days after hatching, the juveniles had six segments, four with chaetae, and one tentacle. The second tentacle developed in subsequent days. These juveniles dug into the bottom after hatching, where their development and growth continued.

### C) Larvae and reproduction in the bitentaculate hard substrate species of *Dodecaceria*

The life cycle of *Dodecaceria* species includes both sexual and asexual reproduction. Unfortunately, there is considerable confusion historically relative to species names associated with different types of reproduction. Some species were established for certain types of reproduction, where earlier names have now been shown to apply. Petersen (1999) attempted to summarize this, but the current usage of names remains inconsistent. A proposal by Gibson and Heppell (1995) to the International Commission on Zoological Nomenclature (ICZN) to establish a neotype for *D. concharum* based on specimens from SE England instead of the type-locality in Denmark was rejected in part (ICZN 2003) because other workers had historically defined the species differently and specimens considered to be *D. concharum* were available in Danish waters (George and Petersen 1991, Petersen 1999).

Based on the summary presented by Petersen (1999) and subsequent usage of this followed by Bellan (2001), Dauvin *et al.* (2003), Bleidorn *et al.* (2003a), Elias and Rivero (2009a), Aguilar-Camacho and Salazar-Vallejo (2011), and Weidhase *et al.* (2015), an updated list of *Dodecaceria* species is here provided for those species where information on reproduction is known (Tab. 7.3.1.5.1).

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**Tab. 7.3.1.5.1:** Modes of reproduction observed in species of *Dodecaceria*.

| Species | Sexual reproduction | Larval development | Asexual reproduction | Locality | References |
|---|---|---|---|---|---|
| *Dodecaceria ater* | Eggs (150–200 µm); parthenogenetic; eggs develop without fertilization. | Viviparous; spawned and brooded in adult tubes. | Not observed. | NE France and UK | Caullery and Mesnil (1898) (as *Dodecaceria concharum* Form A, ?C); Marcel (1962) and Gibson (1977, 1981) (all as *D. concharum*); Petersen (1999) |
| *Dodecaceria berkeleyorum* | Epitokes observed for both sexes. | Unknown: larvae reported by Knox (1971) are actually *Polydora* sp. | Binary fission. | New Zealand | Knox (1971); Gibson (1978) (as *D. berkeleyi*). |
| *Dodecaceria concharum* | Epitokes observed for both sexes; eggs up to 185 µm in diameter. | Not described. | Schizometamery. | Northern Europe; Sea of Japan;?California | Caullery and Mesnil (1898) (as *D. concharum* Form B); Dehorne (1933) (as *D. caulleryi*); Gibson and Clark (1976) and (Gibson 1978, 1979, 1981) (as *D. caulleryi*); George and Petersen (1991); Petersen (1999). |
| *Dodecaceria coralii* | Short headed sperm; eggs 70–90 µm; no epitokes observed. | Not reported. | Not observed. | NE USA | Martin (1933), Petersen (1999) |
| *Dodecaceria* cf. *diceria* | Epitokes observed; sex not stated. | Not reported. | Binary fission, | N. North Sea | Gibson (1996) (as *D. diceria*) |
| *Dodecaceria fewkesi* | Male and female colonies separate; eggs 100 µm; sperm observed, not measured. | Fertilized eggs develop into swimming trochophore; ciliated lecithotrophic larvae developed in culture to ca. 4 segments. | Binary and multiple fission. Colonies of a single sex suggesting clones from original regenerates. | Eastern Pacific: Canada to California | Berkeley and Berkeley (1954) |
| *Dodecaceria fimbriata* | Epitokes observed for both sexes; details of gametes not reported. | Not reported. | Fragmentation of anterior and posterior ends and single segments; each fragment regenerates entire worms. | Eastern Canada; New England | Martin (1933), Gibson (1979) |
| *Dodecaceria meridiana* | Atokous; large eggs observed. | Not reported. | Fragmentation, with regeneration of whole worm. | Argentina, Mar del Plata | Elias and Rivero (2009a) |
| *Dodecaceria pulchra* | Parthenogenic; females with eggs present, size not reported. | Not reported. | Fragmentation of anterior and posterior ends and single segments; each fragment regenerates entire worms. | South Africa | Gibson (1977), Petersen (1999) |

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**Tab. 7.3.1.5.1** (Continued)

| Species | Sexual reproduction | Larval development | Asexual reproduction | Locality | References |
|---|---|---|---|---|---|
| *Dodecaceria saxicola* | Epitokes observed with red eyespots present; males with short-headed sperm; eggs of females not measured. | Not reported. | Not observed. | Mediterranean | Petersen (1999) |
| *Dodecaceria sextentaculata* | Epitokes not observed; eggs 85 µm. | Not reported. | Fragmentation. | Naples, Italy | Petersen (1999) |

Some observations on reproduction are scattered among different references under various names. This list is followed by the few accounts of descriptions of *Dodecaceria* larvae. Other details of asexual reproduction by species of *Dodecaceria* are provided in the "Asexual Reproduction" section, which follows. More comments on the validity and synonymy of names currently applied to *Dodecaceria* species are presented in the taxonomic section for the genus.

**D) Larvae of *Dodecaceria***

Despite the numerous accounts of epitokes and gametes in different species of *Dodecaceria*, the larvae of only two species have ever been described: (1) *D. ater* as *D. concharum* Form A (Caullery and Mesnil 1898, Marcel 1962, Gibson 1977) and (2) *D. fewkesi* (Berkeley and Berkeley 1954). The few observations of larvae for *Dodecaceria* species is likely due to the prolonged periods of asexual fragmentation and regeneration by several species, coupled with a short period where spawning takes place. Larvae of *D. berkeleyorum* illustrated by Knox (1971) are clearly larvae of a spionid, *Polydora* sp., most likely from egg capsules that occurred in the same shells.

The larval development of *D. ater* (as *D. concharum* Form A), a parthenogenic species, was described by Caullery and Mesnil (1898) and commented on by Marcel (1962) and Gibson (1977) (both as *D. concharum*). Development was viviparous with the young developing in the body of the female. Larvae included a trochophore stage with a broad prototroch; these larvae progressed to a three-segment stage with apical cilia, prototroch, telotroch, and a pair of red eyespots. The three-segment larvae were released from the body of the female and subsequently lost their cilia but developed chaetae on segment 2. Posthatching development was followed by Caullery and Mesnil (1898) until juveniles with 16–17 chaetigerous segments were present with a pair of tentacles and the first branchiae. Marcel (1962) observed the same sequence of development but also found deformed and defective embryos and larvae. Gibson (1981) related this to the parthenogenetic nature of the species and that by lacking males; progeny carry only one set of chromosomes and a reduced genetic diversity.

Berkeley and Berkeley (1954) collected colonies of *D. fewkesi* and transferred them to aquaria with running seawater in the laboratory. Individual colonies were either all males or all females as products of asexual reproduction. Recently spawned eggs were pink in color (Fig. 7.3.1.5.8 K) and found in groups on the bottom of the aquaria. Fertilized eggs were obtained in June and July 1952. Fertilized eggs were recognized due to the elevation of a thick fertilization membrane and inward contraction of the cytoplasm. The authors observed cleavage to about 32 cells, after which the cells were too dense to count. After 18 hours, the embryos were rotating ciliated spheres (Fig. 7.3.1.5.8 L). Trochophores with a prototroch, telotroch, and apical cilia were observed after 24 hours (Fig. 7.3.1.5.8 M). These trochophores remained near the bottom of the culture vessels but would swim if disturbed. The authors were able to trace the development through one, three, and four segment stages (Fig. 7.3.1.5.8 N–P); the latter was reached after 100 hours. Their illustrations clearly show the development of an akrotroch anterior to the prototroch, a neurotroch along the venter, and a partial band of cilia on the second segment, which may correspond to a gastrotroch. Chaetae and tentacles were not present. These early larvae were not cultured further but appear to be similar in morphological development to those of *C. tentaculata* and *C. moorei* of Wilson (1936) and Blake (1975).

**Asexual reproduction.** Asexual reproduction is widespread among cirratulids and, according to Petersen (1999), is likely to occur in many species in addition to sexual reproduction. In cirratulids, architomy, where one individual

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divides into single segments or groups of segments, each of which regenerates the missing parts and can become a new individual, is the only form of asexual reproduction; paratomy, or stolonization as occurs in some syllids, spionids, and ctenodrilids, has never been observed in cirratulids.

Petersen (1999) defined the terms that have been used to describe the different types of fission that have been reported in cirratulids: (1) binary and trinary fission, or division into two to three parts; (2) fragmentation into variable number of fragments, each consisting of several segments; and (3) schizometamery, where larger middle segments break off singly and each in turn regenerates a new individual. Additionally, the remaining anterior and posterior sections may also regenerate missing parts.

Asexual reproduction has been observed in species of *Caulleriella*, *Cirratulus*, *Cirriformia*, *Protocirrineris,* and *Timarete* but is best known in the genus *Dodecaceria*. George and Petersen (1991) reviewed the species of *Zeppelina*, a genus of Ctenodrilidae, whose species were based entirely on regenerating specimens; they referred most species of *Zeppelina* to *Dodecaceria*. The type species *Zeppelina monostyla* was referred to *D. concharum*. Other species of *Zeppelina* were referred to species of *Kirkegaardia* (as *Monticellina*) and *Raphidrilus*.

Caullery and Mesnil (1898) reported anterior and posterior fragmentations in *Caulleriella viridis* (as *Heterocirrus viridis*). Petersen (1999) noted that other more common species of *Caulleriella* have not exhibited evidence of asexual reproduction. She did, however, illustrate a specimen of *Caulleriella* sp. from Naples regenerating both anterior end posterior ends. Asexual fragmentation was observed by McIntosh (1915) and by Curtis (1977) for *Cirratulus incertus* (as *C. cirratus*). This species is reported to reproduce asexually for one or more years before becoming epitokous (Petersen 1999). Small species of *Protocirrineris* and *Timarete* are believed to also reproduce asexually (Petersen 1999). Gherardi *et al*. (2007) identified asexual reproduction in *T. filigera* from the Adriatic Sea with specimens regenerating both anterior and posterior ends; females were also observed for the first time. Individuals of *T. punctata* have also been collected showing anterior and posterior ends in the process of regeneration (Petersen 1999: Fig. 3 M; Çinar 2007). Magalhães *et al*. (2014) found numerous specimens of *T. caribous* regenerating anterior and posterior ends and suggested that asexual reproduction was taking place (Fig. 7.3.1.5.11 A–C). Similar observations were made for *T. ceciliae* and *T. oculata* in the same study. An example of anterior regeneration of *T. hawaiensis* is shown in Fig. 7.3.1.5.11 D. Weidhase *et al*. (2014a) as part of an experimental study of anterior regeneration of *C.* cf. *cirratus* assumed that their species was reproducing asexually because epitokes were not observed while the population was increasing at a rapid rate.

Asexual reproduction is widespread in species of *Dodecaceria* and is an integral part of the life cycle for several species. The best known example is *D. concharum*, first reported by Caullery and Mesnil (1898) and subsequently described and illustrated by Dehorne (1933) (as *D. caulleryi*). This species undergoes schizometamery. At the initiation of asexual reproduction, the middle body segments become individually swollen and assume a spherical form and with the string of segments appearing moniliform or beadlike in appearance (Fig. 7.3.1.5.10 A). These individual rounded segments then separate from one another and accumulate in the burrow or tube of the adult. Each of these separated "generator" segments then begins to regenerate anterior and posterior ends while also developing a functional gut through the new regenerating worms. This developing "worm" has narrow anterior and posterior ends growing from the much larger original "generator" segment. This temporary worm fragments into its three components: (1) the former anterior end regenerates a posterior end (Fig. 7.3.1.5.10 E); (2) the former posterior end regenerates an anterior end (Fig. 7.3.1.5.10 D); and (3) the original "generator" segment repeats the process by regenerating new anterior and posterior ends. The new individuals produced from the first set of anterior and posterior ends are called schizozooids. The original generator appears to be limited to producing two sets of schizozooids before expending its internal metabolic reserves. Thus, the individual segments that become enlarged and break off from the parent worm are each capable of producing four new worms. The diagram in Fig. 7.3.1.5.10 B illustrates the pattern of schizometamery. To date, *D. concharum* (as *D. caulleryi* in some accounts) is the only species known with this full capacity. Martin (1933) suggested that *D. fimbriata* had the capacity to produce at least two individuals from a single segment. It is likely that other species of *Dodecaceria* will also be found with this capability.

**Regeneration**

Cirratulids, like many polychaetes, have well-developed regenerative abilities. In conjunction with widespread evidence of architomic fragmentation in the reproduction of many cirratulids, others are capable of regenerating anterior and posterior ends after ablation. Most observations are, however, casual and based on specimens collected having evidence of anterior (Fig. 7.3.1.5.11 D, E) or posterior regeneration. An example of abnormal regeneration

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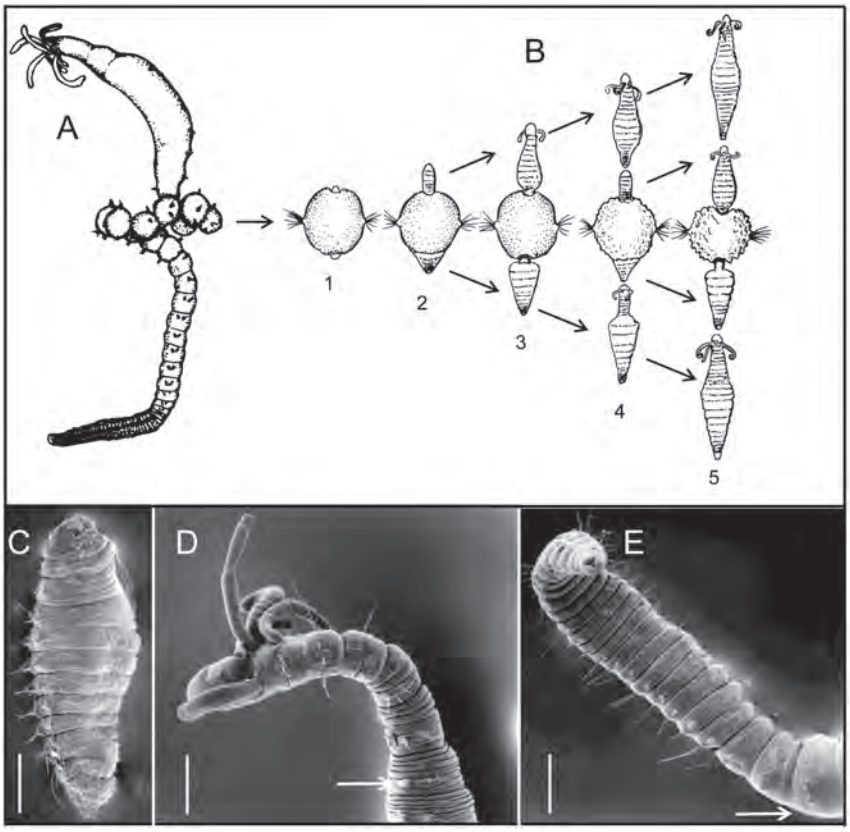


**Fig. 7.3.1.5.10:** Asexual reproduction in *Dodecaceria*. A, B, diagrammatic representation of schizometamery in *Dodecaceria*: A, adult worm with enlarged middle segments prior to fragmentation; B, diagram showing the sequence of regeneration and additional fragmentation from original budded segment. C–E, *Dodecaceria concharum* (Denmark): C, regenerating fragment; D, regenerating anterior end, arrow denotes original adult segments; E, regenerating posterior end, arrow denotes original adult segments. Scale bars: A, B, not to scale; C, 100 µm; D, E, 200 µm. A, B, New illustrations based on Martin (1933) and Dehorne (1933); C, E, original scanning electron microscopy images by the late Mary E. Petersen; D, modified after George and Petersen (1991).

is shown in Fig. 7.3.1.5.11 E. While experimental studies of annelid regeneration are numerous, there have been few based on cirratulids. Two recent studies by Weidhase *et al.* (2014a, 2015) are directed toward evaluation of regeneration of external and internal morphology after ablation of anterior ends and anterior/posterior ends of two multitentaculate species: *Cirratulus* cf. *cirratus* and *Timarete* cf. *punctata*, respectively.

For *Cirratulus* cf. *cirratus*, Weidhase *et al.* (2014a) identified five sequential phases of anterior regeneration: (1) wound closure, (2) blastema formation, (3) blastema differentiation, (4) resegmentation, and (5) growth. These authors determined that all ablated anterior segments were regenerated simultaneously. The nervous system regenerates earlier than the musculature does and initially forms an unusual tripartite loop-like structure that later becomes the circumesophageal connectives that connect to the brain. The authors note that the loop-like structure has not been previously reported for annelids. The longitudinal and circular musculature regenerates independently within the blastema. Complete regeneration of the anterior nervous system and musculature, together with anterior segmentation, takes about 22 days.

For *Timarete* cf. *punctata*, Weidhase *et al.* (2015) evaluated both anterior and posterior regeneration processes. These authors determined that for anterior regeneration, unlike *C.* cf. *cirratus*, *T.* cf. *punctata* initially regenerates the prostomium and peristomium, followed by three of the ablated segments with the three remaining ones added sequentially. Anterior regeneration of the nervous system and musculature is similar to that of *C.* cf. *cirratus*. In posterior regeneration, the blastema formation is followed by patterning into a new pygidium and development of a segmental growth zone with new segments added sequentially.

## Biology and ecology

### Habitat

Cirratulids are most common in soft sediments, where they often dominate benthic assemblages. In nearshore habitats such as Massachusetts Bay, the bitentaculates *Tharyx acutus* and *Kirkegaardia baptisteae* (as *Monticellina baptisteae*) are among the most abundant species (Hilbig and Blake 2000). In deep-water assemblages off California (2,200–3,200 m), two species of *Chaetozone*, *C. brunnea* and *Chaetozone allanotai*, were among the top 10 species identified after 10 years of monitoring (Blake *et al.* 2009).

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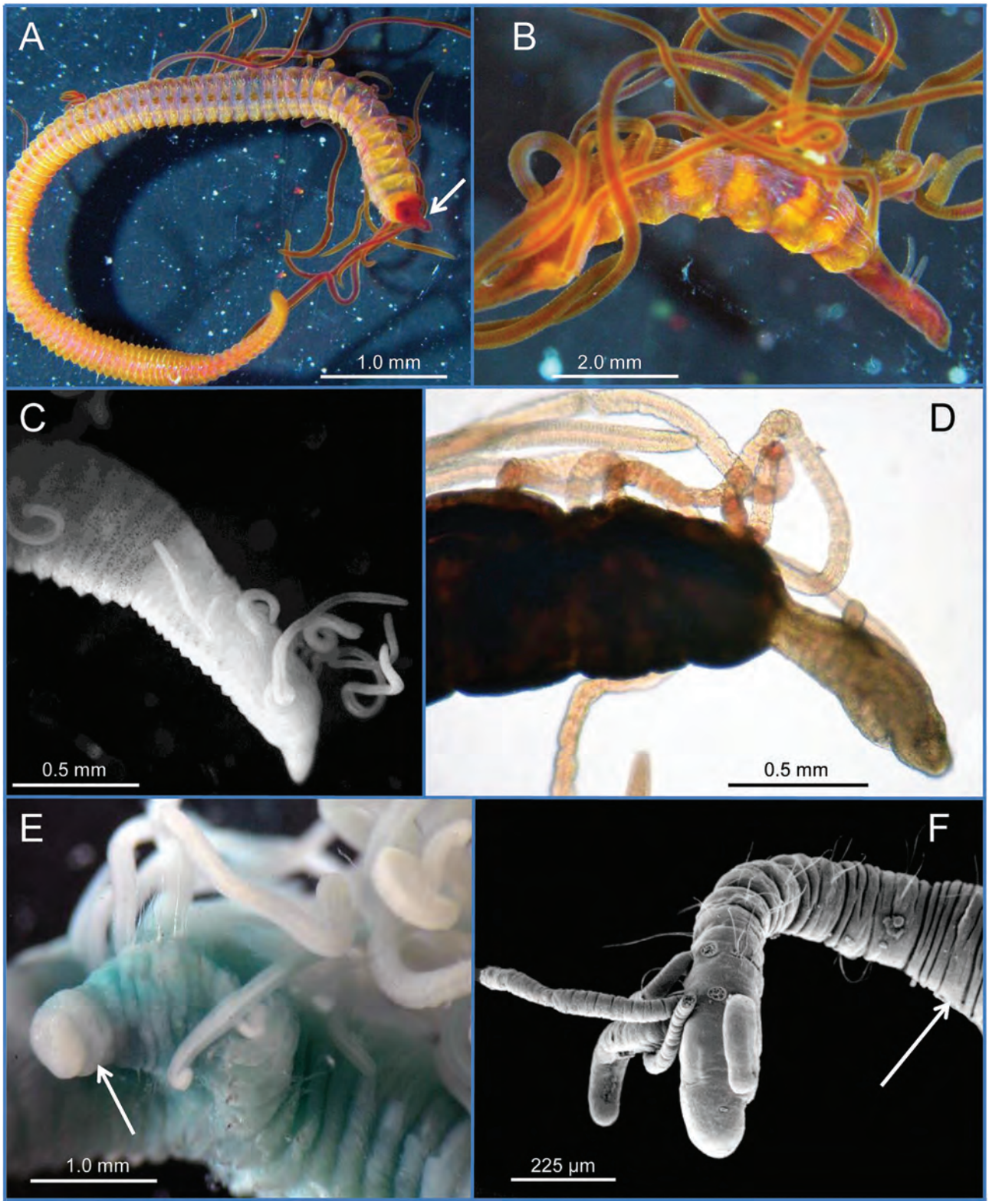


**Fig. 7.3.1.5.11:** Regeneration in Cirratulidae. A, Recently fragmented posterior end of *Timarete caribous* showing the formation of blastema prior to regeneration. B, Midbody fragment regenerating anterior and posterior ends, including the first pair of branchiae in *T. caribous*. C, Completely regenerated anterior end of *T. caribous* showing lighter color. D, Detail of a recently regenerated anterior end of *Timarete hawaiensis*. E, Anomalous regeneration of an anterior end on midbody segments of *T. caribous*. F, Anterior regeneration in *Dodecaceria concharum* (Denmark). A–E, Original; F, original scanning electron microscopy iamge by the late Mary E. Petersen (unpublished).

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Multitentaculate cirratulids live in a variety of habitats including muds and sands, crevices in rocks, or associated with live substrata such as bryozoans, sponges, algae, or oyster shells. *Cirriformia moorei* is one of the most common polychaetes found in the low intertidal zone of mudflats of estuaries and embayments in central California (Blake 1996). The species is often associated with beds of the eelgrass, *Zostera marina*. The worms respire through branchiae that they project into clear overlying water. The red branchiae are clearly visible on the surface of the sediment at the bottom of tidal pools. The species feeds at or just below the sediment-water interface (Ronan 1977). When populations of the species are dense, the numerous branchiae look like hundreds of red worms on the surface (Blake 1996). In contrast, *C. spirabrancha, Timarete perbranchiata*, and *Protocirrineris socialis*, also from intertidal zones of central California, are found in rocky habitats that are exposed to wave action. These worms typically live in crevices or pockets of sand among the rocks (Blake 1996).

*Dodecaceria* species bore into mollusk shells and calcareous rocks (Fig. 7.3.1.5.2 F). Evans (1969), working with shell borers of the sea scallop *Placopecten magellanicus* in Newfoundland, observed that *D. fimbriata* (as *D. concharum*) settle as juveniles into previously bored burrows of *Polydora* species (Spionidae) in mollusk shells and proceeded to enlarge them and as such they are secondary borers (Evans 1969). Another species, *Dodecaceria fewkesi,* from the NE Pacific, constructs hardened rocklike structures that are riddled with tubes containing the worms and are attached to boulders and other hard surfaces in the intertidal zone along the open coast. The hardened colonies are gray in color, and after storms, these are sometimes found on beaches (Berkeley and Berkeley 1954). Exactly how these worms construct such rocks is not known, but it is apparent that some sort of cementing material is used.

The tube walls of *Dodecaceria* species are composed of thin calcareous lamellae with a prismatic ultrastructure (Vinn 2009). This type of biomineralization is nearly identical to that of calcareous cirratulid tubes from the Oligocene and most similar to that of extant sabellids.

### Burrowing and feeding

The literature on burrowing and feeding of Cirratulidae and other polychaetes has recently been thoroughly reviewed by Jumars *et al.* (2015). Cirratulids that live in soft sediments are typically burrowers that lie just beneath the surface of the sediment where they extend their branchiae into the overlying water for aeration and/or extend their dorsal tentacles or tentacular cirri to collect sediment or other particles for ingestion.

**Burrowing.** Cirratulids that live in defined tubes or mud balls or are shell borers like *Dodecaceria* are likely sedentary or sessile once their burrows are established (Jumars *et al.* 2015). Other cirratulids that form temporary burrows and actively move as part of their mode of life are considered mobile or discretely mobile burrowers *sensu* Jumars *et al.* (2015).

Some of the bitentaculate cirratulid species form tubes, composed of mucus and silt. These tubes sometimes have a tattered or tessellated appearance as in several species of *Kirkegaardia* (Blake 2016). The presence of openings for anterior dorsal tentacles and groups of segmental branchiae along the length of hardened tessellated tubes of *Kirkegaardia neotesselata* from off Massachusetts (Blake 2016) suggests that the worms lie in a horizontal or oblique position relative to the surface so that these filaments can easily extend on to the surficial sediment and overlying water. The tube of one undescribed species of *Aphelochaeta* from deep water off northern California was observed to have a spiraled shape (Blake unpublished).

The mudball worms of the genus *Kirkegaardia* have an enlarged prechaetigerous and thoracic region that together provides a bulbous anterior end that might be used to block or plug the tube opening; the rest of their body is narrow and twisted and conforms to the shape of their burrows with the mud ball habitat (Jumars 1975, Blake 2016).

The concept and mechanics of crack propagation as a method of burrowing through muddy cohesive sediments by benthic polychaetes was first introduced by Dorgan *et al.* (2005) as part of observations of burrowing by *Nereis virens*. Simply put, the worm everts its pharynx and exerts a force normal to the direction of movement, which causes a crack to open in the sediment and propagate, releasing energy. The worm then retracts the pharynx and moves forward into the crack before repeating the process. In this manner, the worm is able to move into and through otherwise cohesive sediments.

The mechanics and energetics of burrowing and crack propagation in the large cirratulid *Cirriformia moorei* from California have been elegantly described by Che and Dorgan (2010a,b) and Dorgan *et al.* (2011). Instead of everting a proboscis, *C. moorei* opens cracks using its hydrostatic skeleton to exert a dorso-ventral force against the walls of the burrow to open and extend a crack and then move the body forward (Che and Dorgan 2010a). These authors identified four distinct burrowing phases as the

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worms move through sediment. First, the worm stretches and elongates its anterior body toward the initial crack. The worm then thickens its body and continues to move forward, extending the crack to a maximal distance. After this, the anterior end thickens to its maximum, causing the dorsoventral stress to be amplified at the tip of the crack so that it extends laterally. The sequence ends with a peristaltic wave that moves the rest of the body forward into the crack. Repetition of this process moves the worm forward through the sediment. In a subsequent paper, Che and Dorgan (2010b) determined that *C. moorei* is also able to burrow backward with its posterior end using a similar mechanism of crack propagation and the same phases of burrowing. Pauses in burrowing were observed in aquaria at times when the worms extended their branchiae to the surface (Jumars *et al.* 2015).

There are little data on how deep in the sediments cirratulids burrow. For multitentaculates, Ronan (1977) determined that *C. moorei* (as *C. spirabrancha*) form burrows in fine grained sediment up to 22 cm deep that ranged from straight vertical shafts to J-shaped burrows having one or more apertures. The worms actively moved within their burrows from place to place but had periods where they were apparently sessile.

Some data on burrow depth for smaller bitentaculate cirratulids from deep-water habitats off North Carolina were collected by Blake (1994). Two bitentaculate cirratulid species, *Kirkegaardia baptisteae* (as *M. baptisteae*) and *Tharyx kirkegaardi*, were investigated. *K. baptisteae* was more or less uniformly distributed over the 0–10 cm depth interval. In contrast, *T. kirkegaardi* was mostly concentrated in the 0–2 cm fraction and effectively absent deeper than 5 cm. Both species were common along the 500–1,000 m isobaths in fine sediments. Specimens of the abyssal cirratulid, *Kirkegaardia fragilis*, were collected from the 0–2 cm depth interval at the Clarian-Clipperton Fracture Zone in 4,800 m in the Central Pacific Ocean (Blake 2016). These results, although scanty, suggest that different deep-water species of bitentaculate cirratulids occupy different depth intervals in the sediment perhaps related to their size. Both *K. baptisteae* and *K. fragilis* have been found to inhabit thin, tattered tubes with openings through which the tentacles and branchiae project (Blake 2016).

**Feeding.** Feeding in cirratulids has been reviewed by Jumars *et al.* (2015). Cirratulids have been observed to feed both at the surface and as subsurface feeders within their burrows. Observations of feeding with multitentaculates have mainly been with species of *Cirriformia* and *Timarete*. Several investigators have observed species to burrow, pause, and then extend their tentacles into the sediment-water interface to collect particles and transport them to the mouth: Ronan (1977) for *C. moorei* as *Cirriformia spirabrancha*, Shull and Yasuda (2001) for *Cirriformia grandis*, and Pardo and Amaral (2004) for *Timarete* sp. as *Cirriformia filigera*. In Tomales Bay, California, the numerous red-colored tentacles and branchiae of *C. moorei* are seen in shallow tidal pools on mudflats, where the species occurs in dense populations (Blake 1996). Jumars *et al.* (2015) suggested that *C. moorei*, while burrowing, backed up and extended its tentacles anteriorly into the newly opened crack to feed on particles on the burrow walls.

Ronan (1977) observed that *C. moorei* (as *C. spirabrancha*) feeds by collecting mineral grains and detritus with its tentacles that were observed to actively probe both at and below the sediment-water interface. Ronan (1977) determined that the worms selected for small encrusted mineral grains. These were prevalent in the stomach, and he classified this species as a surface and subsurface omnivore. Other items in the stomach included fecal pellets, pieces of *Zostera*, small metazoans, and diatoms. The worms were observed to reverse themselves in their burrows and defecate from the burrow aperture. These worms also play an important role in bioturbation by moving particles from the surface to depth as part of their burrowing and feeding activities.

Experiments on particle size selection by cirratulids have shown that there is a clear preference for particles smaller than 30 μm in diameter; Whitlatch (1980) observed the digestive tracts of *Chaetozone* sp. and *Tharyx* sp. with a predominance of particles of 10 μm and 30 μm, respectively; the multitentaculate species *C. grandis* was observed with guts having particles of the size range 16–32 μm (Shull and Yasuda 2001). Magalhães (2015) experimentally offered three different size ranges of glass beads (0–20 μm, 40–70 μm, and 70–110 μm) to 20 specimens of each *T. hawaiensis* and *A. honouliuli* and observed that both species significantly favored the collection of the smallest glass bead size range (0–20 μm).

Shull and Yasuda (2001) observed *C. grandis* from Boston Harbor in burrows oriented in an oblique position with tentacles and branchiae extended to the surface. Feeding by the worms results in a net downward movement of particles that are directed toward the mouth. Glass bead selection using a range of sizes was tested in experiments by Shull and Yasuda (2001), who were able to demonstrate particle selection of the smallest sizes for *C. grandis*. In nature, most cirratulids ingest sediment and detrital particles (Jumars *et al.* 2015). There have been few observations on feeding by bitentaculates, but Farke

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(1979), working with *Aphelochaeta* sp. (as *Tharyx marioni*), noted that specimens were active burrowers and depleted surficial sediments of fine particles, suggesting a feeding behavior similar that of *C. grandis*.

Pardo and Amaral (2004) observed feeding behavior of a species of *Timarete* (identified as *C. filigera*) collected from beaches in Brazil. The worms are positioned below the surface in a J-shaped temporary burrow. The tentacular filaments and some branchiae were extended on to the surface. When feeding, up to four tentacular filaments extended over the sediment surface, where food particles were captured and carried along the ciliated grooves of each tentacle directly to the mouth. The authors noted that only fine sand particles were selected and carried to the mouth; larger particles were retained on the surface. Gut contents included Foraminifera, Radiolaria, diatoms, and plant detritus, in addition to sand grains. A more extensive study of food resources available to a species of *Timarete* and other polychaetes on sandy beaches of SE Brazil was carried out by Checon *et al*. (2016). *Timarete* sp. (as *C. filigera*) was identified as a surface deposit feeder. Gut contents of 198 specimens of *Timarete* sp. were examined, 26% of which were filled. The majority of food items consisted of a wide variety of diatoms (82.7%), the majority of which were benthic species. The remainder of food items in the gut consisted of detritus, Foraminifera, and Radiolaria. The identity of *Timarete* species from Brazil was recently evaluated, and the occurrence of *T. filigera* was not confirmed for the southeast Atlantic; instead, the species *T. punctata*, *Timarete oculata*, *T. ceciliae*, and *T. caribous* are present in Brazil (Magalhães *et al*. 2014). Based on the collection localities of the material studied by Pardo and Amaral (2004) and Checon *et al*. (2016), these authors could be dealing with either *T. oculata* or *T. caribous*, but examination of the studied material would be necessary to confirm the identification.

These studies of large species of *Cirriformia* and *Timarete* having numerous tentacular filaments that extend to the surface and are used in feeding indicate that smaller particles are selected and that benthic diatoms are likely the primary source of organic material. Feeding in other cirratulids, however, is poorly known. Taboada *et al*. (2012) suggested that *Cirratulus balaenophilus,* which occupies cavities in whale bones, might feed on bacterial surface films.

Farke (1979) made observations on feeding in *Tharyx killariensis* (as *T. marioni fide* Petersen 1999). When feeding, the worms stayed in burrows and extended their two dorsal tentacles to the surface, where they collected sediment particles, debris, and diatoms and transported them to the mouth along the ciliated channel on the ventral side of the tentacle. These same particles were observed in the gut. Blake (1994) as part of the study of depth intervals of deep-water infauna off North Carolina (see previous discussion), suggested that *K. baptisteae* (as *Monticellina*) and *T. kirkegaardi* were subsurface deposit feeders.

*Dodecaceria* species extend their tentacles outside their burrows and collect sediment particles from the surface of shale rock (Gibson 1992). The particles became attached to mucous in each ciliated groove; the worms drew their tentacles across their head in a wiping action and transferred the mucous with particles to the mouth. Large and small particles were collected in the same manner, and Gibson (1992) indicated that they were nonselective.

As reviewed in the "Morphology" section, cirratulids, in general, have simple tubular guts that require less through time to process their food resource (Penry and Jumars 1990). This is would be an advantage for species that occur in sediments with high organic enrichment.

## Ecology

Christie (1985) studied the reproductive cycles of three British populations of *Chaetozone setosa* and discovered evidence of a sibling-species complex. Morphological differences in the structure and arrangement of dorsal tentacles, branchiae, and arrangement of the spines on posterior segments were documented. Although gametogenesis and larval development were similar in the three populations, the timing of gametocyte development and spawning differed on a seasonal basis. The differences in morphology and breeding support Christie's (1985) suspicion that the three populations represent three distinct species. One of these siblings was later described as a new species, *Chaetozone christiei* by Chambers (2000).

Hily (1987), working in the Bay of Brest, on *Chaetozone* sp. (as *C. setosa*), focused his investigations on the relationship of the species to gradients of organic enrichment. This effort was thus ecological rather than reproductive in its approach. The species was found to prefer fine sediments. The highest population densities (10,000 individuals $m^{-2}$) were found in sediments with high organic content. This species of *Chaetozone* was found as an opportunistic early-stage colonizer in sediments that had been defaunated by dredging, anoxic events, and oil spills.

High densities of cirratulids recorded in some sediments such as reported by Hily (1987) are likely due to colonization by settling larvae or direct development of postlarvae of species having direct development. However, Consentino (2013), after conducting a series of colonization experiments with *C. bioculata* and *C. tentaculata*,

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concluded that migration of adults from adjacent sites to newly disturbed source sediments was an active process for these two species.

For the most part, cirratulids have rarely been considered as alien or invasive species although several species have been reported widely. Many of these records for species such as *C. setosa* and *C. cirratus* have and will eventually be found to refer to other species. *Chaetozone corona*, a species originally described from southern California by Berkeley and Berkeley (1941) and now known to range south to Mexico and Costa Rica (Blake 1996, Dean and Blake 2007), however, does appear to be invading new geographic areas, including Brazil (Omena and Creed 2004), the eastern Mediterranean Sea and Sea of Marmara (Çinar and Ergen 2007, Çinar *et al*. 2011, Simboura *et al*. 2010), and the Atlantic coast of France (Le Garrec *et al*. 2017). *Chaetozone corona* is a distinctive species in having neuropodial acicular spines from chaetiger 1, a dome-shaped peristomial dorsal crest, prominent prostomial eyespots, and a distinctive methyl green staining pattern and as such is easy to identify and distinguish from local congeners and other species of *Chaetozone* globally. The mechanism of dispersal is not known but is likely via ballast water (Le Garrec *et al*. 2017). Other cirratulids with wide distributions include *T. punctata* and *T. caribous*, both described from the Caribbean Sea. *Timarete caribous* may have invaded the Mediterranean via ballast water as most collected specimens were found in artificial substrates near large commercial harbors (Çinar 2009), and *T. punctata* may have migrated from the Red Sea to the Mediterranean through the Suez Canal (Çinar 2007).

Paiva *et al*. (2016) investigated the phylogeographic patterns of two mitochondrial markers (COI and 16S) of five populations of *T. punctata* from the central Pacific, Caribbean Sea, and South Atlantic. The authors found evidence of two cryptic species within *T. punctata*: one collected from a single site in northern Brazil and a second one present in the southern Atlantic, Caribbean, and central Pacific. This wide geographic distribution was suggested by the authors to be human mediated because of the very low level of genetic diversity and high frequency of shared haplotypes along the sampled sites.

Cirratulids have sometimes been assessed with regard to uptake of metals and other contaminants. One of the most intriguing results was the discovery of Gibbs *et al*. (1983) that *Aphelochaeta* sp. (as *T. marioni*) was able to accumulate high levels of arsenic in its tissues with no apparent toxic effect. The species was found to concentrate arsenic at levels that were far above those found in ambient sediments. Milanovich *et al*. (1976) determined that *C. moorei* (as *C. spirabrancha*) was able to accumulate high levels of copper in its tissues with no toxic effect, providing the accumulation was gradual.

The ability of some cirratulids to concentrate metals in their tissues may account for the interesting observation of Yoshiyama and Darling (1982) that *T. perbranchiata* (as *Cirriformia luxuriosa*) was distasteful to intertidal fishes in central California rocky habitats. These authors suggested that the polychaete possessed a predation-deterring chemical in its tentacles (=branchiae). Judd (1968) had earlier found a similar predation-deterring substance (an amine) in *C. moorei* (as *C. spirabrancha*) in sand flats in central California.

Kicklighter *et al*. (2003) and Barsby *et al*. (2003) identified 2-alkylpyrrole sulfamates as the chemicals responsible for unpalatability of exposed tentacles of *C. tentaculata* as prey of the bluehead wrasse in southern Florida. In contrast, the bodies of the worms that were in their burrows and not exposed were found to be palatable when offered separately to the fish. These observations are the first confirmed chemical defense system in a marine annelid. Meredith *et al*. (2007) found a similar evidence of chemical defense in the Caribbean species *T. punctata*.

## Phylogeny and taxonomy

### Phylogeny – Morphological Studies

Cirratulids have long been known as a dumping group for many polychaete genera of unknown phylogenetic placement (Day 1967). Genera now belonging to Acrocirridae (*Acrocirrus* and *Macrochaeta*), Cossuridae (*Cossura*), and Ctenodrilidae (*Raricirrus*) were originally placed within Cirratulidae. This had clearly made Cirratulidae a polyphyletic assemblage, and it is very likely that it is still paraphyletic with the current exclusion of Ctenodrilidae (Halt *et al*. 2006).

**Relationships with other polychaete families.** The clade Cirratuliformia was named in Rouse and Pleijel (2001) and included seven families based on the results of a morphological phylogeny by Rouse and Fauchald (1997): Acrocirridae, Cirratulidae, Flabelligeridae, Ctenodrilidae, Fauveliopsidae, Poeobiidae (now within Flabelligeridae), and Sternaspidae. The synapomorphies of the clade composed of Acrocirridae, Flabelligeridae, and Cirratulidae included the presence of similar parapodial rami, anterior excretory pair of nephridia, and posterior gonoducts (Rouse and Fauchald 1997). Rouse and Pleijel (2003), in a preliminary morphology-based cladistics analysis of

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Cirratuliformia, included 17 ingroup taxa, and only three of them represented Cirratulidae genera (*Aphelochaeta*, *Dodecaceria*, and *Cirratulus*). They found clear evidence that Cirratulidae, Ctenodrilidae, Fauveliopsidae, and Flabelligeridae were not monophyletic. Osborn and Rouse (2011) considered the Cirratuliformia to be composed of only Cirratulidae, Acrocirridae, and Flabelligeridae, and some distinctive features present in these three families are the paired palps, large anterior nephridia, chlorocruorin as blood pigment, and the presence of a heart body (Banse 1969, Rouse and Fauchald 1997).

Salazar-Vallejo *et al.* (2008) provided a morphology-based phylogeny of flabelligerids and included several cirratuliform genera. The analysis recovered the clade Cirratulidae-*Sternaspis* with a synapomorphy related to the median notochaetae arrangement in a tuft, transversal to the body axis. They discussed that this novel finding was probably due to the limited taxonomic sampling, combined to a lack of information on some critical features. The Cirratulidae-*Sternaspis* clade was recovered as sister to fauveliopsids rather than to the ctenodrilid clade.

On the basis of ultrastructural studies of nuchal organs, eyespots, and palps in *Aphelochaeta*, *Cirriformia*, *Dodecaceria*, and *Chaetozone*, Brauer (2014) proposed two hypotheses for the relationships within Cirratuliformia. The first hypothesis considered a monophyletic Cirratulidae with the thickening of the cuticle above the nuchal organs and the segmental origin of tentacles as apomorphies. Cirratulids would then be composed of two clades (i.e., bitentaculate and multitentaculate) with the multitentaculates having as synapomorphy the multiplication of tentacles. According to the author, Flabelligeridae-Acrocirridae, *Sternaspis*, and Fauveliopsidae would be the sister group to cirratulids or to a clade composed of Cirratulidae-Ctenodrilidae. The synapomorphies of this sister group would be the presence of integument with papillae and a retractable head. The second hypothesis considered Cirratulidae as paraphyletic and the bitentaculate clade appearing as a basal group to the cirratuliforms. Brauer (2014) argued that the first hypothesis would represent the most likely scenario because the segmental tentacles are homologous in bitentaculate and multitentaculate cirratulids.

**Relationships of the genera.** Fauchald and Rouse (1997) did not identify any evidence of monophyly in the Cirratulidae. The authors discussed that all cirratulids have paired grooved tentacles as juveniles and that in some taxa such as *Cirratulus*, the tentacles are organized longitudinally, forming two dense patches, and appear a few segments back on a projection of the peristomial fold. Weidhase *et al.* (2015) verified that in regenerating the anterior fragments of *T.* cf. *punctata*, one pair of tentacles was regenerated first on chaetiger 3 and then duplicated on chaetiger 4. The presence of more than a pair of tentacles was hypothesized to be a derived state; therefore, the ancestral condition in cirratulids would be having a pair of palps, a similar character state to acrocirrids. The tentacles in bitentaculate and multitentaculate cirratulids were recently found to be segmental rather than peristomial in origin (Brauer 2014). Blake (1996) organized the cirratulid genera into three groups based on the number of palps and habitat (i.e., multitentaculate, bitentaculate of soft substrates, and bitentaculate of hard substrates).

In a preliminary effort to test the monophyly of cirratulids using morphological data, Magalhães (2015) selected 37 morphological, anatomical, and reproductive characters for all 11 cirratulid genera and four ctenodrilid genera. The Cirratulidae was recovered as monophyletic if all ctenodrilid genera were included within it. Three clades were recognized: a multitentaculate clade composed of five cirratulid genera having two groups of tentacles, a bitentaculate clade composed of five cirratulid genera having a pair of dorsal tentacles, and a third clade composed of all ctenodrilid genera and *Dodecaceria*.

The anterior branchiae in *Dodecaceria* were suggested to be homologous to the branchiae in Acrocirridae and Flabelligeridae (Rouse and Pleijel 2001). The similarities between *Acrocirrus* and *Dodecaceria* also include the presence of paired palps and anterior pairs of segmental organs. This has led to the suggestion that acrocirrids could be sister group to cirratulids (Rouse and Pleijel 2003), but recent morphology-based phylogenies of acrocirrids and flabelligerids have confirmed their sister-group relationships (Salazar-Vallejo *et al.* 2008, Osborn and Rouse 2011).

The relationships between cirratulid and ctenodrilid genera have a long, confusing, and clearly unresolved history. Mesnil and Caullery (1897) argued that ctenodrilids shared many similarities with Cirratulidae, and subsequent authors have considered them either as synonymous (e.g., Fauvel 1927, Day 1967) or distinct (e.g., Fauchald 1977, Hartmann-Schröder 1996) families. Rouse and Pleijel (2003), in a strict consensus tree based on 15 morphological characters, recovered *Dodecaceria*, *Cirratulus*, *Aphelochaeta*, *Ctenodrilus*, and *Raphidrilus* in a polytomy with acrocirrids, fauveliopsids, and flabelligerids. Magalhães (2015) found *Dodecaceria* to be a sister taxon to *Raphidrilus* and related to *Ctenodrilus* and *Aphropharynx*,

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which would together form the ctenodrilid-*Dodecaceria* clade. However, no supporting synapomorphies were detected.

**Phylogeny – Molecular Studies**

The first available cirratulid sequence was 18S rRNA of *D. concharum* published in Winnepenninckx *et al.* (1998). This sequence was subsequently used aiming to resolve broader annelid relationships (e.g., McHugh 2000, Struck *et al.* 2002). Ctenodrilidae have constantly been placed within Cirratulidae (Bleidorn *et al.* 2003a, Rouse and Pleijel 2003) and Sternaspidae, and Fauveliopsidae have been suggested to be sister groups rather than placed within Cirratuliformia (Struck *et al.* 2007, Rousset *et al.* 2007). Molecular data have suggested that Cirratuliformia as originally proposed are not monophyletic unless if composed of only Cirratulidae, Acrocirridae, and Flabelligeridae (e.g., Colgan *et al.* 2006, Osborn and Rouse 2011, Struck *et al.* 2011).

**Relationships with other polychaete families.** Zrzavý *et al.* (2009), in a combined dataset using morphology and six molecular partitions (i.e., 18S, 28S, and 16S rRNA, EF1α, H3, COI), found support for the Cirratuliformia, but with the inclusion of the Histriobdellidae, although the latter is most likely part of Eunicida (Struck *et al.* 2006). Osborn and Rouse (2011) compiled 29 morphological characters and provided molecular data (i.e., 18S rDNA, 28S rDNA, COI, and CytB, 16S) to investigate the relationships between acrocirrids and flabelligerids, using sequences of four cirratulid genera and the ctenodrilid *Ctenodrilus serratus* as outgroups. In a combined molecular and morphological analysis, the authors found a well-supported clade including all cirratulid genera and *Ctenodrilus*. The majority consensus trees from Bayesian analyses using isolated genes recovered different tree topologies of the cirratulid clade. Trees built with 18S and 28S data showed a multitentaculate clade with *Cirratulus* and *Cirriformia*, whereas a clade containing bitentaculate genera was not observed in any isolated gene tree.

Phylogenomic data suggest the placement of cirratulids within Sedentaria, a clade comprised of Clitellata and Echiura, as well as the polychaete taxa Capitellidae, Opheliidae, Arenicolidae, Terebelliformia, Cirratuliformia, Siboglinidae, Serpulidae, and Spionidae (Struck *et al.* 2011). Struck *et al.* (2015) recovered the clade Cirratuliformia/Siboglinidae as sister to Sabellida/Spionida, whereas Weigert *et al.* (2014) placed Cirratuliformia/Siboglinidae as sister to Orbiniidae. The exact placement of Cirratuliformia within Sedentaria is still questionable and it will depend on the number of taxa and characters used in the phylogenomic analyses (Weigert *et al.* 2014, Struck *et al.* 2015, Weigert and Bleidorn 2016).

**Relationships of the genera.** The affiliation of *Ctenodrilus* and *Dodecaceria* is unquestionable. Bleidorn *et al.* (2003b) included 18S rDNA sequence data for *C. parva*, Cirratulidae sp., *D. ater*, *D. concharum*, and *C. serratus* and found out that *Ctenodrilus* appeared as ingroup of *Dodecaceria* (99% maximum parsimony bootstrap). This relationship has been further investigated with additional genes and species of *Dodecaceria* and *Ctenodrilus*. Using only 16S rDNA, *C. serratus* was nested within *Dodecaceria* (Weidhase *et al.* 2016). Rousset *et al.* (2006) provided a combined analysis of 16S, 18S, particular 28S, and histone H3 genes and recovered *C. serratus* as a sister group to two species of *Dodecaceria*. Weidhase *et al.* (2016) provided a larger COI sampling of *Dodecaceria* and found a sister group relationship. Magalhães *et al.* (2016) found that for 16S, *Ctenodrilus* was nested within *Dodecaceria*, whereas for COI, both genera were resolved as reciprocal monophyletic groups.

Preliminary results shown in Weidhase *et al.* (2014b) include the most extensive taxa and sequence sampling (16S, 18S rRNA, and CO1), providing the first picture of the molecular phylogeny of cirratulids. Most genera were recovered as not monophyletic. The monophyly in *Cirratulus* would be achieved with the exclusion of *C. balaenophilus*, and *Dodecaceria* would be monophyletic if *Ctenodrilus* was included within it (Weidhase *et al.* 2014b). Fauchald and Rouse (1997) assumed that the presence of a pair of palps is a plesiomorphic condition in cirratulids, and according to the results of Weidhase *et al.* (2014b), the paired palps would have been lost at least twice in the clades *Dodecaceria*-*Ctenodrilus* and *Raricirrus*-multitentaculate cirratulid genera and the presence of multiple pairs of tentacles appeared up to four times. The loss of tentacles in *Ctenodrilus* and *Raricirrus* was explained as a result of progenetic evolution (Weidhase *et al.* 2014b, 2016), and at least for *Ctenodrilus*, there are several morphological affinities with juvenile *Dodecaceria* (George and Petersen 1991, Bleidorn *et al.* 2003b, Weidhase *et al.* 2016).

## Taxonomy

### Phylogeny and taxonomy

### Family Cirratulidae Ryckholt, 1851

**Diagnosis:** Body elongate with numerous short segments; not divided into distinct regions, but anterior

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and/or posterior segments sometimes expanded and crowded. Prostomium narrow and conical or broad and wedge shaped, without appendages; eyespots present or absent; paired nuchal organs present dorsolateral. Peristomium achaetous, smooth or with two or more distinct annuli. Grooved dorsal tentacles arise as a single pair or as multiple groups of filaments on posterior margin of peristomium or on one or more anterior chaetigerous segments. Branchiae long, filamentous, usually occurring over numerous segments. Parapodia biramous with rudimentary podial lobes. Chaetae simple, including capillaries, acicular spines or bidentate hooks. Pygidium a simple lobe sometimes with sub-anal disk, or terminal cirri. Pharynx ventral, unarmed. Sexual and asexual reproduction may occur.

**Remarks:** The concept of the Cirratulidae has changed in recent decades as several groups were removed to separate families (e.g., Ctenodrilidae, Cossuridae, and Acrocirridae). The remaining genera are roughly divided into three groups: (1) the multitentaculate genera (e.g., *Cirratulus, Cirriformia, Fauvelicirratulus, Protocirrineris*, and *Timarete*), (2) the bitentaculate soft-substrate genera (e.g., *Aphelochaeta, Caulleriella, Chaetozone, Kirkegaardia*, and *Tharyx*), and (3) the bitentaculate hard-substrate genera (*Dodecaceria*). The ctenodrilids most likely are an ingroup taxon of the Cirratulidae closely related to *Dodecaceria* based on recent phylogenetic studies (see previous discussion) but are treated as a separate family in this handbook (see chapter 7.3.1.4).

The multitentaculate cirratulids have tentacular filaments located on 1–2(3) segments on *Cirratulus*, *Cirriformia*, and *Fauvelicirratulus* and on several segments on *Timarete* and *Protocirrineris*. The greater majority of multitentaculate species have been known for a long time, with only four new species described since 2000. However, several species such as *C. cirratus, T. filigera, T. punctata,* and others have been widely reported, and it is likely that additional species will be identified from these widespread records with further study.

The bitentaculate sediment dwelling species have been the subject of numerous taxonomic papers over the past 25 years, with more than half of the known species being described. This is largely due to extensive exploration of offshore and deep-water habitats where they dominate. In contrast, the multitentaculate species are largely known from intertidal and nearshore habitats.

The *Dodecaceria* complex was reviewed by Gibson (1978, 1979), George and Petersen (1991), and Petersen (1999). The systematics of this genus is closely tied to an understanding of the patterns of asexual reproduction that characterize the group. Failure to consider the mode of reproduction to led the erroneous descriptions of many species of *Dodecaceria* as species of *Zeppelina* (George and Petersen, 1991).

**Descriptions of species:** The following section documents 278 species in 11 genera that are currently considered as valid. Each genus is defined and relevant references are indicated. A few synonyms are indicated, as well as a limited number of new combinations within the genera. The geographic location of each species is also noted, as well as its depth range where easily available. Among the species and genera, 87 species and five genera of multitentaculate cirratulids are listed; 171 species and five genera of bitentaculate sediment dwelling species are listed; and 20 species of the calcareous inhabiting species of *Dodecaceria* are listed.

### A) Multitentaculate genera

The cirratulids having groups of tentacular filaments instead of paired dorsal tentacles are more or less organized into five genera: *Cirratulus* Lamarck, 1801, *Cirriformia* Hartman, 1936, *Fauvelicirratulus* Çinar & Petersen, 2011, *Protocirrineris* Czerniavsky, 1881, and *Timarete* Kinberg, 1866. These genera are separated from one another on the basis of the kind(s) of chaetae present, the segment(s) from which the tentacular filaments arise, the segment(s) from which the first branchiae arise, the position of the branchiae in relation to the notopodial tori, and the shape of the prostomium. The first three genera and the fifth have a more or less wedge-shaped prostomium, capillary chaetae, and acicular spines (aciculars); the fourth has a bluntly conical to wedge-shaped prostomium and only capillary chaetae. *Cirratulus* has numerous tentacular filaments arising from a single segment on either side of the dorsum, usually the posterior edge of the peristomium or one of chaetigers 1–7, and branchiae beginning on the same segment as the tentacular filaments, whereas *Cirriformia* usually has tentacular filaments over one to two anterior chaetigers and branchiae usually begin on chaetiger 1 in adults (may be present on the posterior edge of the peristomium in juveniles). *Timarete* and *Protocirrineris* have tentacular filaments arising over two or more anterior segments, with the first branchiae typically arising from the posterior edge of the peristomium in *Timarete* and usually from the same segment as the first tentacular filaments in *Protocirrineris* (but sometimes branchiae occur on a few segments anterior to the tentacular filaments). Moreover, some species of *Timarete* may have multiple branchiae on some segments. The newly described genus *Fauvelicirratulus* is similar to *Cirratulus* in relation to the segmental origin of tentacular and branchial filaments on chaetiger 1 but differs by the presence of multiple pairs of branchial

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filaments per segment and presence of long, straight spines instead of the short acicular ones.

Unlike the bitentaculate cirratulids where numerous new species have been reported over the past 25 years, only 9 of the 87 known species of multitentaculates (<10%) have been newly described during the same year period. This is probably because the majority of multitentaculates are more or less limited to shallower near-coastal habitats and are easier to collect, whereas the sediment-dwelling bitentaculates not only occur in nearshore habitats but are also one of the major components in offshore shelf and slope habitats that have only been extensively explored in recent years. Recent systematic literature on multitentaculates includes Blake (1996), Çinar (2007), Elias and Rivero (2009b), Çinar and Petersen (2011), Magalhães and Bailey-Brock (2010, 2013b), Taboada *et al*. (2012), Magalhães *et al*. (2014), and Lezzi *et al*. (2016).

**Genus *Cirratulus* Lamarck, 1801**

38 species

**Type species:** *Lumbricus cirratus* Müller, 1776

**Diagnosis** (modified after Blake 1996): Prostomium wedge shaped, elongate or blunt, usually with transverse rows of eyespots (Fig. 7.3.1.5.12 A, F); peristomium with two to three annulations. Two or more grooved tentacular filaments arising from a single anterior segment. Branchiae first present from same chaetiger as tentacular filaments, occurring singly, and continuing over most of body to posterior end. Parapodial rami well separated (Fig. 7.3.1.5.12 B). Chaetae including capillaries and acicular spines (Fig. 7.3.1.5.12 C–E and I–K). Pygidium with one or more lobes surrounding anus (Fig. 7.3.1.5.12 H).

**Remarks:** Taxonomic problems with the genus *Cirratulus* include identifications of *C. cirratus* from widespread areas. Upon study, these will likely be found to consist of multiple species. Blake (1996) evaluated records of *C. cirratus* and others in the NE Pacific and was able to separate five species, one new, none of which agreed with species he had seen from the North Atlantic. Similar reviews of *Cirratulus* records are needed elsewhere.

The following list of 38 species is in need of review because many names are old and largely unreported in recent literature. Some of these older taxa are not included; readers are referred to Hartman (1959) for additional information. Type specimens of numerous species of *Cirratulus* were examined by the late Mary E. Petersen. We are currently evaluating her notes and drawings of these.

1. *Cirratulus abyssorum* Hansen, 1878. Indeterminate, perhaps *Aphelochaeta*.
2. *Cirratulus africanus* Gravier, 1906. Indeterminate, juvenile.
3. *Cirratulus annamensis* Gallardo, 1968. Bay of Nha Trang, South Vietnam, 10–20 m.
4. *Cirratulus assimilis* McIntosh, 1885. North Atlantic, off Bermuda.
5. *Cirratulus balaenophilus* Taboada, Doner, Blake & Avila, 2012. Antarctic Peninsula associated with whale bones.
6. *Cirratulus branchioculatus* Khlebovitch, 1959. Kuril Islands.
7. *Cirratulus caudatus* Levinsen, 1893. Denmark.
   [*Cirratulus dunmanni* McIntosh, 1911]. Ireland, Dunmanus Bay. *Fide* M.E. Petersen, unpublished records.
8. *Cirratulus cingulatus* Johnson, 1901. NE Pacific, British Columbia and Washington, intertidal. *Fide* Blake (1996).
9. *Cirratulus cirratus* (O.F. Müller, 1776). Western Europe. Widely reported globally; these likely other species.
   [*Cirratulus flavescens* Johnston, 1825]. *Fide* Hartman (1959).
   [*Cirratulus blainvillei* Grube, 1855]. *Fide* Hartman (1959).
   [*Cirratulus fuscescens* Johnston, 1825]. *Fide* Hartman (1959).
   [*Cirratulus medusa* Johnston, 1833]. *Fide* Hartman 1959.
10. *Cirratulus concinnus* Ehlers, 1908. Off South Africa. See Day (1967).
11. *Cirratulus dillonensis* Blake, 1996. NE Pacific, northern California, intertidal in rocks.
12. *Cirratulus elongatus* Treadwell, 1901. Panama. Indeterminable according to Hartman (1959).
13. *Cirratulus exuberans* Chamberlin, 1919. Panama.
14. *Cirratulus flavescens* Grube, 1872. Unresolved Homonym. *Fide* Hartman (1959).
15. *Cirratulus gibbosus* Moore, 1903. Japan, off Honshu Island.
16. *Cirratulus gilchristi* Day, 1961. Off South Africa.
17. *Cirratulus glandularis* (Langerhans, 1884). North Atlantic, Madeira.
18. *Cirratulus hedgpethi* Hartman, 1951. Gulf of Mexico, Texas coast, intertidal.
19. *Cirratulus incertus* McIntosh, 1916. UK, England.
20. *Cirratulus jucundus* Kinberg, 1866. Strait of Magellan.
21. *Cirratulus longicephalus* Imajima, 1964. Japan.
22. *Cirratulus megalus* Chamberlin, 1919. SE Pacific, off Peru, 980 m.
23. *Cirratulus miniatus* Schmarda, 1861. Jamaica.
24. *Cirratulus multioculatus* (Hartman, 1961). NE Pacific, central California, from rocks 40–168 m. *Fide* Blake (1996).

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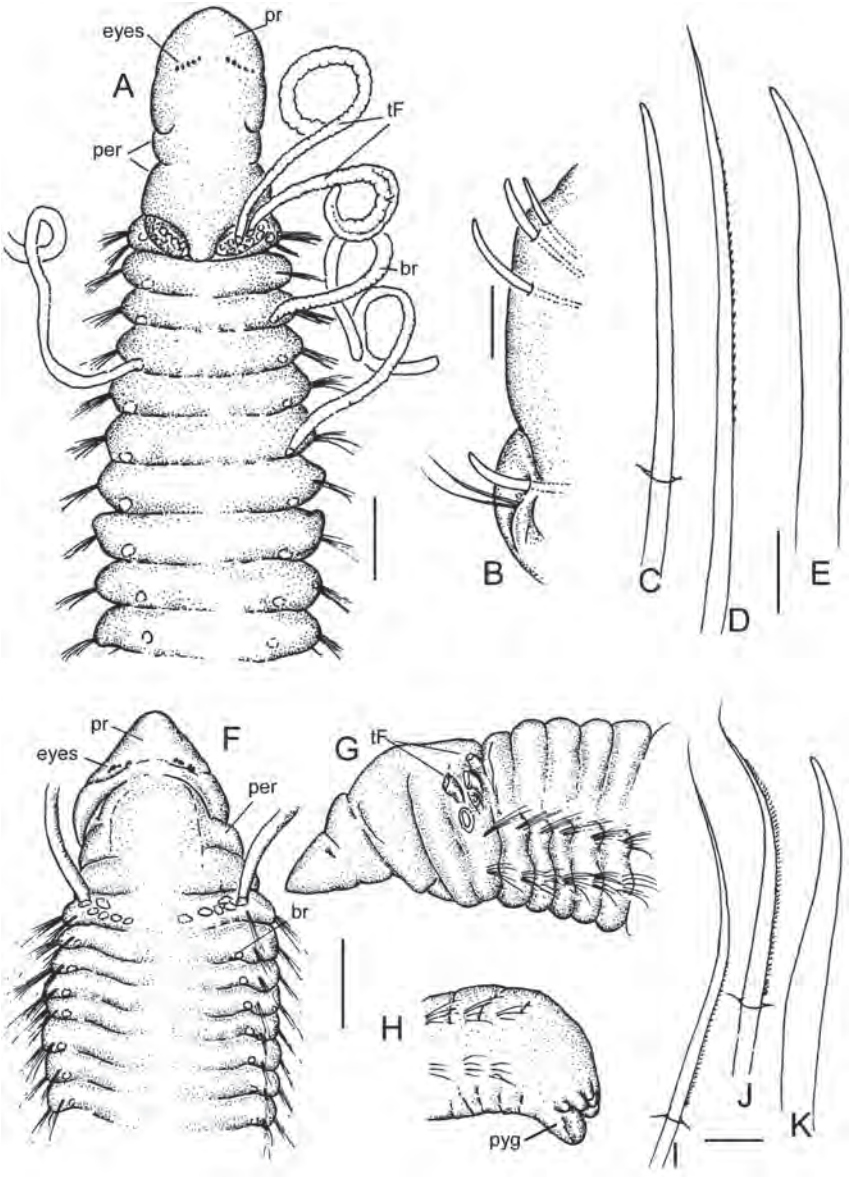


**Fig. 7.3.1.5.12:** Examples of species of *Cirratulus*. A–E, *Cirratulus dillonensis*: A, anterior end, dorsal view; B, posterior parapodium, anterior view; C, notoacicular spine; D, capillary notochaeta from anterior chaetiger; E, neuroacicular spine. F–K, *Cirratulus spectabilis*: F, anterior end, dorsal view; G, same, lateral view; H, posterior end, lateral view; I–J, anterior notochaetae; K, neuroacicular spine. Scale bars: A, 500 µm; B, 100 µm; F–H, 200 µm; C, D, 20 µm; I–K, 10 µm. All after Blake (1996).

25. *Cirratulus multifiligera* (Hartmann-Schröder, 1962). NE Pacific, Chile, Punta Arenas, Strait of Magellan. As *Dodecaceria*.
26. *Cirratulus obscurus* Quatrefages, 1865. Brazil.
27. *Cirratulus pallidus* Treadwell, 1931. Caribbean Sea, Jamaica, Montego Bay.
28. *Cirratulus parafiliformis* Hartmann-Schröder & Rosenfeldt, 1989. South Shetland Islands, King George Island, 265 m.
29. *Cirratulus parvus* Moore, 1907. Massachusetts, low water.
30. *Cirratulus patagonicus* (Kinberg, 1866). South America, Patagonia.
31. *Cirratulus revillagigedoensis* Rioja, 1961. NE Pacific, Mexico.
32. *Cirratulus robustus* Johnson, 1901. NE Pacific, Washington to California, intertidal to shelf depths.
33. *Cirratulus serratus* Hartmann-Schröder, 1974. SE Atlantic, Namibia.
34. *Cirratulus sinincolens* Chamberlin, 1919. Gulf of California, deep water.
35. *Cirratulus spectabilis* (Kinberg, 1866). NE Pacific, British Columbia to central California, intertidal in rocks. [*Chaetozone berkeleyorum* Banse & Hobson, 1968]. *Fide* Blake (1996).
36. *Cirratulus tumbesiensis* Carrasco, 1977. SE Pacific, Chile, Bahia de Concepcion, shallow subtidal.
37. *Cirratulus wladislavi* Buzhinskaja, 1985. Sakhalin Island, shelf depths.
38. *Cirratulus zebuensis* McIntosh, 1885. Philippine Islands.

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**Genus *Cirriformia* Hartman, 1936**

23 species

**Type species:** *Terebella tentaculata* Montagu, 1808

**Diagnosis** (after Blake 1996): Prostomium elongate or blunt, usually without eyespots (Fig. 7.3.1.5.13 A, G, and H); peristomium with two to three annulations. Grooved tentacular filaments limited to one to three anterior segments, arising between chaetigers 2 and 7 (Fig. 7.3.1.5.13 A, G, and H). Branchiae occurring singly, usually first present from chaetiger 1, arising close to notopodia throughout, not becoming dorsal in middle body segments and not forming dorsolateral branchial bulges. Parapodial rami well separated (Fig. 7.3.1.5.13 B–D and I). Chaetae including capillaries and acicular spines (Fig. 7.3.1.5.13 E–F and J–K).

**Remarks:** Blake (1996) reviewed *Cirriformia* from the northeastern Pacific and determined that two species, widely reported from California and the eastern Pacific in general, *C. luxuriosa* and *C. spirabrancha*, were misconstrued. After examining type materials, *C. luxuriosa* was referred to the genus *Timarete* and *C. spirabrancha*, which was considered a common intertidal mud flat species, was redefined and found to be more or less restricted to rocky habitats; specimens previously referred to *C. spirabrancha* and occurring in mud flats were redescribed as a new species, *C. moorei*. Magalhães *et al.* (2014) recently reviewed species of *Cirriformia* from Brazil and described two new species. These results suggest that examination of type materials and new collections of *Cirriformia* will identify additional species and clarify older records. At present, 23 species are known.

1. *Cirriformia afer* (Ehlers, 1908). West Africa, Angola, Nigeria subtidal.
2. *Cirriformia capensis* (Schmarda, 1861). West Africa, South Africa, intertidal to low water. *Fide* Day (1967).
3. *Cirriformia capillaris* (Verrill, 1900). Bermuda. *Fide* Hartman (1959).
4. *Cirriformia capixabensis* Magalhães *et al.*, 2014. Southern Brazil, intertidal.
5. *Cirriformia chefooensis* (Grube, 1877). China.
6. *Cirriformia chicoi* Magalhães *et al.*, 2014. Brazil, intertidal.
7. *Cirriformia chrysodermoides* Pillai, 1965. Philippines, Luzon, Dupan City, intertidal.
8. *Cirriformia comosa* (von Marenzeller, 1870). Southern Japan.
9. *Cirriformia crassicollis* (Kinberg, 1866). Hawaiian Islands, intertidal. *Fide* Magalhães and Bailey-Brock (2010).
10. *Cirriformia grandis* (Verrill, 1873). W North Atlantic, New England, intertidal to subtidal.
11. *Cirriformia limnoricola* Kirkegaard & Santhakumaran, 1967. India, Bombay Harbor, in wood in *Limnoria* tunnels.
12. *Cirriformia maryae* Silva, 1961. Indian Ocean, Sri Lanka.
13. *Cirriformia moorei* Blake, 1996. NE Pacific, California embayments, intertidal to 25 m.
14. *Cirriformia multicirratus* (Treadwell, 1936). Bermuda.
15. *Cirriformia multitentaculata* Hartmann-Schröder & Rosenfeldt, 1989. Antarctic Peninsula, Joinville Island, 133 m.
16. *Cirriformia pentatentaculata* Hartmann-Schröder & Rosenfeldt, 1989. Antarctic Peninsula, 50 m.
17. *Cirriformia pygidia* (Treadwell, 1936). North Atlantic, Bermuda. *Fide* Magalhães *et al.* (2014).
18. *Cirriformia quetalmahuensis* Hartmann-Schröder, 1962. SE Pacific, southern Chile
19. *Cirriformia saxatilis* (Gravier, 1906). Red Sea.
20. *Cirriformia semicincta* (Ehlers, 1905). Hawaiian Islands; widespread in Indo-Pacific. *Fide* Hartman (1966).
21. *Cirriformia spirabrancha* (Moore, 1904). NE Pacific, California, intertidal in rocks. *Fide* Blake (1996).
22. *Cirriformia tentaculata* (Montagu, 1808). NE Atlantic, widespread in Western Europe; UK; North Sea; Mediterranean Sea; Black Sea; intertidal to low water.
23. *Cirriformia tortugaensis* (Augener, 1922). W North Atlantic, southern Florida.

**Genus *Fauvelicirratulus* Çinar & Petersen, 2011**

one species

**Type species:** *Cirratulus dollfusi* Fauvel, 1928. Designated by Çinar and Petersen (2011).

**Diagnosis** (modified after Çinar and Petersen 2011): Body large, dorso-ventrally flattened. Prostomium broadly rounded anteriorly; eyespots absent. Tentacular filaments emerging on dorso-lateral area of chaetiger 1, arranged in two dense groups of about 25 filaments each in a circular pattern. Branchial filaments multiple in anterior segments, arising as one to two filaments from each of four to eight raised notopodial lobes on parapodia of anterior and middle segments, with lobes reducing in size and fewer or no branchiae posteriorly. Two types of chaetae: long, fine capillaries, and straight, tapering spines each in noto- and neuropodia; spines from about chaetiger 12.

**Remarks:** *Cirratulus dollfusi* Fauvel, 1928 was redescribed based on new material from the Sea of Marmara and compared with the holotype from Morocco (Çinar and Petersen 2011). The species is a multitentaculate and multibranchiate cirratulid; it differs from all other known cirratulid genera in chaetal morphology and the manner with which the multiple branchial filaments arise from the notopodia. Chaetae are of two types: numerous long, fine capillaries in both rami throughout, also two to four shorter, wider, finely tapering spines in noto- and

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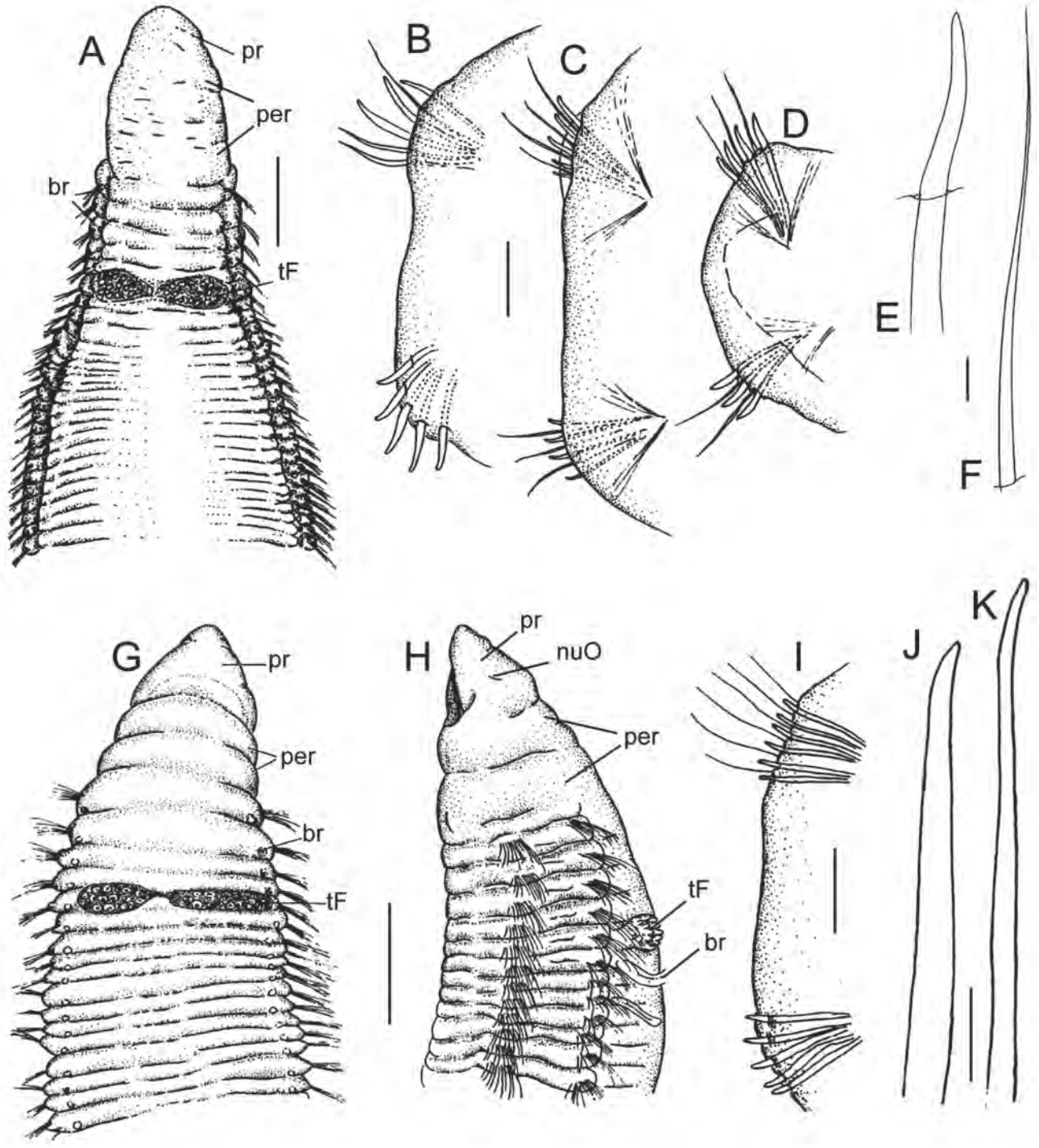


**Fig. 7.3.1.5.13: Examples of species of *Cirriformia*.** A–F, *Cirriformia moorei*: A, anterior end, dorsal view; B, parapodium 100; C, parapodium 150; D, parapodium 300; E, neuroacicular spine; F, capillary notochaeta. G–K, *Cirriformia luxuriosa*: G, anterior end, dorsal view; H, same, left lateral view; I, parapodium 150; J, neuroacicular spine; K, notoacicular spine. Scale bars: A, G, H, 2 mm; B–D, 300 µm; E, F, 25 µm; I, 200 µm; J, K, 20 µm. All after Blake (1996).

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neuropodia. There are no slightly flattened sigmoid spines, typical of most *Cirratulus* species. Very short, slender grooved tentacles arise in a small circular group on either side of chaetiger 1. Branchial filaments are multiple, arising as one to two filaments from each of four to eight raised notopodial lobes on anterior and middle parapodia; branchiae are few or absent posteriorly. No other cirratulid genera appear to have straight, tapering spines plus so many fine capillaries. However, *Cirratulus hedgpethi* Hartman from the Gulf of Mexico does have straight spines, but the numbers and nature of the branchiae were not reported by Hartman (1951). The species has not been reported since the original report and the type has not been reexamined to determine if this species might belong to *Fauvelicirratulus*.

1. *Fauvelicirratulus dollfusi* (Fauvel, 1928). Mediterranean Sea; Sea of Marmara; SW Atlantic off West Africa; subtidal to 450 m. *Fide* Çinar and Petersen (2011).

**Genus *Protocirrineris* Czerniavsky, 1881**

10 species

**Type species:** *Cirratulus tenuisetis* Grube, 1860, designated by Hartman, 1959

**Diagnosis** (after Blake 1996): Prostomium bluntly conical to wedge shaped, with or without eyespots (Fig. 7.3.1.5.14 A, B, and D). Body nearly round in cross-section, with segments distinct. Grooved tentacular filaments few, arising singly or in paired groups on several anterior chaetigers following chaetiger 1 (Fig. 7.3.1.5.14 A, B, and D). Branchiae occurring singly, first present from segments with tentacular filaments, sometimes on more anterior chaetigers. Chaetae all capillaries. Pygidium a simple lobe (Fig. 7.3.1.5.14 C).

**Remarks:** The genus *Protocirrineris* was resurrected by Petersen (1991) and defined by Blake (1996). The genus is characterized having the tentacular filaments arranged in rows within paired groups and by having only capillary chaetae throughout. Blake (1996) described both adults and juveniles of a new species, *P. socialis*. The juveniles had only a single longitudinal row of tentacular filaments over chaetigers 5–7, whereas large adults had three rows of tentacular filaments over chaetigers 7–9. The type species, *P tenuisetis* from the Adriatic is poorly known as *P. chrysoderma* from the Gulf of Naples, Italy. Both species need redescription and comparison with recently described species such as *P. puramentorum* from the Ionian Sea, Italy. To date 10 species are known.

1. *Protocirrineris angelicollatio* Elías & Rivero, 2009. SW Atlantic, Argentina, Mar del Plata, intertidal on limestone.
2. *Protocirrineris antarctica* (Monro, 1930). Subantarctic locations: South Georgia; Kerguelen Islands; subtidal to 310 m. New combination.
3. *Protocirrineris chrysoderma* (Claparède, 1868). Gulf of Naples, Italy. *Fide* Lezzi *et al.* (2016).
   [*Cirrineris fuscus* Grube, 1872]. *Fide* Lezzi *et al.* (2016).
4. *Protocirrineris indicus* (Day, 1973). India, intertidal. New combination.
5. *Protocirrineris mascaratus* Magalhães & Bailey-Brock, 2013b. Hawaii, off Oahu, low water to 100 m; Maui, 30 m.
6. *Protocirrineris nuchalis* (Ehlers, 1907). New Zealand, North Island. *Fide* Magalhães and Bailey-Brock (2013b).
7. *Protocirrineris purgamentorum* Lezzi, Çinar & Giangrande, 2016. Ionian Sea, Italy, shallow subtidal.
8. *Protocirrineris socialis* Blake, 1996. NE Pacific, California, intertidal to shallow subtidal, in rocks.
9. *Protocirrineris violacea* (Westheide, 1981). Galápagos Islands, Santa Cruz Island, subtidal. New combination.
10. *Protocirrineris tenuisetis* Grube, 1860. Adriatic.

**Genus *Timarete* Kinberg, 1866**

15 species

**Type species:** *Cirratulus anchylochaetus* Schmarda, 1861, by original designation

**Synonym:** *Ambo* Chamberlin, 1918.

**Type species:** *Ambo perbranchiata* Chamberlin, 1918, p. 177, by priority

**Diagnosis** (after Blake 1996): Prostomium wedge shaped, rounded on anterior margin (Fig. 7.3.1.5.15 A, C), with or without eyespots. Body nearly round in cross-section, with segments distinct. Grooved tentacular filaments arising in two groups from the dorsum of two or more anterior chaetigers, posterior to chaetiger 1. Branchiae occurring singly or with several filaments per parapodium, individual branchial filaments robust, becoming more dorsal in origin in middle body segments (Fig. 7.3.1.5.15 B, D), with each sometimes forming a dorsolateral bulge over notopodium. Chaetae including capillaries and acicular spines (Fig. 7.3.1.5.15 B, D).

**Remarks:** Species of *Timarete* are distinguished from other multitentaculate genera mainly in the arrangement and number of branchiae per segment. Anterior branchiae arise dorsal to and near the notochaetae. In middle and posterior segments, the branchiae shift dorsally to a location higher on the body wall and come to arise near the dorsal midline. Multiple branchiae may also arise from a single location, and groups of these sometimes form a bulge dorsal to the notopodia. Most species of *Timarete* were described more than 50 years ago. Blake (1996) reviewed species of *Timarete* from California and Magalhães *et al.* (2014) reviewed the genus from Brazil. These works resulted in several

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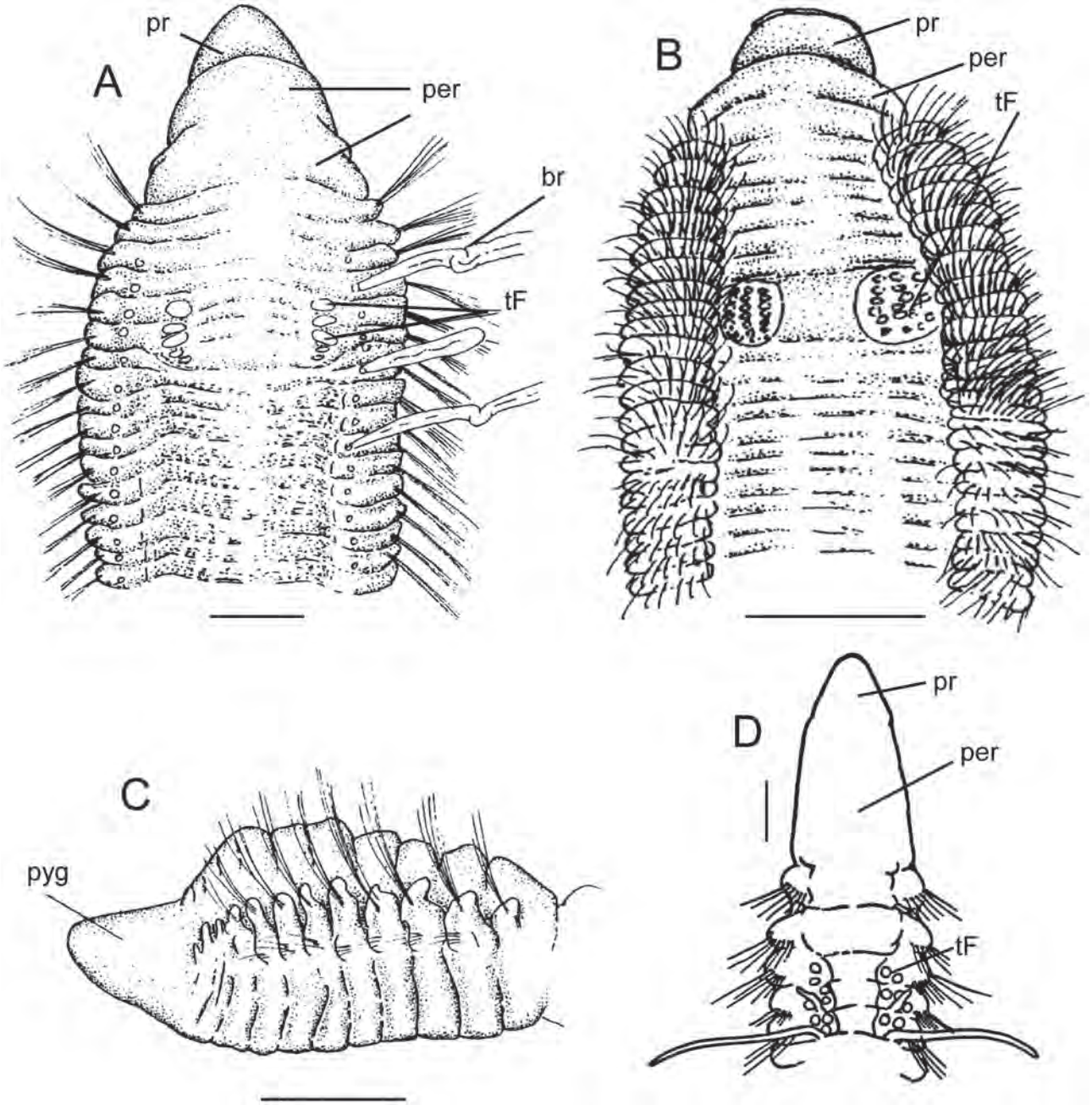


**Fig. 7.3.1.5.14:** Examples of *Protocirrineris*. A–C, *Protocirrineris socialis*: A, anterior end of small paratype, dorsal view; B, anterior end, dorsal view of holotype; C, posterior end, right lateral view of paratype. D, *Protocirrineris antarctica*, dorsal view. Scale bars: A, C, 200 µm; B, 1.0 mm; D, 1 mm. A–C, After Blake (1996): D, after Monro (1930).

species being redescribed and synonyms clarified; one new species from Brazil was described. Fifteen species are known.

1. *Timarete anchylochaeta* (Schmarda, 1861). New Zealand; various records from Europe are likely erroneous. *Fide* Çinar (2007).
2. *Timarete caribous* (Grube, 1859). Caribbean Sea and Gulf of Mexico, Florida to Colombia; Brazil, intertidal to shallow subtidal; Mediterranean Sea (introduced). Magalhães *et al.* (2014).
   [*Cirriformia melanacantha* (Grube, 1872)]. Brazil. *Fide* Magalhães *et al.* (2014).
   [*Cirratulus danielseni* Hansen, 1882]. Brazil. *Fide* Hartman (1959) and Magalhães *et al.* (2014).
3. *Timarete ceciliae* Magalhães, Seixas, Paiva & Elias, 2014. Brazil, intertidal.

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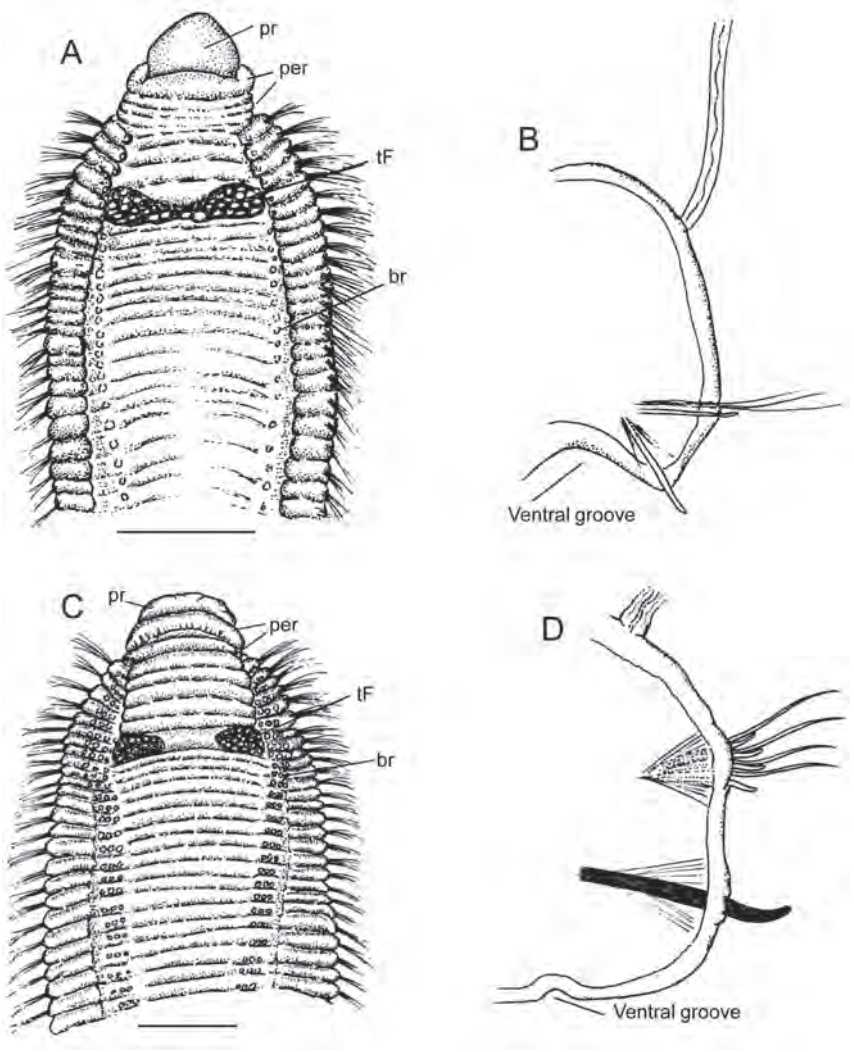


**Fig. 7.3.1.5.15:** Examples of species of *Timarete*. A, B, *Timarete luxuriosa*: A, anterior end, dorsal view; B, parapodium from middle of body. C, D, *Timarete perbranchiata*: C, anterior end, dorsal view; D, parapodium from middle of body. Scale bars: A, 2 mm; C, 2 cm; B, D, not to scale. All after Blake (1996).

4. *Timarete dasylophius* (von Marenzeller, 1879). Japan; Sri Lanka.
5. *Timarete filigera* (Delle Chiaje, 1828). Mediterranean Sea.
6. *Timarete gibbosa* (Moore, 1903). Japan.
7. *Timarete hawaiensis* (Hartman, 1956). Hawaii, Oahu, offshore and Pearl Harbor. *Fide* Magalhães and Bailey-Brock (2010).
8. *Timarete japonica* Zachs, 1933. Japan.
9. *Timarete luxuriosa* (Moore, 1904). NE Pacific, southern California, intertidal. *Fide* Blake (1996).
10. *Timarete nasuta* Ehlers, 1897. South America, Patagonian region including Straits of Magellan, Tierra del Fuego and Staten Island, intertidal to shallow subtidal; Falkland Islands.
11. *Timarete norvegica* (de Quatrefages, 1866). Northern Europe. *Fide* Southern (1914).
12. *Timarete oculata* (Treadwell, 1932). Brazil, intertidal. *Fide* Magalhães *et al.* (2014).
13. *Timarete perbranchiata* (Chamberlin, 1918). NE Pacific, California, intertidal. *Fide* Blake (1996).
    [*Ambo americana* Monro, 1933]. Galapagos. *Fide* Hartman (1959).
    [*Ambo convergens* Chamberlin, 1918. California. *Fide* Hartman (1959).
14. *Timarete polytricha* (Schmarda, 1861). SE Pacific, Chile.
15. *Timarete punctata* (Grube, 1859). Caribbean Sea, intertidal to shallow subtidal; Mediterranean Sea (possibly introduced); Brazil. *Fide* Çinar (2007) and Magalhães *et al.* (2014).

**B) Soft-bottom Bitentaculate genera**

The infaunal bitentaculate genera include numerous species, many yet undescribed, which are poorly known and often difficult to distinguish from one another. Until about 1990, the definitions of *Chaetozone*, *Caulleriella*,

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and *Tharyx* were those established by Hartman (1961). All three genera were considered similar in the placement of the single pair of dorsal tentacles, reduction of the parapodia, and general appearance of the anterior and posterior ends of the body. The only reliable differences were in the form and arrangement of the chaetae. According to Hartman's system, species of *Tharyx* had only capillary-tipped chaetae, species of *Caulleriella* had acicular chaetae with bifid tips, whereas species of *Chaetozone* had acicular spines with distally entire tips. Hartman's concept of *Caulleriella* and *Chaetozone* differed from definitions of Fauvel (1927), Berkeley and Berkeley (1952), and Day (1967), who defined *Chaetozone* on the basis of whether or not the spines formed cinctures encircling the posterior body segments.

As part of a review of some bitentaculate cirratulids from the western North Atlantic, Blake (1991) established that the type species of the genus *Tharyx*, *T. acutus* Webster & Benedict, had knob-tipped hooks or spines in addition to capillaries. Blake (1991) therefore restricted *Tharyx* to species having these knob-tipped spines and established a new genus, *Aphelochaeta*, for former *Tharyx* species having simple, nonserrated capillary chaetae. *Tharyx monilaris* Hartman, originally described from off California, was designated as the type species of this new genus. Species having serrated capillaries were referred to the genus *Monticellina* Laubier, which was revalidated. All three of these genera, together with *Chaetozone* and *Caulleriella*, are well represented globally, and in the 25 years since Blake's (1991) paper, the number of described species of the five bitentaculate genera has more than doubled from 70 to 171. Further refinement of the definitions of these genera and descriptions of numerous new species have been presented by Blake (1996, 2006, 2015a,b, 2016), Chambers (2000), Chambers and Woodham (2003), Dean and Blake (2007, 2009, 2016), Doner and Blake (2006, 2009), Elias and Rivero (2008, 2009b, 2011), Elias *et al.* (2016), Magalhães and Bailey-Brock (2013a, 2015), Blake and Lavesque (2017), and Lezzi *et al.* (2016). Most recently, Blake (2016) determined that *Monticellina* Laubier was preoccupied in the Rhabdocoela and renamed the polychaete genus *Kirkegaardia*. In the same paper, he described 24 species, 16 of which were new to science.

**Genus *Aphelochaeta* Blake, 1991**

32 species

**Type species:** *Tharyx monilaris* Hartman, 1961. Designated by Blake 1991

**Diagnosis** (modified after Doner and Blake 2009): Prostomium conical, tapering (Fig. 7.3.1.5.16 A, B, and F–H); peristomium elongate with one to four annulations, with pair of grooved dorsal tentacles arising either on or anterior to chaetiger 1; first pair of branchiae arising either on or anterior to chaetiger 1; thoracic region frequently expanded, with crowded segments; abdominal segments variable, sometimes moniliform; noto- and neuropodia close to one another, not widely separated (Fig. 7.3.1.5.16 C, D); chaetae simple capillaries (Fig. 7.3.1.5.16 J–K), with distinct serrations or sawtooth edge not visible in light microscopy, but fibril endings sometimes seen with SEM; far posterior segments frequently expanded, tapering to simple pygidial lobe.

**Remarks:** Blake (1991) assigned bitentaculate cirratulid species having only simple, nonserrated capillary chaetae to the genus *Aphelochaeta*. The species belonging to *Aphelochaeta* are among the most difficult to identify among the bitentaculate cirratulids due to the lack of obvious variability in chaetal morphology. Although the capillaries differ in thickness and length among species, they are difficult to quantify and depict in a manner that readily distinguishes one species from another. In the absence of obvious chaetal characters, species can be distinguished on prostomial shape, form and size of the peristomium in relation to the prostomium and first chaetiger, placement of the dorsal tentacles and first pair of branchiae, degree of elaboration of the thoracic region, presence or absence of moniliform segments, presence of absence of a dorsal and/or ventral groove along the body, degree of enlargement of the posterior segments, and species-specific methyl green staining patterns. The obvious differences in several of these characters between two sympatric species, *Aphelochaeta bullata* and *Aphelochaeta guttata* from deep-water off California, are readily apparent in the illustrations by Doner and Blake (2009). Despite the specific nature of combinations of these characters, closely related species are often difficult to distinguish from one another, and it is usually only at the local or regional level that keys to species have any utility.

▸ **Fig. 7.3.1.5.16:** Examples of species of *Aphelochaeta*. A, *Aphelochaeta monilaris*: A, anterior and middle segments, left lateral view with methyl green stain patterns on thorax and tip of prostomium. B–E, *Aphelochaeta glandaria*: B, anterior end, dorsal view; C, parapodium from middle body segment; D, parapodium from posterior part of body; E, posterior end, left lateral view. F, G, *Aphelochaeta bullata:* F, anterior end, left lateral view; G, anterior end, dorsal view. H–K, *Aphelochaeta tigrina*: H, anterior end, dorsal view; I, posterior end with methyl green stained bands depicted; J, capillary neurochaetae; K, capillary notochaetae. Scale bars: A, C, D, H, 200 µm; B, E, 500 µm; F, G, I, 300 µm; J, K, 20 µm. A–E, H–K, after Blake (1996); F, G, after Doner and Blake (2009).

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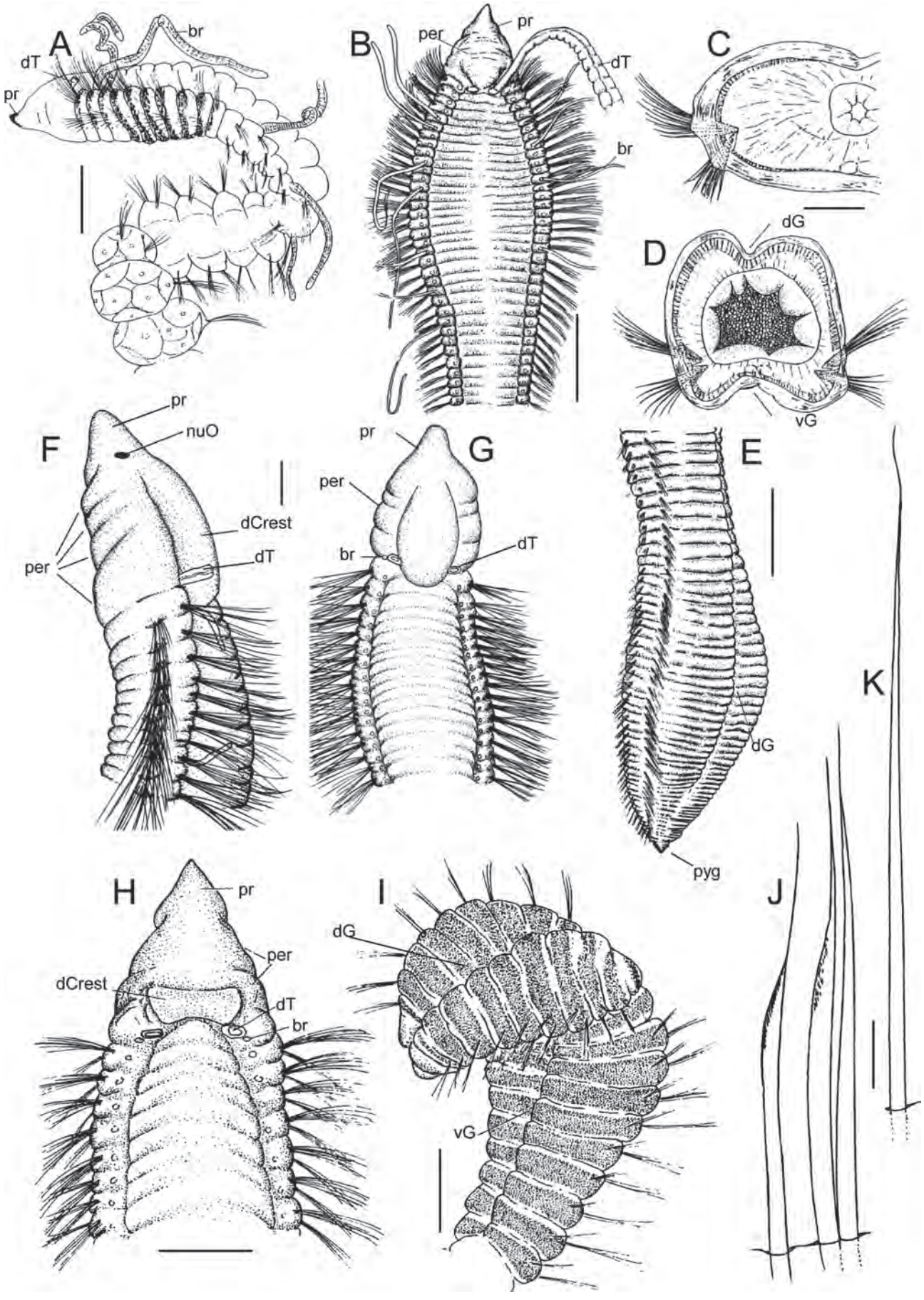


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Thirty-two species of *Aphelochaeta* are listed as valid in the World Register of Marine Species (WoRMS) and are reviewed here. Among these, *Aphelochaeta filiformis, A. marioni, Aphelochaeta mcintoshi, Aphelochaeta multibranchus, Aphelochaeta nigrorostrum*, *Aphelochaeta retierei*, and *Aphelochaeta serrata* are poorly known and need further study. *Aphelochaeta marioni*, for example, has been identified globally, yet no types are available and the original description and illustrations suggest that more than one species is involved. *Aphelochaeta retierei* and *A. serrata* have unusual capillaries that appear to be jointed or compound. The holotype of *A. nigrorostrum* has been examined by one of us (JAB). The specimen is very small, is in poor condition, and cannot be characterized in a manner necessary to separate the species from its congeners. In addition, recent offshore surveys have revealed the presence of numerous undescribed species, largely from deep water.

1. *Aphelochaeta aequiseta* (Hartmann-Schröder, 1962). SE Pacific, Peru.
2. *Aphelochaeta antelonga* Dean & Blake, 2016. Pacific Costa Rica, 11–18 m.
3. *Aphelochaeta arizonae* Magalhães & Bailey-Brock, 2013a. Hawaii, Pearl Harbor, intertidal.
4. *Aphelochaeta bullata* Doner & Blake, 2009. NE Pacific, slope depths, 2,160–3,775 m.
5. *Aphelochaeta cincinnata* (Ehlers, 1908). Southern Indian Ocean, Kerguelin Islands, 88 m; Antarctic records refer to other species (Blake unpublished).
6. *Aphelochaeta elongata* Blake, 1996. NE Pacific, California, Tomales Bay, intertidal.
7. *Aphelochaeta filibranchia* (Day, 1961). South Africa, shallow subtidal.
8. *Aphelochaeta filiformis* (Keferstein, 1862). Western Europe.
9. *Aphelochaeta glandaria* Blake, 1996. NE Pacific: off California, shelf depths, 77–200 m; off Costa Rica, 11–200 m.
10. *Aphelochaeta guimondi* Dean & Blake, 2016. Pacific Costa Rica, 11–26 m.
11. *Aphelochaeta guttata* Doner & Blake, 2009. NE Pacific, slope depths, 2,420–3,666 m.
12. *Aphelochaeta honouliuli* Magalhães & Bailey-Brock, 2013a. Hawaii, Mamala Bay, off Oahu, 50–105 m.
13. *Aphelochaeta longisetosa* (Hartmann-Schröder, 1965). SE Pacific, off Chile, low water to 200 m.
14. *Aphelochaeta malefica* Elías & Rivero, 2009. SW Atlantic, Argentina, Mar del Plata, 12–13 m.
15. *Aphelochaeta marioni* (de Saint-Joseph, 1894). Western Europe.
16. *Aphelochaeta mcintoshi* (Southern, 1914). Northern Europe.
17. *Aphelochaeta monilaris* (Hartman, 1960). NE Pacific, widespread, shelf and slope depths; Atlantic records likely refer to other species.
18. *Aphelochaeta multibranchis* (Grube, 1863). E North Atlantic, North Sea, Mediterranean Sea, Black Sea.
19. *Aphelochaeta multifilis* (Moore, 1909). NE Pacific, southern California, shallow subtidal.
20. *Aphelochaeta nigrorostrum* (Hartman & Fauchald, 1971). Western North Atlantic, 1,102–4,825 m.
21. *Aphelochaeta pacifica* (Annenkova, 1937). Tartar Strait between Sakhalin Island and Russian mainland.
22. *Aphelochaeta petersenae* Blake, 1996. NE Pacific, southern California, intertidal to low subtidal.
23. *Aphelochaeta phillipsi* Blake, 1996. NE Pacific, off California, 60–98 m.
24. *Aphelochaeta praeacuta* Dean & Blake, 2016. Pacific Costa Rica, 11–28 m.
25. *Aphelochaeta retierei* (Lechapt, 1994). NE Atlantic Ocean off Morocco, 25–35 m.
26. *Aphelochaeta saipanensis* Magalhães & Bailey-Brock, 2013a. Central Pacific Ocean, Mariana Islands, Saipan, intertidal on reef flats.
27. *Aphelochaeta serrata* (Eliason, 1962). Sweden, Skagerrak.
28. *Aphelochaeta striata* Dean & Blake, 2016. Pacific, Costa Rica, 11–28 m.
29. *Aphelochaeta tigrina* Blake, 1996. NE Pacific, off central California, 90–160 m.
30. *Aphelochaeta whiteavesi* (McIntosh, 1911). Eastern Canada, Gulf of St. Lawrence. New combination, Blake unpublished; syntypes: BMNH ZK 1921.5.1.3241/44.
31. *Aphelochaeta williamsae* Blake, 1996. NE Pacific, off Central California, 90–150 m.
32. *Aphelochaeta zebra* Dean & Blake, 2016. Pacific Costa Rica, shallow water.

### Genus *Caulleriella* Chamberlin, 1919

34 species

**Type species:** *Cirratulus viridis* Langerhans, 1880, original designation by Chamberlin (1919)

**Diagnosis** (modified after Blake 1996): Prostomium elongate, conical to pointed (Fig. 7.3.1.5.17 A, B, and E); peristomium elongated to short, dorsal tentacles usually beginning anterior to chaetiger 1 (Fig. 7.3.1.5.17 A, B, and E). Middle body segments not beaded; parapodia often with noto- and neuropodia widely separated laterally (Fig. 7.3.1.5.17 B, C, E, and F). Modified chaetae including capillaries and bidentate, crotchet-like hooks, not arranged into modified cinctures. In some species, unidentate hooks may occur in some regions of the body in addition to bidentate hooks (Fig. 7.3.1.5.17 G–D). Pygidium either a simple conical lobe (Fig. 7.3.1.5.17 C, F) or with two anal cirri.

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**Remarks:** Among the bitentaculate cirratulids, species of *Caulleriella* are often easy to recognize because the noto- and neuropodia of middle and posterior segments are widely separated from one another. In extreme examples, the four chaetae-bearing podial lobes of a single segment when viewed in cross-section have the chaetae arising at four corners of the body. Examples of such widely separated podia are in Blake (1996) for *C. apicula*, *Caulleriella cristata*, and *Caulleriella pacifica*. In these species, the podia are widely separated throughout the body. A less extreme example is *Caulleriella venefica* from off New England where the noto- and neuropodia of middle body segments are close to one another in anterior segments, then diverge in middle segments to become widely separated, but not as wide as in the Pacific examples (Doner and Blake 2006). All species of *Caulleriella* have bidentate hooks. At least one species, *Caulleriella trispina*, has unidentate hooks in middle body segments that transition to bidentate hooks posteriorly. *Chaetozone armata*, described by Hartman (1963) from off California, has widely separated podia as in *Caulleriella* species defined in Blake (1996) and here. There are only single spines in these podia in middle and posterior segments, and they superficially are unidentate, not bidentate. However, a closer examination of these spines on the holotype (LACM-AHF Poly 0566) suggests that a short accessory tooth or sheath on the convex side has been worn; in addition, juveniles of this species have been found with bidentate hooks. Therefore, *C. armata* is here transferred to *Caulleriella*. Two other species of *Caulleriella* have spines with reduced teeth suggesting wear: *Caulleriella cucula* and *Caulleriella murilloi* from Costa Rica (Dean and Blake 2009). An undescribed species from off the U.S. Atlantic coast has bidentate hooks where the apical "tooth" is actually a broad hood (Fig. 7.3.1.5.4 L, M). There are currently 34 species considered valid in WoRMS and here. However, several of the older species such *Caulleriella alata*, *C. bioculata*, and *Caulleriella fragilis* have either been reported widely or rarely and need to reevaluated.

1. *Caulleriella acicula* Day, 1961. South Africa, subtidal.
2. *Caulleriella alata* (Southern, 1914). E North Atlantic, Ireland, low water; numerous additional records globally.
3. *Caulleriella antarctica* Hartman, 1978. Antarctica, deep water.
4. *Caulleriella apicula* Blake, 1996. E North Pacific, southern California, 24 m.
5. *Caulleriella armata* (Hartman, 1963). NE Pacific, southern California, 27–180 m. New combination.
6. *Caulleriella bioculata* (Keferstein, 1862). E North Atlantic, France; reported widely: South Africa, California, Australia, Hawaii.
7. *Caulleriella bransfieldensis* Hartmann-Schröder & Rosenfeldt, 1989. Antarctica, Bransfield Strait, 68 m.
8. *Caulleriella bremecae* Elias & Rivero, 2008. SW Atlantic, Argentina, Mar del Plata, intertidal.
9. *Caulleriella cabbsi* Pocklington & Coates, 2010. Bermuda, intertidal.
10. *Caulleriella capensis* (Monro, 1930). S and SW Africa, shallow water.
11. *Caulleriella cordiformia* Magalhães & Bailey-Brock, 2013a. Hawaii, Mamala Bay, off Oahu, 102 m.
12. *Caulleriella cristata* Blake, 1996. E North Pacific, central California, intertidal, in rocks.
13. *Caulleriella cucula* Dean & Blake, 2007. Pacific, Costa Rica, 9–46 m.
14. *Caulleriella dulcensis* Dean & Blake 2007. Pacific, Costa Rica, intertidal.
15. *Caulleriella fragilis* (Leidy, 1855). W North Atlantic, Rhode Island intertidal in rocks.
16. *Caulleriella galeanoi* Elias & Rivero, 2008. SW Atlantic, Argentina, Mar del Plata, intertidal.
17. *Caulleriella glabra* Gallardo, 1968. Bay of Nha Trang, South Vietnam, 9–17 m.
18. *Caulleriella hamata* (Hartman, 1948). NE Pacific, Alaska to Washington; ?California; intertidal to shallow subtidal.
19. *Caulleriella homosetosa* Hartmann-Schröder & Rosenfeldt, 1989. Antarctic Peninsula.
20. *Caulleriella lajolla* Blake, 1996. E North Pacific, southern California, subtidal in algal holdfasts.
21. *Caulleriella longisetosa* Hutchings & Murray, 1984. New South Wales, Australia, intertidal.
22. *Caulleriella magnaoculata* Hartmann-Schröder, 1962. Peru.
23. *Caulleriella minuta* Dean & Blake, 2007. Pacific, Costa Rica, intertidal.
24. *Caulleriella moralensis* Dean & Blake, 2007. Pacific, Costa Rica, intertidal.
25. *Caulleriella murilloi* Dean & Blake, 2007. Pacific, Costa Rica, intertidal with mangroves.
26. *Caulleriella obtusa* Hartmann-Schröder & Rosenfeldt, 1990. Antarctic Peninsula.
27. *Caulleriella pacifica* E. Berkeley, 1929. E North Pacific, British Columbia and Puget Sound, shallow subtidal; Guam. *Fide* Magalhães & Bailey-Brock, 2015.
28. *Caulleriella parva* Gillandt, 1979. North Sea, Helgoland, intertidal to shallow subtidal.
29. *Caulleriella petersenae* Díaz-Díaz, Cárdenas-Oliva & Liñero-Arana, 2014. Caribbean Sea, NE Venezuela, shallow subtidal.
30. *Caulleriella tricapillata* Hutchings & Rainer, 1979. Australia, New South Wales, intertidal.

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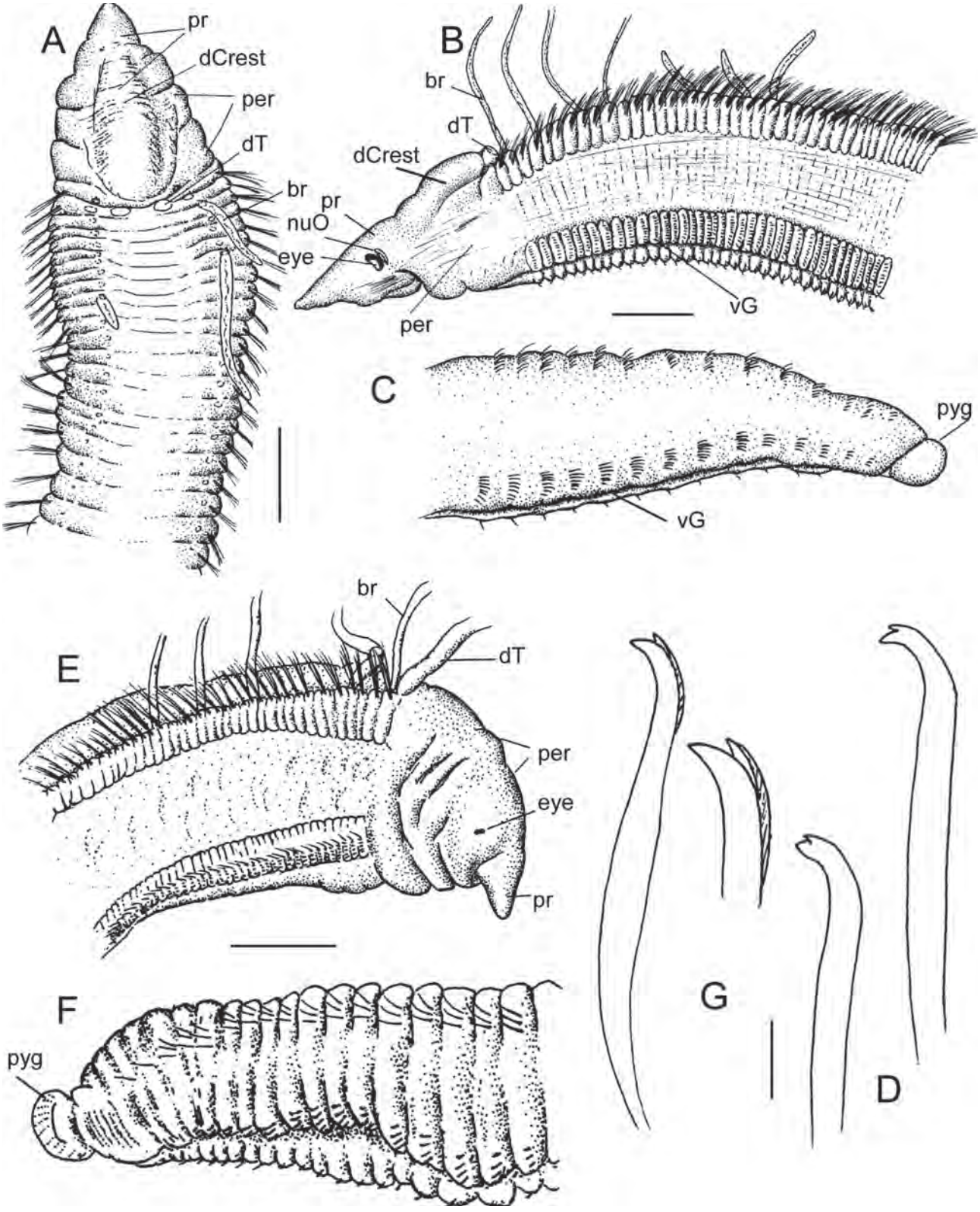


**Fig. 7.3.1.5.17:** Examples of species *Caulleriella*. A, *Caulleriella cristata*: A, anterior end, dorsal view. B–D, *Caulleriella apicula*: B, anterior end, left lateral view; C, posterior end, left lateral view; D, neuropodial bidentate hooks. E–G, *Caulleriella pacifica*. E, anterior end, right lateral view; F, posterior end, right lateral view; G, neuropodial hooks. Scale bars: A, 300 µm; B, C, 200 µm; E, F, 500 µm; D, G, 20 µm. All after Blake (1996).

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31. *Caulleriella trispina* Elías & Rivero, 2011. SW Atlantic, Argentina, Mar del Plata, intertidal, 12–16 m; SE Brazil, 35–89 m.
32. *Caulleriella typhlops* (Willey, 1905). Indian Ocean, Gulf of Manaar.
33. *Caulleriella venefica* Doner & Blake, 2006. W North Atlantic, Long Island Sound, Massachusetts Bay, Georges Bank, 30–85.
34. *Caulleriella viridis* (Langerhans, 1880). E North Atlantic, Madeira.

### Genus *Chaetozone* Malmgren, 1867

54 species

**Type species:** *Chaetozone setosa* Malmgren, 1867, by monotypy

**Diagnosis** (modified after Blake 2015): Prostomium blunt to conical, usually lacking eyespots (Fig. 7.3.1.5.18 A, F, I, and J), with a pair of small nuchal slits or depressions at posterior edge, with a single pair of grooved dorsal tentacles arising from posterior edge of peristomium (Fig. 7.3.1.5.18 A, F, I, and J), or sometimes more posterior on an achaetous anterior segment, or rarely an anterior chaetiger. First pair of branchiae arising from an achaetous segment or first chaetiger (Fig. 7.3.1.5.18 I), or sometimes with first two pairs of branchiae on a single anterior segment. Body basically thick and fusiform over many segments, rarely with middle or posterior body segments beaded or moniliform. Chaetae include capillaries on most chaetigers and acicular spines in neuropodia and notopodia, spines typically concentrated in posterior segments, forming distinct cinctures with spines emerging from elevated membranes (Fig. 7.3.1.5.3 E–G); cinctures with few to many spines alternating with capillaries (Figs. 7.3.1.5.4 J and 7.3.1.5.18 C–E, H, and K); some species with posterior noto- and neuropodial sigmoid acicular spines numerous, encircling entire posterior segments; bidentate spines sometimes present in juveniles or occasionally in ventral most position of far posterior chaetigers of adults accompanying unidentate spines in cinctures; some species with long, natatory-like capillaries, sometimes limited to gravid individuals. Pygidium a simple lobe (Fig. 7.3.1.5.18 G), disk like (Fig. 7.3.1.5.18 B, K), or with long, terminal cirrus.

**Remarks:** This generic definition (previous) includes additional characters necessary to identify existing species and potentially apply to future taxa that may be different. In general, species of *Chaetozone* are characterized by having posterior acicular spines arranged in spreading fascicles that either partially or completely encircle the posterior end of the body producing distinctive parapodia called cinctures, with the numerous protruding spines forming a conspicuous armature. The acicular spines are typically unidentate and either blunt tipped or pointed and are accompanied by alternating capillaries. One group of *Chaetozone* species has spines with a fine tip that curves and attaches to the concave side of the shaft (Figs. 7.3.1.5.4 K and 7.3.1.5.4.18 L). In a few species, bidentate spines occur in the ventral parts of fascicles containing acicular spines. These are more typical in smaller or juvenile specimens and have been recorded by Christie (1985) in some *Chaetozone* specimens he examined; by Woodham and Chambers (1994) in smaller specimens of *C. zetlandica*; by Blake (1996) in the newest spines in neuropodia of *Chaetozone lunula*; and by Doner and Blake (2006), where a few bidentate spines were present in the spinal array of *Chaetozone diodonta*. However, in no instances have the cinctures of spines included more than one or two bidentate hooks.

Some species of *Chaetozone* in the following list, all from deep water, do not fully agree with the earlier definition and likely belong elsewhere. For example, *Chaetozone gracilis* is an abyssal species redescribed by Blake (1996) as having spines limited to the neuropodia. *Chaetozone andersenensis*, *Chaetozone pinguis*, *Chaetozone benthaliana* and possibly *Chaetozone gayheadia* are all deep-sea species having large inflated bodies, with few spines in the noto- and neuropodia not forming cinctures, and with a broad prostomium reminiscent of those found in multitentaculate genera. Some of these are being redescribed and placed in a new genus a forthcoming paper on South American and Antarctic cirratulids (Blake unpublished). Several species in the following list are older taxa that have not been recently reported; in a few cases, more recent descriptions or unpublished observations are noted.

With 54 species, *Chaetozone* is by far the largest cirratulid genus. Additional species are known, mostly from offshore shelf and slope habitats.

1. *Chaetozone abranchiata* (G.A. Hansen, 1878). North Sea.
2. *Chaetozone acuminata* Dean & Blake, 2007. NE Pacific, Costa Rica, 35 m.
3. *Chaetozone acuta* Banse & Hobson, 1968. NE Pacific, Puget Sound, 15–35 m.
4. *Chaetozone allanotai* Blake, 2006. NE Pacific, off California, slope depths, 1,800–3,200 m.
5. *Chaetozone anasima* Doner & Blake, 2006. W North Atlantic, New England, Maine to Massachusetts, 20–85 m.
6. *Chaetozone andersenensis* (Augener, 1932). Antarctica, widespread in shelf depths.
   [*Tharyx fusiformis* Monro, 1939]. New synonymy.
7. *Chaetozone atlantica* McIntosh, 1885. West Indies, deep water. M.E. Petersen (unpublished notes) examined the type specimen (BMNH 85.12.1.277) which was

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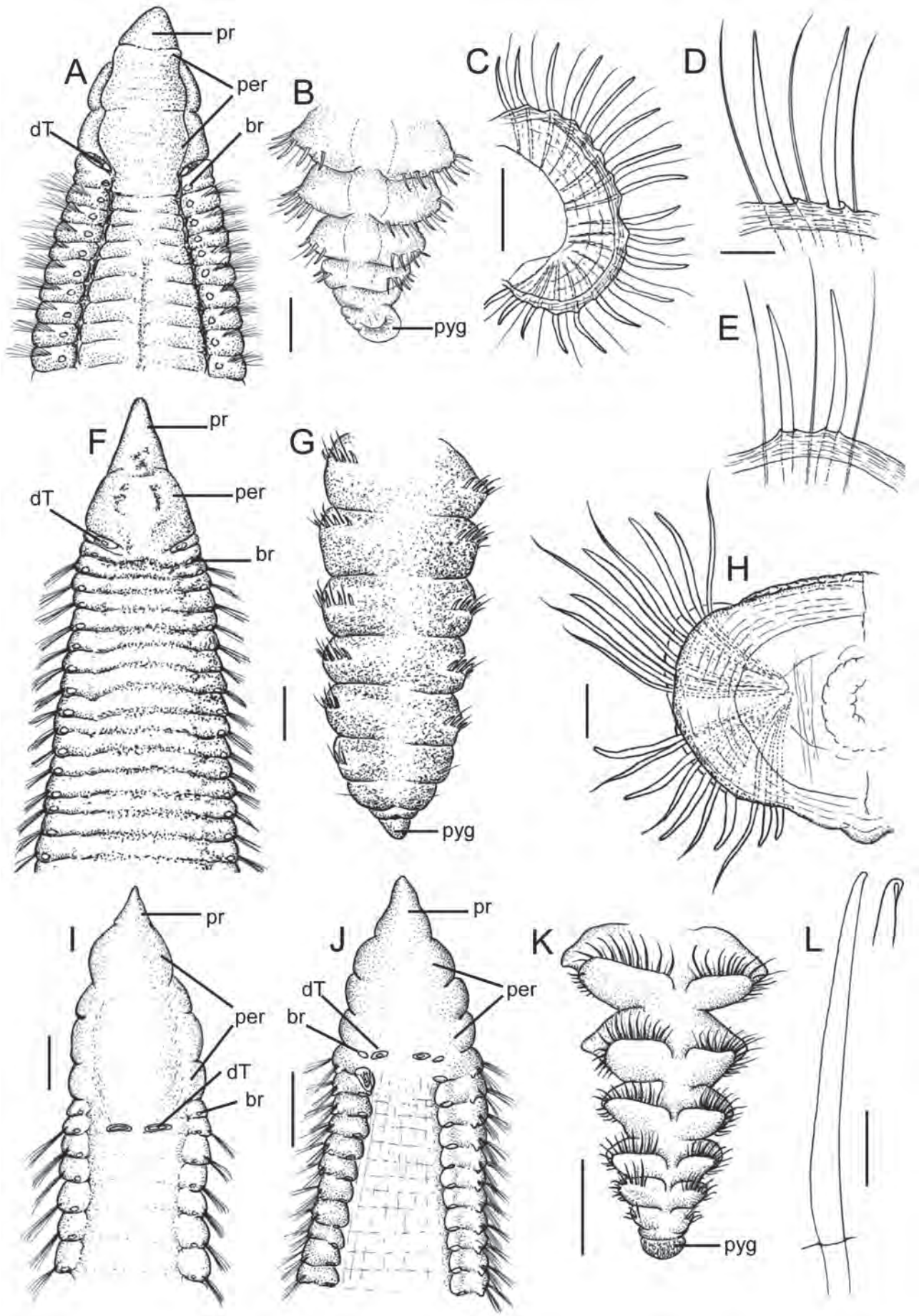


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in two parts; she was unable to find posterior aciculars and confirm that the species belongs in *Chaetozone*.

8. *Chaetozone bansei* Blake, 1996. NE Pacific, California, 10–35 m.
9. *Chaetozone bathyala* Blake, 2015. Alaskan and Canadian Arctic and subarctic, intertidal to 55 m.
10. *Chaetozone benthaliana* McIntosh, 1885. Eastern Canada, off Halifax, Nova Scotia, abyssal depths.
11. *Chaetozone brunnea* Blake, 2006. NE Pacific, off northern California, slope depths, 2,000–3,200 m.
12. *Chaetozone camasetosa* Blake, 2015. NE Pacific, SE Alaska to British Columbia, 12–95 m.
13. *Chaetozone caputesocis* (de Saint-Joseph, 1894). France.
14. *Chaetozone careyi* Blake, 2015. Alaskan Arctic, Beaufort Sea, 10–55 m; Canadian subarctic, Hudson Strait, intertidal.
15. *Chaetozone carpenteri* McIntosh, 1911. Mediterranean Sea; Adriatic Sea; Tyrrhenia Sea; subtidal, 30–98 m. *Fide* Chambers *et al.* (2011).
16. *Chaetozone christiei* Chambers, 2000. N Atlantic, E coast of Britain, North Sea, intertidal to shallow subtidal.
17. *Chaetozone cimar* Dean & Blake, 2007. NE Pacific, off Costa Rica, 50 m.
18. *Chaetozone cincinnata* Augener, 1923. New Zealand, Auckland Islands. Augener (1923) considered his specimens to be the same as *Heterocirrus cincinnatus* of Ehlers (1908) (see: *Aphelochaeta cincinnata*) from Kerguelen, but they differ in having noto- and neuropodial acicular spines in posterior chaetigers; the Ehlers' species has only capillaries. Hartman (1959) considered that Augener's name was a homonym of Ehlers' species. To date, this has not been addressed.
19. *Chaetozone columbiana* Blake, 1996. NE Pacific, Oregon to Washington, subtidal.
20. *Chaetozone commonalis* Blake, 1996. NE Pacific, off central California, shelf depths, 90–410 m.
21. *Chaetozone corona* Berkeley & Berkeley, 1941. NE Pacific, southern California to Costa Rica, 24–120 m; Alien species in E North Atlantic, Brittany coast, Adriatic Sea and Mediterranean Sea. *Fide* Blake (1996), Le Garrec *et al.* (2017), Grossi *et al.* (2017).
22. *Chaetozone curvata* Hartmann-Schröder, 1965. SE Pacific, off Chile, 250 m. Notes on the holotype (ZMH P-15050) were recorded by Blake (1996).
23. *Chaetozone dimorphosetosa* (Hutchings & Murray, 1984). Australia, New South Wales, subtidal.
24. *Chaetozone diodonta* Doner & Blake, 2006. W North Atlantic, New England, Georges Bank, 100–160 m.
25. *Chaetozone elakata* Blake & Lavesque, 2017. E North Atlantic, offshore Bay of Biscay, 60 m.
26. *Chaetozone flagellifera* Gallardo, 1968. Bay of Nha Trang, South Vietnam, 19–43 m; Central Pacific, Guam, subtidal. *Fide* Magalhães and Bailey-Brock (2015).
27. *Chaetozone gayheadia* Hartman, 1965. W North Atlantic, off New England, 300 m. Petersen (1991, 1999) suggested that this species belonged to *Cirratulus*, not *Chaetozone*. New collections from off the U.S. Atlantic shelf are being evaluated (Blake unpublished).
28. *Chaetozone gibber* Woodham & Chambers, 1994. North Atlantic, of SW and SE England; Mediterranean Sea; shallow subtidal.
29. *Chaetozone gracilis* (Moore, 1923). NE Pacific, off California, abyssal depths, 4,016 m. Redescribed by Blake (1996).
30. *Chaetozone hartmanae* Blake, 1996. NE Pacific, off southern California, basins and canyons, 542–914 m. [*Caulleriella gracilis* Hartman, 1969] Not Moore 1923. *Fide* Blake (1996).
31. *Chaetozone hedgpethi* Blake, 1996. NE Pacific, northern California, shallow subtidal; Costa Rica, 18–24 m.
32. *Chaetozone hobsonae* Blake, 2015. NE Pacific, SE Alaska to British Columbia, low water to 95 m.
33. *Chaetozone hystricosa* Doner & Blake, 2006. W North Atlantic, Massachusetts, 25–100 m.
34. *Chaetozone jubata* Chambers & Woodham, 2003. E North Atlantic, North Sea, Faroe-Shetland Channel, 700–1,000 m.
35. *Chaetozone larae* Elias, Rivero & Orensanz, 2016. SW Atlantic, off Argentina, 70 m.
36. *Chaetozone lunula* Blake, 1996. NE Pacific, central California, shelf depths, 77–190 m.
37. *Chaetozone macrophthalma* Langerhans, 1881. E North Atlantic, Madeira.
38. *Chaetozone malmgreni* Blake, 2015. NE Pacific, off Oregon, 109 m.
39. *Chaetozone maotienae* Gallardo, 1968. Bay of Nha Trang, South Vietnam, 11–30 m.
40. *Chaetozone michellae* Magalhães & Bailey-Brock, 2013a. Hawaii, off Oahu, 417–597 m.

◂ **Fig. 7.3.1.5.18:** Examples of species of *Chaetozone*. A–E, *Chaetozone pugettensis*: A, anterior end, dorsal view; B, posterior end, dorsal view; C, posterior parapodium, anterior view; D, posterior notopodial spines and capillaries; E, posterior neuropodial spines and capillaries. F–H, *Chaetozone pigmentata*: F, anterior end, dorsal view; G, posterior end, dorsal view; H, posterior parapodium, anterior view. I, *Chaetozone careyi*: I, anterior end, dorsal view. J–L, *Chaetozone camasetosa*: J, anterior end, dorsal view; K, posterior end, dorsal view; L, notopodial spine from posterior parapodium with recurved tip (inset). Scale bars: A, B, F, G, I, J, K, 200 µm; C, 100 µm; D, E, H, L, 50 µm. All after Blake (2015).

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41. *Chaetozone nicoyana* Dean & Blake, 2007. NE Pacific, Costa Rica, 9–44 m.
42. *Chaetozone pacifica* McIntosh, 1885. New Zealand, North Island, off East Cape, 1,280 m. Type (BMNH 85.12.1.279) examined by M.E. Petersen (unpublished notes). Posterior chaetigers with few aciculars and capillaries.
43. *Chaetozone palaea* Blake, 2006. NE Pacific, off California, slope depths, 1,675–3,130 m.
44. *Chaetozone pigmentata* Blake, 2015. North American Arctic: Alaska to Baffin Island and Labrador Sea, 38–245 m.
45. *Chaetozone pinguis* Hartman, 1978. Weddell Sea and Antarctic Peninsula in shelf and upper slope depths.
46. *Chaetozone platycera* Hutchings & Murray, 1984. Australia, New South Wales, intertidal.
47. *Chaetozone pugettensis* Blake, 2015. NE Pacific, Puget Sound, shallow water.
48. *Chaetozone ronaldi* Magalhães & Bailey-Brock, 2013a. Hawaii, off Oahu, 408–481 m.
49. *Chaetozone ruffi* Blake, 2015. Alaskan Arctic in shallow water.
50. *Chaetozone senticosa* Blake, 1996. NE Pacific, north and central California, nearshore 5–10 m.
51. *Chaetozone setosa* Malmgren, 1867. Norwegian Arctic, Spitsbergen and subarctic latitudes of Northern Europe, 30–110 m. *Fide* Blake 2015.
52. *Chaetozone spinosa* Moore, 1903. NW Pacific, off Japan, 280 m; NE Pacific, off California, slope depths 2,623–2,955 m. Redescribed by Blake (1996).
53. *Chaetozone vivipara* (Christie, 1984). N Atlantic, UK, NE coast of Britain, subtidal, 1–13 m.
54. *Chaetozone zetlandica* McIntosh, 1911. E North Atlantic, Ireland and off Scotland, subtidal to 170 m. Redescribed by Woodham and Chambers (1994).

### Genus *Kirkegaardia* Blake, 2016

38 species

**Type species:** *Monticellina heterochaeta* Laubier, 1961. Designated by Blake (2016)

**Homonym:** *Monticellina* Laubier, 1961. Preoccupied by *Monticellina* Westblad, 1953

**Diagnosis** (after Blake 2016): Bitentaculate cirratulids with distinct body regions and all chaetae distally pointed. Prechaetigerous typically elongate, cylindrical, with short, blunt prostomium and long peristomium with none to many weakly developed annulations (Fig. 7.3.1.5.19 A, D, and G) or peristomium short and thick (Fig. 7.3.1.5.19 I); dorsal tentacles arising on posterior margin of peristomium, anterior to chaetiger 1 (Fig. 7.3.1.5.19 A, D, G, and I). Thoracic notopodia often shifted dorsally, elevated, producing distinct dorsal groove along thoracic region (Fig. 7.3.1.5.19 A, G); other species with thoracic parapodia more lateral, leaving broad elevated dorsum (Fig. 7.3.1.5.19 D); parapodia of middle and posterior region lateral. Middle body segments longer than wide, frequently beadlike; posterior segments wider than long, somewhat crowded, with posterior most segments usually expanded or enlarged. Chaetae including simple capillaries with fibrils observed under SEM and denticulated capillaries with distinct denticles present along one edge of chaeta (Figs. 7.3.1.5.4 B–E and 7.3.1.5.19 B, C, F, H, and J); denticles visible at 400–1,000×; blades usually basally expanded. Pygidium with simple ventral lobe (Fig. 7.3.1.5.19 E).

**Remarks:** Blake (2016) established *Kirkegaardia* a new name for *Monticellina* Laubier, preoccupied in the Rhabdocoela, and reviewed and redescribed all known species and described 16 additional new species. The genus was emended to accommodate a longer list of species having several new characters and character states. At present, 38 species are assigned to *Kirkegaardia*.

1. *Kirkegaardia acunai* (Dean & Blake, 2009). Pacific Costa Rica, 9–46 m.
2. *Kirkegaardia annulosa* (Hartman, 1965). W North Atlantic, off New England, upper slope depths, 250–550 m.
3. *Kirkegaardia antelaxa* (Dean & Blake, 2009). Pacific Costa Rica, 18 m.
4. *Kirkegaardia anterobranchiata* (Magalhães & Bailey-Brock, 2013a). Hawaii, off Oahu, 20 m.
5. *Kirkegaardia antonbruunae* Blake, 2016. SE Pacific, off Peru, slope depths, 737–1,000 m.
6. *Kirkegaardia aphelocephala* (Hutchings & Murray, 1984). Australia, New South Wales, 4–12 m.
7. *Kirkegaardia araiotrachela* Blake, 2016. SE Pacific, off Peru, slope depths, 520–805 m.
8. *Kirkegaardia baptisteae* (Blake, 1991). W North Atlantic shelf & slope, 30–640 m.
9. *Kirkegaardia brigitteae* Blake, 2016. Antarctica: Weddell Sea; Powell Basin; off South Shetland Islands; Bellingshausen Sea; slope depths, 1,500–3,864 m.

▸ **Fig. 7.3.1.5.19:** Examples of species of *Kirkegaardia*. A–C, *Kirkegaardia heterochaeta*: A, anterior end, dorsal view; B, denticulated neurochaeta (inset not to scale); C, denticulated notochaeta. D–F, *Kirkegaardia baptisteae*: D, anterior end, dorsal view; E, posterior end, dorsal view; F, abdominal denticulated neurochaeta (inset not to scale). G, H, *Kirkegaardia hampsoni*: G, anterior end, dorsal view; H, denticulated neurochaeta (inset not to scale). I, J, *Kirkegaardia jumarsi*: I, anterior end, dorsal view; J, abdominal denticulated neurochaeta (inset not to scale). Scale bars: A, D, 100 µm; E, G, 200 µm; I, 300 µm; B, C, F, H, J, 10 µm. All after Blake (2016).

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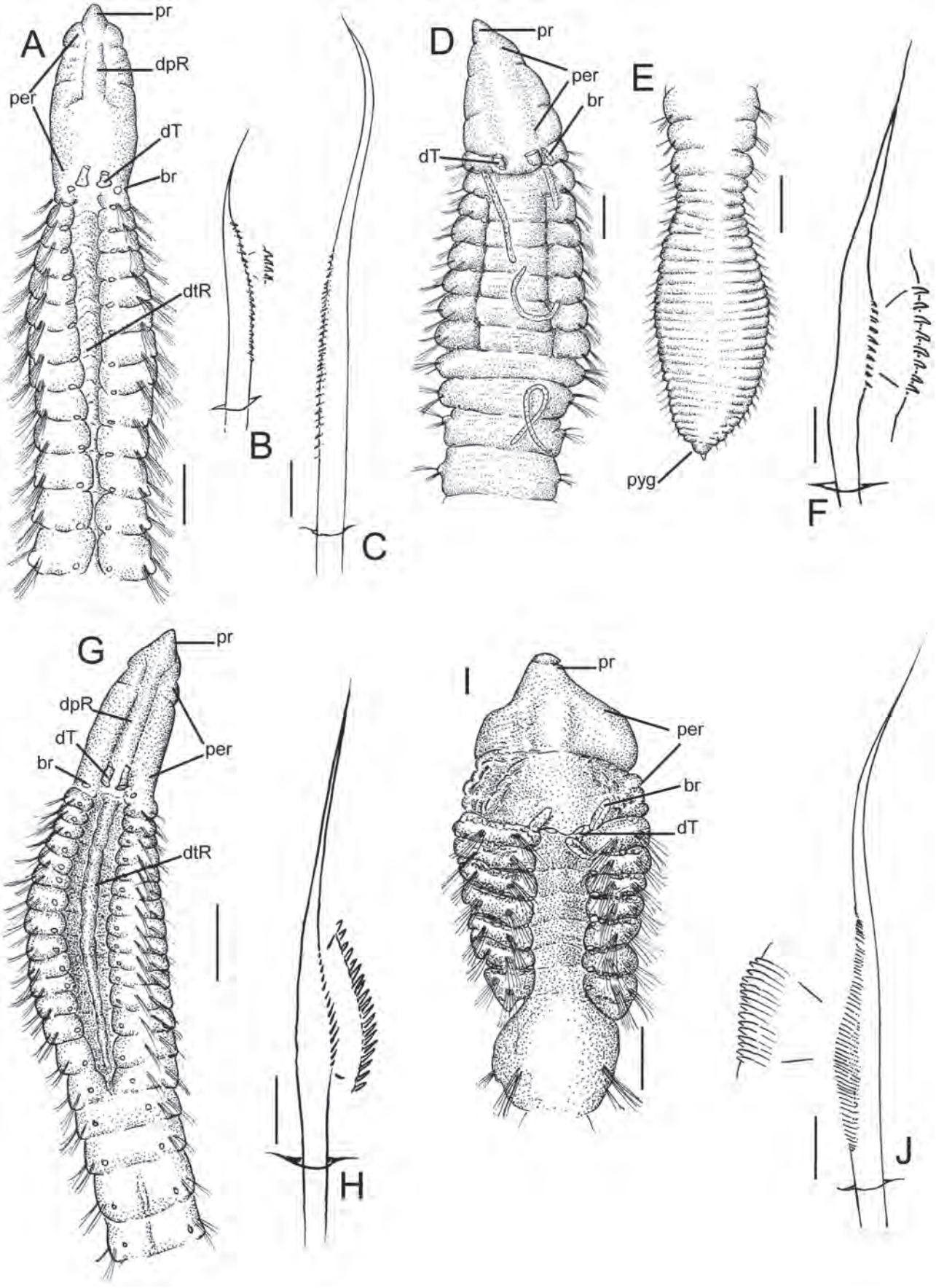


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10. *Kirkegaardia carinata* Blake, 2016. NE Pacific, off northern California, slope depths, 2,820–3,864 m.
11. *Kirkegaardia carolina* Blake, 2016. W North Atlantic, off North Carolina, slope depths, 500–1,000 m.
12. *Kirkegaardia carrikeri* (Dean & Blake, 2009). Pacific, Costa Rica, 11–24 m.
13. *Kirkegaardia chilensis* Blake, 2016. SE Pacific, off Chile, slope depths, 624–957 m.
14. *Kirkegaardia cristata* Blake, 2016. NE Pacific, Puget Sound, 20 m.
15. *Kirkegaardia cryptica* (Blake, 1996). NE Pacific, off California, shelf & slope depths, 92–585 m.
16. *Kirkegaardia dorsobranchialis* (Kirkegaard, 1959). SE Atlantic, off West Africa, 20–30 m; off South Africa, 120 m.
17. *Kirkegaardia dutchae* Blake, 2016. NE Pacific, Puget Sound, 14–82 m.
18. *Kirkegaardia elongata* (Dean & Blake, 2009). Pacific, Costa Rica, 18 m.
19. *Kirkegaardia fragilis* Blake, 2016. Central Pacific, abyssal depths, 4,858–4,879 m.
20. *Kirkegaardia franciscana* Blake, 2016. NE Pacific, off northern California, slope depths, 2,237–2,983 m.
21. *Kirkegaardia giribeti* (Dean & Blake, 2009). Pacific, Costa Rica, intertidal; off Ecuador, 90 m.
22. *Kirkegaardia hampsoni* Blake, 2016. W North Atlantic, shelf depths, 30–150 m.
23. *Kirkegaardia hanaumaensis* (Magalhães & Bailey-Brock, 2013a). Hawaii, off Oahu in coral rubble.
24. *Kirkegaardia heroae* Blake, 2016. Southern Ocean off Tiera del Fuego, Staten Island, 33–41 m.
25. *Kirkegaardia heterochaeta* (Laubier, 1961). Mediterranean Sea, shallow subtidal.
26. *Kirkegaardia jumarsi* Blake, 2016. SE Pacific, Peru-Chile Trench, 5,430 m.
27. *Kirkegaardia kladara* Blake, 2016. W North Atlantic, off North Carolina, slope depths, 500–1,000 m.
28. *Kirkegaardia lueldredgei* (Magalhães & Bailey-Brock, 2015). Central Pacific Ocean, Marianas Islands, Guam, 14–17 m.
29. *Kirkegaardia luticastella* (Jumars, 1975). NE Pacific, deep basins, slope depths, 1,200–2,637 m.
30. *Kirkegaardia marypetersenae* (Lezzi, Çinar & Giangrande, 2016). Ionian Sea, off Italy, 4 m.
31. *Kirkegaardia morae* (Elias, Rivero & Orensanz, 2016). SW Atlantic, off Argentina, subtidal.
32. *Kirkegaardia neotesselata* Blake, 2016. W North Atlantic, off New England, upper slope depths, 255 m.
33. *Kirkegaardia olgahartmanae* Blake, 2016. Antarctica, off Antarctic Peninsula, 650–2,000 m.
34. *Kirkegaardia secunda* (Banse & Hobson, 1968). NE Pacific, shallow water.
35. *Kirkegaardia serratiseta* (Banse & Hobson, 1968). NE Pacific, 9–84 m.
36. *Kirkegaardia setosa* (Dean & Blake, 2009). Pacific Costa Rica, 18 m.
37. *Kirkegaardia siblina* (Blake, 1996). NE Pacific, southern California, 7–10 m.
38. *Kirkegaardia tesselata* (Hartman, 1960). NE Pacific, off California shelf and upper slope depths.

### Genus *Tharyx* Webster & Benedict, 1887

13 species

**Type species:** *Tharyx acutus* Webster & Benedict, 1887, by monotypy

**Diagnosis** (after Blake 2015): Prostomium conical; peristomium elongate, narrow with pair of grooved dorsal tentacles arising on posterior margin anterior to chaetiger 1 (Fig. 7.3.1.5.20 A, B, E, and F); first pair of branchiae typically arising immediately posterior to dorsal tentacles either on posterior margin of peristomium or on chaetiger 1 (Fig. 7.3.1.5.20 A, B, E, and F); abdominal segments sometimes beadlike (Fig. 7.3.1.5.20 C). Noto- and neurochaetae arising close to one another, not widely separated. Chaetae include simple capillaries in anterior and middle chaetigers, acicular spines in posterior Chaetigers with irregular notched tips, sometimes appearing more or less bidentate, with pair of stunted or rounded knobs but never with distinct, sharply pointed teeth (Figs. 7.3.1.5.4 A and 7.3.1.5.20 H–D); spines present either in both posterior noto- and neuropodia or only in neuropodia. Pygidium with terminal anus and small ventral lobe or disk (Fig. 7.3.1.5.20 C, G).

**Remarks:** Species of *Tharyx* typically have elongate, thin bodies and abdominal regions that sometimes have beadlike segments. Classic examples of *Tharyx* species have the first pair of branchiae arising immediately posterior to the dorsal tentacles. Several species also have black pigment spots on the posterior-lateral margins of the peristomium (Fig. 7.3.1.5.20 A). The modified spines of posterior parapodia are typically short, curved, and with blunt or sub-bidentate tips, but never pointed.

◂ **Fig. 7.3.1.5.20:** Examples of species of *Tharyx*. A–D, *Tharyx kirkegaardi*: A, anterior end, left lateral view; B, anterior end, dorsal view; C, posterior end, left lateral view; D, knob-shaped hooks. E–H, *Tharyx parvus*: E, anterior end, left lateral view; F, anterior end, dorsal view; G, posterior end, right lateral view; H, capillary neurochaeta and knob-shaped hook. Scale bars: A–C, 200 µm; E–G, 300 µm; D, H, 20 µm. All after Blake (1996).

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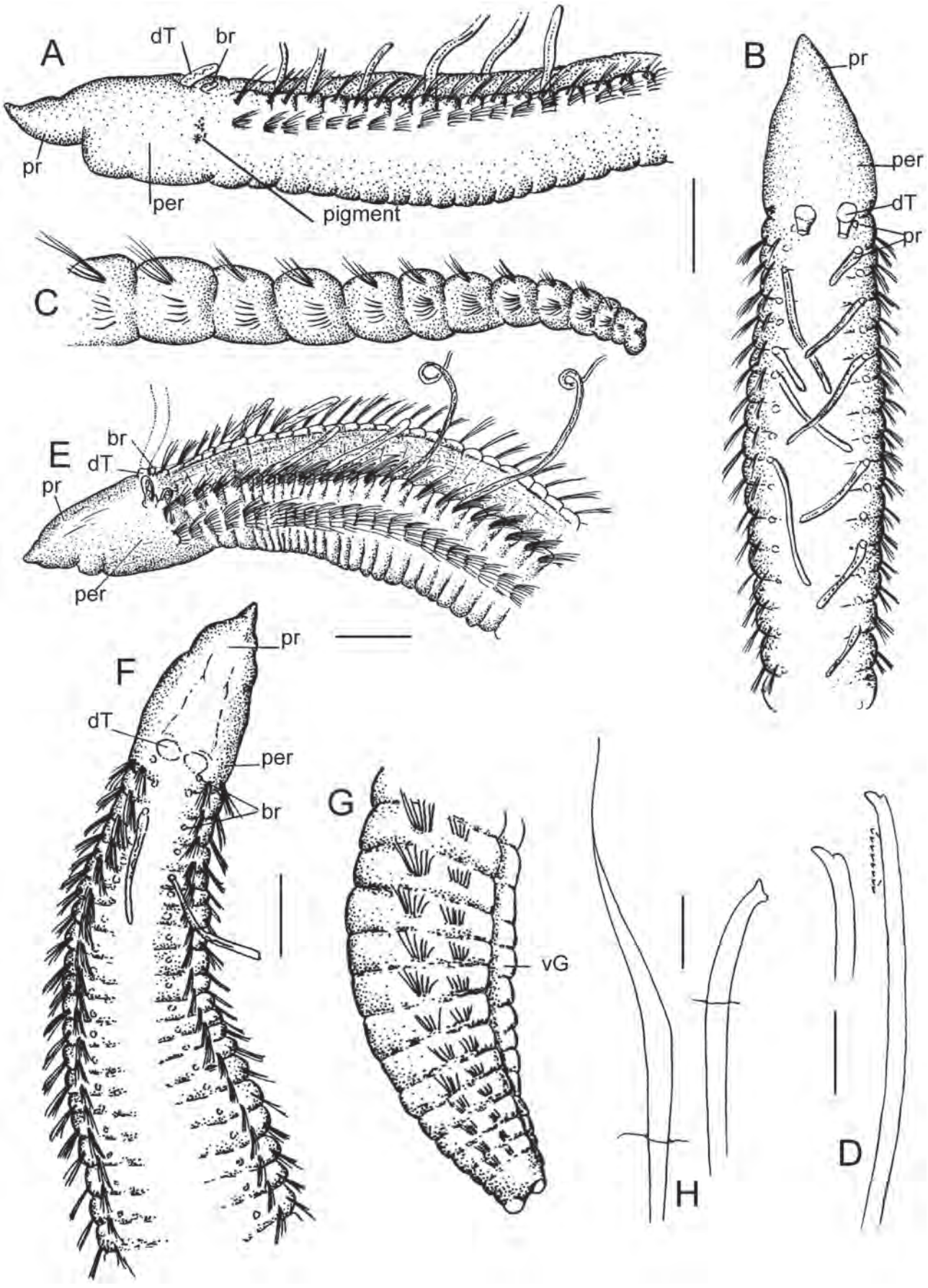


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The list of species currently includes 13 species. Additional undescribed species are known to us from North America and Antarctica, several from deep water.

1. *Tharyx acutus* Webster & Benedict, 1887. W North Atlantic, intertidal to shelf depths.
2. *Tharyx alaskensis* Blake, 2015. Alaskan Arctic, 2.5–128 m.
3. *Tharyx circacutus* Blake, 2015. NE Pacific, Puget Sound, 30 m.
4. *Tharyx killariensis* (Southern, 1914). E North Atlantic, European waters, subtidal.
5. *Tharyx kirkegaardi* Blake, 1991. W. North Atlantic & NE Pacific, shelf and slope depths.
6. *Tharyx longisetosus* (Hutchings & Murray, 1984). Australia, New South Wales, shallow subtidal.
7. *Tharyx maryae* Blake & Göransson, 2015. E. North Atlantic, Sweden, Kattegat, shallow subtidal.
8. *Tharyx parvus* Berkeley, 1929. NE Pacific, British Columbia to California, shallow subtidal.
9. *Tharyx retusisetus* (Hutchings & Murray, 1984). Australia, New South Wales, intertidal.
10. *Tharyx robustus* Blake & Göransson, 2015. North Atlantic, Sweden, Kattegat, shallow subtidal.
11. *Tharyx setigera* Hartman, 1945. W North Atlantic, North Carolina, intertidal to shallow subtidal.
12. *Tharyx similis* Webster & Benedict, 1887. W North Atlantic, New England, intertidal.
13. *Tharyx tumulosa* Magalhães & Bailey-Brock, 2013a. Hawaii, off Oahu, subtidal.

### C) Hard-bottom Bitentaculate genus

### Genus *Dodecaceria* Örsted, 1843

20 species

**Type species:** *Dodecaceria concharum* Örsted, 1843, by monotypy

**Synonym:** *Zeppelina* Vaillant, 1890

**Type species:** *Ctenodrilus monostylos* Zeppelin, 1883, by original designation. *Fide* George and Petersen (1991)

**Diagnosis:** Prostomium blunt or rounded on anterior margin (Fig. 7.3.1.5.21 A, C, E, and I), forming hood over mouth. Peristomium long, achaetous, with a pair of thick, grooved latero-dorsal tentacles at junction with chaetiger 1 (Fig. 7.3.1.5.21 A, C, E, and I). One to several pairs of branchial filaments extending over 1 to few anterior segments (Fig. 7.3.1.5.21 A, C, E, and I). Chaetae all simple, including capillaries and stout, acicular hooks that are simple, chizel or spoon shaped, or sometimes serrated (Figs. 7.3.1.5.4 F–I and 7.3.1.5.21 B, D, F–H, J, and K).

**Remarks:** The systematics of *Dodecaceria* species is complicated by the complex life cycles exhibited by several species. The alternation of asexual and sexual reproductive modes has led to differing opinions of the names and validity of what are relatively common species along some shorelines. The 20 species and synonyms listed here are based largely on George and Petersen (1991) and Petersen (1999).

1. *Dodecaceria ater* (de Quatrefages, 1866). Atlantic coast of France, UK. *Fide* George and Petersen (1991) and Petersen (1999).
   [*Dodecaceria concharum* Form A of Caullery & Mesnil 1898; Marcel 1962; Gibson 1977, 1981]. Not Örsted, 1843.
2. *Dodecaceria berkeleyorum* Knox, 1971. New Zealand.
3. *Dodecaceria capensis* Day, 1961. South Africa, shallow subtidal.
4. *Dodecaceria carolinae* Aguilar-Camacho & Salazar-Vallejo, 2011. Caribbean Sea, Mexico, Yucatan Peninsula, subtidal in limestone and corals.
5. *Dodecaceria concharum* Örsted, 1843. NE Atlantic, Denmark, Atlantic coast of France, UK. *Fide* George and Petersen (1991) and Petersen (1999).
   [*Terebella ostreae* Dalyell, 1853]. *Fide* George and Petersen (1991).
   [*Dodecaceria concharum* Form B of Caulleryi & Mesnil, 1898]. *Fide* George and Petersen (1991).
   [*Dodecaceria caulleryi* Dehorne, 1933]. *Fide* George and Petersen (1991).
   [*Dodecaceria caulleryi sensu* Gibson & Clark, Gibson 1976, 1981]. *Fide* Petersen (1999).
   [*Zeppelina monostyla* (Zeppelin 1883)] Germany. *Fide* George and Petersen (1991).
   [*Zeppelina mediopigmentata* Gillandt, 1979. Germany, North Sea, Helgoland; burrows in shells, intertidal]. *Fide* George and Petersen (1991).
6. *Dodecaceria coralii* (Leidy, 1855). W North Atlantic, New England.
7. *Dodecaceria diceria* Hartman, 1951. Gulf of Mexico, SW Florida, 215 m in bivalve shells.
8. *Dodecaceria fewkesi* Berkeley & Berkeley, 1954. NE Pacific, British Columbia to California, intertidal.
   [*Sabella pacifica* Fewkes, 1889. California]. *Fide* Berkeley and Berkeley (1954).
9. *Dodecaceria fimbriata* (Verrill, 1879). W North Atlantic, E Canada to New England, bores into mollusc shells.
10. *Dodecaceria fistulicola* Ehlers, 1901. SE Pacific, Chile.
11. *Dodecaceria gallardoi* Carrasco, 1977b. SE Pacific, Chile. [May be a synonym of *D. opulens*].
12. *Dodecaceria gravieri* (McIntosh, 1911). Off Cadiz, west of Straits of Gibraltar, 415 m.
13. *Dodecaceria inhamata* (Hoagland, 1919). Bermuda. Indeterminate.
14. *Dodecaceria joubini* Gravier, 1906. Red Sea.
15. *Dodecaceria laddi* Hartman, 1954. Central Pacific, Marshall Islands, Eniwetok Atoll.

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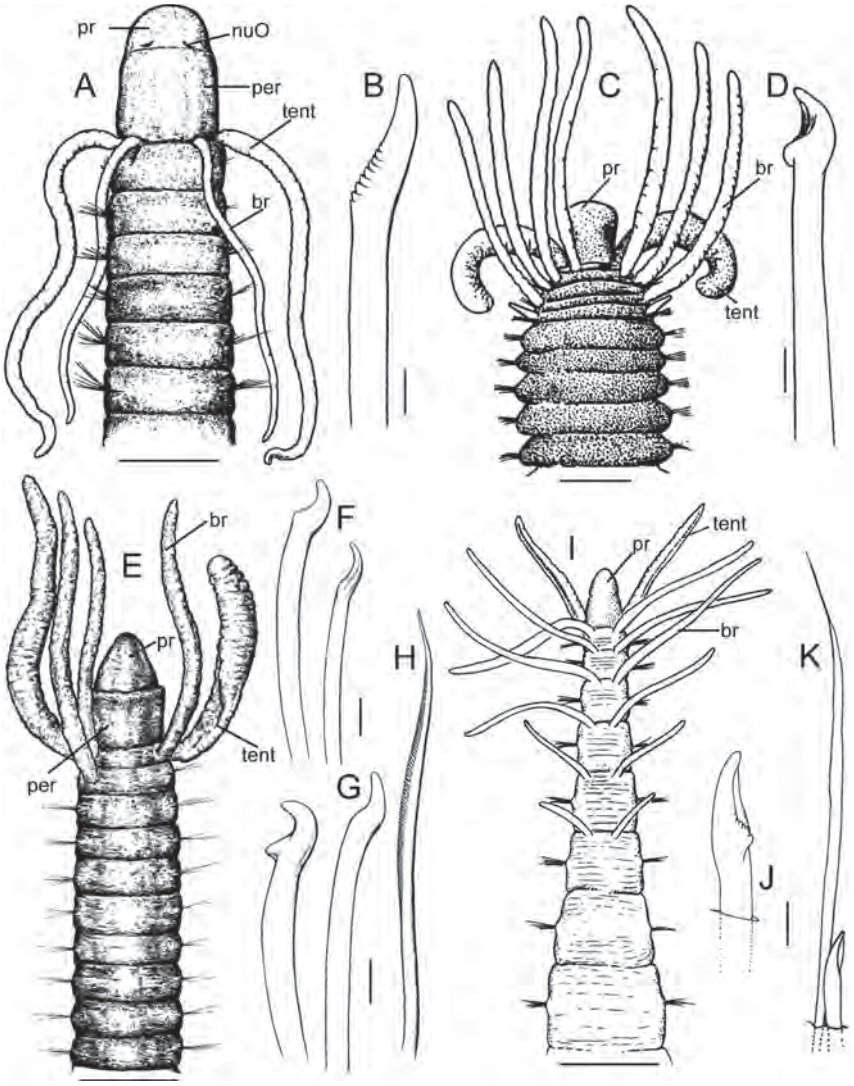


**Fig. 7.3.1.5.21:** Examples of species of *Dodecaceria*. A, B, *Dodecaceria diceria*: A, anterior end, dorsal view; B, neuropodial acicular spine with serrated edge. C, D, *Dodecaceria fewkesi*. C, anterior end, dorsal view; D, neuropodial spoon-shaped hook. E–H, *Dodecaceria laddi*: E, anterior end, dorsal view; F, notopodial acicular spines from an anterior segment; G, neuropodial acicular spines from a far posterior segment; H, capillary chaeta from an anterior segment. I–K, *Dodecaceria* sp. from California: I, anterior end, dorsal view; J, spoon-shaped neuroacicular spine; K, capillary chaeta and acicular spine from a posterior notopodium. Scale bars: A, C, E, I, 500 µm; B, D, F, G, H, J, K, 20 µm. A, B, After Hartman (1951); C, D, after Blake (1996); E, F, after Hartman (1954); I–K after Blake (1996 as *Dodecaceria concharum*).

16. *Dodecaceria meridiana* Elias & Rivero, 2008. SW Atlantic, Argentina. Bores into rock.
17. *Dodecaceria opulens* Gravier, 1908. SE Pacific, Peru. [*Dodecaceria choromytilicola* Carrasco, 1977a]. SE Pacific, central Chile, bores into shells of mussels.
18. *Dodecaceria pulchra* Day, 1955. South Africa.
19. *Dodecaceria saxicola* (Grube, 1855). Mediterranean Sea.
20. *Dodecaceria sextentaculata* (Delle Chiaje, 1828). Naples, Italy.

## References


Aguilar-Camacho, J.M. & Salazar-Vallejo, S.E. (2011): *Dodecaceria carolinae* n. sp. (Polychaeta: Cirratulidae), a shallow-water species from the northwestern Caribbean Sea. *Scientia Marina* 75(1): 95–102.

Augener, H. (1923): Polychaeten von den Auckland und Campbell-Inseln. *Videnskabelige Meddelelser Naturhistorisk Forening i K&benhavn* 75: 1–115, 44 figures.

Banse, K. (1969): Acrocirridae n. fam. (Polychaeta Sedentaria). *Journal of the Fisheries Research Board of Canada* 26: 2595–2620.

Barsby, T., Kicklighter, C.E., Hay, M.E., Sullards, M.C. & Kubanek, J. (2003): Defensive 2-alkylpyrrole sulfamates from the marine annelid *Cirriformia tentaculata*. *Journal of Natural Products* 66: 1110–1112.

Baskin, D.G. (1976): The fine structure of polychaete septate junctions. *Cell and Tissue Research* 174: 55–67.

Bellan, G. (2001): Polychaeta. In: Costello, M.J., *et al.* (ed.) *European Register of Marine Species: A Check-List of the Marine Species in Europe and a Bibliography of Guides to Their Identification. Collection Patrimoines Naturels* 50: 214–231. *Muséum National d'Histoire Naturelle, Institute d'écologie et de gestion de la biodiversité service du patrimoine naturel, Paris*

Berkeley, E. & Berkeley, C. (1952): Annelida. Polychaeta Sedentaria. *Canadian Pacific Fauna* 9b (Part 2) Fisheries Research Board of Canada: 1–139.

Berkeley, E. & Berkeley, C. (1954): Notes on the life-history of the polychaete *Dodecaceria fewkesi* (nom. n). *Journal of the Fisheries Research Board of Canada* 11: 326–334.

Bestwick, B.W., Robbins, I.J. & Warren, L.M. (1989): Metabolic adaptations of the intertidal polychaete *Cirriformia tentaculata*


EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

to life in an oxygen-sink environment. *Journal of Experimental Marine Biology and Ecology* 125: 193–202.

Blake, J.A. (1975): The larval development of Polychaeta from the northern California coast. I. *Cirriformia spirabrancha* (Family Cirratulidae). *Transactions of the American Microscopical Society* 94: 179–188.

Blake, J.A. (1991): Revision of some genera and species of Cirratulidae (Polychaeta) from the western North Atlantic. *Ophelia Supplement* 5: 17–30.

Blake, J.A. (1994): Vertical distribution of benthic infauna in continental slope sediments off Cape Lookout, North Carolina. *Deep-Sea Research II* 41: 919–927.

Blake, J.A. (1996): Chapter 8. Family Cirratulidae Ryckholdt, 1851. Including a revision of the genera and species from the eastern North Pacific. In: Blake, J.A., Hilbig, B. & Scott, P.V. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 6. The Annelida Part 3 – Polychaeta: Orbiniidae to Cossuridae.* Santa Barbara Museum of Natural History, Santa Barbara: 263–384.

Blake, J.A. (2006): New species and records of deep-water Cirratulidae (Polychaeta) from off Northern California. *Scientia Marina* 70S3: 45–57.

Blake, J.A. (2015): New species of *Chaetozone* and *Tharyx* (Polychaeta: Cirratulidae) from the Alaskan and Canadian Arctic and the Northeastern Pacific, including a description of the lectotype of *Chaetozone setosa* Malmgren from Spitsbergen in the Norwegian Arctic. *Zootaxa* 3919: 501–552.

Blake, J.A. (2016): *Kirkegaardia* (Polychaeta: Cirratulidae), new name for *Monticellina* Laubier, preoccupied in the Rhabdocoela, together with new records and descriptions of eight previously known and sixteen new species from the Atlantic, Pacific, and Southern Oceans. *Zootaxa* 4166: 1–93.

Blake, J.A. & Baptiste E.M. (1985): Chapter 6. Life history studies on dominant polychaete species from Georges Bank. In: Maciolek-Blake, N., Grassle, J.F. & Neff, J.M. (eds.) *Georges Bank Benthic Infauna Monitoring Program, Final Report for third year of Sampling*. U.S. Department of the Interior, Minerals Management Service, Herndon, VA.: 140–178. [http://marinecadastre.gov/espis/#/search/study/9111].

Blake, J.A. & Göransson, P. (2015): Redescription of *Tharyx killariensis* (Southern) from Ireland and description of two new species of *Tharyx* from the Kattegat, Sweden (Polychaeta: Cirratulidae). *Zootaxa* 4039: 501–515.

Blake, J.A. & Lavesque, N. (2017): A new species of *Chaetozone* (Polychaeta, Cirratulidae) from the Bay of Biscay offshore France, together with a review of *Chaetozone* species from the North Atlantic and adjacent waters. *Zootaxa* 4312: 565–579.

Blake, J.A., Maciolek, N.J., Ota, A.Y. & Williams, I.P. (2009). Long-term benthic infaunal monitoring at a deep-ocean dredged material disposal site off Northern California, *Deep-Sea Research II* 56: 1775–1803.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003a): A contribution to sedentary polychaete phylogeny using 18S rRNA sequence data. *Journal of Zoological Systematics and Evolutionary Research* 41: 186–195.

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003b): New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 29: 279–288.

Brauer, S. (2014): *Untersuchungen zur Phylogenie der Cirratulidae (Annelida)*. Mathematisch-Naturwissenschaftliche Fakultät – University of Bonn, Bonn, Germany. PhD Thesis.

Bumpus, H.C. (1898): The breeding of animals at Woods Holl during the months of June, July, and August. *Science* 8(207): 850–858.

Buzhinskaja, G.N. (1992): An unusual means of brood protection in the polychaete family Cirratulidae. In: *Polychaeta and Their Ecological Significance. Explorations of the Fauna of the Seas*. Zoological Institute, Russian Academy of Sciences, St. Petersburg: 43(51): 14–18, Figs. 7.3.1.5.1–2 [In Russian, with English abstract; translated April 1995 by Dr. A.V. Verashchaka, Russian Academy of Sciences, Moscow].

Carrasco, F.D. (1977a): *Dodecaceria choromyticola* sp. n. (Annelida, Polychaeta, Cirratulidae) perforador de *Choromytilus chorus* (Mytilidae). *Boletin de la Sociedad de Biologia de Concepcion* 51: 63–66.

Carrasco, F.D. (1977b): Polychaeta (Annelida) de Bahia de Concepcion, Chile. Familias Orbiniidae, Cirratulidae, Cossuridae, Capitellidae y Ampharetidae, con la descripcion de tres especies y una subspecie nuevas. *Boletin de la Sociedad de Biologia de Concepcion* 51: 67–92.

Caullery, M. &. Mesnil, F. (1898): Les formes épitoques et l'évolution des Cirratuliens. *Annales de l'université Lyon* 39: 1–200.

Cazaux, C. (1972): Développement larvaire d'Annélides Polychètes (Bassin d'Arcachon) III. *Archives de Zoologie Expérimentale et Générale* 113: 71–108.

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

Chambers, S.J. (2000): A redescription of *Chaetozone setosa* Malmgren, 1867 including a definition of the genus, and a description of a new species of *Chaetozone* (Polychaeta: Cirratulidae) from the northeast Atlantic. *Bulletin of Marine Science* 67: 587–596.

Chambers, S.J. & Woodham, A. (2003): A new species of *Chaetozone* (Polychaeta: Cirratulidae) from deep water in the northeast Atlantic, with comments on the diversity of the genus in cold northern waters. *Hydrobiologia* 496: 41–48.

Chambers, S., Lanera, P. & Mikac, B. (2011): *Chaetozone carpenteri* McIntosh, 1911 from the Mediterranean Sea and records of other bi-tentaculate cirratulids. *Italian Journal of Zoology* 78 (S1): 41–48. http://dx.doi.org/10.1080/11250003.2011.580565.

Che, J. & Dorgan, K.M. (2010a): It's tough to be small: dependence of burrowing kinetics on body size. *The Journal of Experimental Biology* 213: 1241–1250.

Che, J. & Dorgan, K.M. (2010b): Mechanics and kinematics of backward burrowing by the polychaete *Cirriformia moorei. The Journal of Experimental Biology* 213: 4272–4277.

Checon, H.H., Pardo, E.V. & Amaral, A.C.Z. (2016): Breadth and composition of polychaete diets and the importance of diatoms to species and trophic guilds. *Helgoland Marine Research* 70 (19): 1–11. http://dx.doi/10.1186/s10152-016-0469-4.

Christie, G. (1984): A new species of *Tharyx* (Polychaeta: Cirratulidae) from the estuaries in north-east England. *Sarsia* 69: 69–73.

Christie, G. (1985): A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *Journal of the Marine Biological Association of the United Kingdom* 65: 239–254.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Çinar, M.E. (2007): Re-description of *Timarete punctata* (Polychaeta: Cirratulidae) and its occurrence in the Mediterranean Sea. *Scientia Marina* 71(4): 755–764.

Çinar, M.E. (2009): Alien polychaete species (Annelida: Polychaeta) on the southern coast of Turkey (Levantine Sea, eastern Mediterranean), with 13 new records for the Mediterranean Sea. *Journal of Natural History* 43(37–38): 2283–2328.

Çinar, M.E., Dagli, E. & Açik, S. (2011): Annelids (Polychaeta and Oligochaeta) from the Sea of Marmara, with descriptions of five new species. *Journal of Natural History* 45: 2105–2143.

Çinar, M.E. & Ergen, Z. (2007): The presence of *Chaetozone corona* (Polychaeta: Cirratulidae) in the Mediterranean Sea: an alien or native species? *Cahiers de Biologie Marine* 48: 339–346.

Çinar, M.E. & Petersen, M.E. (2011): Re-description of *Cirratulus dollfusi* (Polychaeta: Cirratulidae), and *Fauvelicirratulus* as a new genus. *Journal of the Marine Biological Association of the United Kingdom* 91(2): 415–418.

Claparède, É. (1868): Les annélides chétopodes du Golfe de Naples. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève* 19(2): 313–584, plates I–XVI.

Colgan, D.J, Hutchings, P.A. & Braune, M. (2006): A multigene framework for polychaete phylogenetic studies. *Organisms Diversity & Evolution* 6: 220–235.

Consentino, A. (2013): Small-scale distribution patterns of two cirratulid species with a description of a peculiar early juvenile stage. *Journal of the Marine Biological Association of the United Kingdom* 93(7): 1761–1771.

Costello, D.P., Davidson, M.E., Eggers, A., Fox, M.H. & Henley, C. (1957): *Methods for Obtaining and Handling Marine Eggs and Embryos*. Marine Biological Laboratory, Woods Hole, Massachusetts: 1–247.

Cunningham, J.T. (1887): On some points in the anatomy of Polychaeta. *Quarterly Journal of Microscopical Science, London* 28: 239–278.

Cunningham, J.T. &. Ramage, G.A. (1888): The Polychaeta Sedentaria of the Firth of Forth. *Transactions of the Royal Society of Edinburgh* 33: 635–684, plates 36–47.

Curtis, M.A. (1977): Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. *Ophelia* 16: 9–58.

Dales, R.P. (1951): Notes on the reproduction and early development of the cirratulid *Tharyx marioni* (St. Joseph). *Journal of the Marine Biological Association of the United Kingdom* 30: 113–117.

Dales, R.P. & Warren, L.M. (1980): Survival of hypoxic conditions by the polychaete *Cirriformia tentaculata*. *Journal of the Marine Biological Association of the United Kingdom* 60(2): 509–516.

Dauvin, J.-C., Dewarumez, J.-M. & Gentil, F. (2003): Liste actualisée des espèces d'Annélides Polychètes présentes en Manche. *Cahiers de Biologie Marine* 44(1): 67–95.

Day, J.H. (1967): *A monograph on the Polychaeta of southern Africa*. British Museum of Natural History, London. Publication No. 656: 1–878.

Dean, H.K. (1995): A new species of *Raricirrus* (Polychaeta: Ctenodrilidae) from wood collected in the Tongue of the Ocean, Virgin Islands. *Proceedings of the Biological Society of Washington* 108(2): 169–179.

Dean, H.K. & Blake, J.A. (2007): *Chaetozone* and *Caulleriella* (Polychaeta: Cirratulidae) from the Pacific coast of Costa Rica, with description of eight new species. *Zootaxa* 1451: 41–68.

Dean, H.K. & Blake, J.A. (2009): *Monticellina* (Polychaeta: Cirratulidae) from the Pacific coast of Costa Rica with descriptions of six new species. *Zoosymposia* 2: 105–126.

Dean, H.K. & Blake, J.A. (2016): *Aphelochaeta* (Polychaeta: Cirratulidae) from the Pacific coast of Costa Rica, with a description of five new species. *Zootaxa* 4103(2): 101–116.

Dehorne, A. (1933): La schizometamerie et les segmentes tetragemmes de *Dodecaceria caulleryi* sp. n. *Bulletin Biologique de la France et de la Belgique* 67: 298–326, plates 10–12.

Doner, S.A. & Blake, J.A. (2006): New species of Cirratulidae (Polychaeta) from the northeastern United States. *Scientia Marina* 70S: 65–73l.

Doner, S.A. & Blake, J.A. (2009): Two new species of *Aphelochaeta* (Polychaeta: Cirratulidae) from deep water off northern California. *Zoosymposia* 2: 127–137.

Dorgan, K.M., Jumars, P.A., Johnson, B., Boudreau, B.P. & Landis, E. (2005): Burrow extension by crack propagation. *Nature* 433: 475.

Dorgan, K.M., Lefebvre, S., Stillman, J.H. & Keohl, M.A.R. (2011): Energetics of burrowing by the cirratulid polychaete *Cirriformia moorei*. *The Journal of Experimental Biology* 214: 2202–2214.

Dyrssen, A. (1912): Zur Kenntnis des feineren Baues des Haemocoels bei einigen Anneliden. *Zeitschrift für Naturwissenschaften, Jena* 48: 365–398.

Ehlers, E. (1908): Die Bodensässignen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898–1899. Im Auftrage des Reichsamtes des Innern, herausgeben von Carl Chun, Professor der Zoologie in Leipzig, Leiter der Expedition* 16(1): 1–168.

Elias, R. & Rivero, M.S. (2008): Two new species of *Caulleriella* (Polychaeta: Cirratulidae) from Argentina. *Iheringia Serie Zoología* 98: 225–230.

Elias, R. & Rivero, M.S. (2009a): First new *Dodecaceria* (Polychaeta: Cirratulidae) species from the SW Atlantic (38ºS – 57ºW, Argentina). *Revista de Biologia Marina y Oceanografia* 44: 131–136.

Elias, R. & Rivero, M.S. (2009b): Two new species of Cirratulidae (Annelida: Polychaeta) from Mar del Plata, Argentina (SW Atlantic). *Zoosymposia* 2: 139–148.

Elias, R. & Rivero, M.S. (2011). A new species of Cirratulidae (Polychaeta) with characteristics of three genera, and a key to the known species around Mar del Plata (south-western Atlantic). *Journal of the Marine Biological Association of the United Kingdom* 91: 1529–1535.

Elias, R., Rivero, M.S. & Orensanz, J.M. (2016): New species of *Monticellina* and *Chaetozone* (Polychaeta: Cirratulidae) in the SW Atlantic, and a review of Monticellina species. *Journal of the Marine Biological Association of the United Kingdom* 1–11. [published online, June 6, 2016]. http://dx.doi.org/10.1017/s0025315416000771.

Evans, J.W. (1969): Borers in the shell of the sea scallop, *Placopecten magellanicus*. *American Zoologist* 9: 775–782.

Farke, H. (1979): Population dynamics, reproduction and early development of *Tharyx marioni* (Polychaeta, Cirratulidae) on tidal flats of the German Bight. *Veröffentlichungen des Instituts für Meeresforschung.in Bremerhaven* 18: 69–99.

Fauchald, K. (1977): The polychaete worms, definitions and keys to the orders, families and genera. *Natural History Museum of*

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

*Los Angeles County: Los Angeles, CA (USA), Science Series* 28: 1–188.
Fauchald, K. & Rouse, G.W. (1997): Polychaete systematics: Past and present. *Zoologica Scripta* 26: 71–138.
Fauvel, P. (1916): Annélides polychètes des Iles Falkland recuellies par M. Rupert Vallentin Esqre (1902–1910). *Archives de Zoologie Experimentale de Generale* 55: 417–482, plates VIII–IX.
Fauvel, P. (1927): Polychètes sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. *Faune de France* 16: 1–494.
Gallardo, V. (1967): Polychaeta from the Bay of Nha Trang, South Viet Nam. *NAGA Report, Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand 1959–1961*, 4(3): 35–279.
Gardiner, S.L. (1992): Chapter 2.2. Polychaeta: General organization, integument, musculature, coelom, and vascular system. In: Harrison, F.W. & Gardiner, S.L. (eds.) *Microscopic Anatomy of Invertebrates Volume 7: Annelida*. Wiley-Liss Inc.: 19–52. New York.
George, J.D. (1963): Behavioural differences between larval stages of *Cirriformia tentaculata* (Montagu) from Drake's Island (Plymouth Sound) and from Southampton Water. *Nature* 199: 195.
George, J.D. (1964a): The life history of the cirratulid worm, *Cirriformia tentaculata* on an intertidal mudflat. *Journal of the Marine Biological Association of the United Kingdom* 44: 47–65.
George, J.D. (1964b): On some environmental factors affecting the distribution of *Cirriformia tentaculata*, on an intertidal mudflat. *Journal of the Marine Biological Association of the United Kingdom* 44: 473–478.
George, J.D. (1967): Cryptic polymorphism in the cirratulid polychaete *Cirriformia tentaculata*. *Journal of the Marine Biological Association of the United Kingdom* 47: 75–79.
George, J.D. (1968): The effect of the 1962–63 winter on the distribution of the cirratulid polychaetes, *Cirratulus cirratus* (Müller) and *Cirriformia tentaculata* (Montagu) in the British Isles. *Journal of Animal Ecology* 37: 321–337.
George, J.D. & Petersen, M.E. (1991): The validity of the genus *Zeppelina* Vaillant (Polychaeta: Ctenodrilidae). *Ophelia* Supplement 5: 89–100.
Gherardi, M., Margherita, S., Lepore, E., Todisco, G. & Giangrande, A. (2007): The role of schizogenesis in population dynamics of *Timarete filigera* (Polychaeta: Cirratulidae): 2 years observations in the Port of Bari (South Adriatic Sea). *Marine Ecology* 28: 306–314.
Gibbs, P.E. (1971): A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. *Journal of the Marine Biological Association of the United Kingdom* 51: 745–769.
Gibbs, P.E., Langston, W.J., Burt, G.R. & Pascoe, P.L. (1983): *Tharyx marioni* (Polychaeta): a remarkable accumulator of arsenic. *Journal of the Marine Biological Association of the United Kingdom* 63: 313–325.
Gibson, P.H. (1977): Reproduction in the cirratulid polychaetes *Dodecaceria concharum* and *D. pulchra*. *Journal of Zoology London* 182: 89–102.
Gibson, P.H. (1978): Systematics of *Dodecaceria* (Annelida: Polychaeta) and its relation to the reproduction of its species. *Zoological Journal of the Linnaean Society* 63: 275–287.
Gibson, P.H. (1979): The specific status of the two cirratulid polychaetes, *Dodecaceria fimbriata* and *D. caulleryi*, compared by their morphology and methods of reproduction. *Canadian Journal of Zoology* 57: 1443–1451.
Gibson, P.H. (1981): Gametogenesis in the cirratulid polychaetes *Dodecaceria concharum* and *D. caulleryi*. *Journal of Zoology, London* 193: 355–370.
Gibson, P.H. (1992): The feeding in the cirratulids *Dodecaceria fimbriata* and *D. concharum*. *Polychaete Research* 14: 4.
Gibson, P.H. (1996): Distribution of the cirratulid polychaetes *Dodecaceria fimbriata*, *D. concharum*, and *D. diceria* in European waters between latitudes 48°N and 70°N. *Journal of the Marine Biological Association of the United Kingdom* 76: 626–635.
Gibson, P.H. (1997): The nuchal organs and the nervous system of the head of four species of the cirratulid *Dodecaceria*. *Polychaete Research* 17: 6–8.
Gibson, P.H. & Clark, R.B. (1976): Reproduction in *Dodecaceria caulleryi* (Polychaeta: Cirratulidae). *Journal of the Marine Biological Association of the United Kingdom* 56: 649–674.
Gibson, P.H. & Heppell, D. (1995): Case 2899. *Dodecaceria concharum* Örsted, 1843 and *Heterocirrus fimbriatus* Verrill, 1879 (currently *D. fimbriata*) (Annelida, Polychaeta): proposed conservation of the specific names by the designation of a neotype for *D. concharum*. *Bulletin of Zoological Nomenclature* 52: 27–33.
Goodrich, E.S. (1945): The study of nephridia and genital ducts since 1895. *Quarterly Journal of Microscopical Science, London* 86(2–4): 113–392.
Grossi, L, Bertasi, F. & Trabucco, B. (2017): New records of the alien polychaete *Chaetozone corona* (Polychaeta: Cirratulidae) in the Adriatic Sea. *Acta Adriatica* 58: 235–244.
Halt, M.N., Rouse, G.W., Petersen, M.E. & Pleijel, F. (2006): Chapter 11. Cirratuliformia. In: Rouse, G. & Pleijel, F. (eds.) *Reproductive Biology and Phylogeny of Annelida.* Science Publishers, Enfield, NH, USA: 497–520.
Hartman, O. (1951): The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Sciences* 2: 7–124.
Hartman, O. (1954): Marine annelids of the northern Marshall Islands. *U.S. Geological Survey Professional Paper* 260-Q: 619–643.
Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation Publications, Occasional Paper* 23: 1–628.
Hartman, O. (1960): Systematic account of some marine invertebrate animals from the deep basins of Southern California. *Allan Hancock Pacific Expeditions* 22: 69–215, 19 plates.
Hartman, O. (1961): Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* 25: 1–226, 34 plates.
Hartman, O. (1963): Submarine canyons of Southern California Part III. Systematics: Polychaetes. *Allan Hancock Pacific Expeditions* 27: 1–93.
Hartman, O. (1966): Polychaetous annelids of the Hawaiian Islands. *Occasional Papers of Bernice P. Bishop Museum* 23(11): 163–252.
Hartmann-Schröder, G. (1962): Zweiter Beitrag zur Polychaetenfauna von Peru. *Kieler Meeresforschungen* 18: 109–147.
Hartmann-Schröder, G. (1996): *Annelida, Borstenwürmer, Polychaeta*. 2nd ed. Die Tierwelt Deutschlands 58: 1–648. Gustav Fischer, Jena.
Hilbig, B. & Blake, J.A. (2000): Long-term analysis of polychaete-dominated benthic infaunal communities in Massachusetts Bay. *Bulletin of Marine Science* 67: 147–164.

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Hily, C. (1987): Spatio-temporal variability of *Chaetozone setosa* (Malmgren) populations on an organic gradient in the Bay of Brest, France. *Journal of Experimental Marine Biology and Ecology* 112: 201–216.

Hutchings, P. & Murray, A. (1984): Taxonomy of polychaetes from the Hawkesbury River and the southern estuaries of New South Wales, Australia. *Records of the Australian Museum* 36: 1–118 + Supplement 3.

International Commission on Zoological Nomenclature. (2003). Opinion 2019 (Case 2899) *Dodecaceria concharum* Örsted, 1843 and *Heterocirrus fimbriatus* Verrill, 1879 (currently *D. fimbriata)* (Annelida, Polychaeta): Conservation of usage of the names by the designation of a neotype for *D. concharum* not approved. *Bulletin of Zoological Nomenclature* 60: 66–67.

Jenner, R. (1932): Evolution morphologique et fonctionnelle du stomodeum des polychètes. *Recueil de l'Institut Zoologique Torley-Rousseau* 4: 5–30.

Judd, T.E. (1968): *The presence of an amine which discourages predation on* Cirriformia spirabrancha. Unpublished manuscript, Hopkins Marine Station, Stanford University, Pacific Grove, California.

Jumars, P.A. (1975): Target species for deep-sea studies in ecology, genetics, and physiology. *Zoological Journal of the Linnaean Society* 57: 341–348.

Jumars, P.A., Dorgan, K.M. & Lindsey, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520 [+ Supplemental Appendix A. Family-by-Family Updates: A1–A350 + Supplemental Table of Guild Characteristics: 1–14].

Keferstein, W. (1862): Untersuchungen über niedere Seethiere. *Zeitschrift für wissenschaftliche Zoologie* 12: 1–147.

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

Khlebovich, V.V. (1958): On two forms of the polychaete *Cirratulus cirratus* (O.F. Müller). *Reports of the Academy of Sciences of the USSR* 123(2): 375–376 [In Russian, Translated to English in 1958 in *Doklady Akademyia Nauk SSSR* (Biological Section Translations) 123:1004–1005].

Kicklighter, C.E., Kubanek, J., Barsby, T. & Hay, M.E. (2003): Palatability and defense of some tropical infaunal worms: alkylpyrrole sulfamates as deterrents to fish feeding. *Marine Ecology Progress Series* 263: 299–306.

Knox, G.A. (1971): *Dodecaceria berkelyi* n.sp., a polychaete (family Cirratulidae) from New Zealand. *Journal of the Fisheries Research Boar of Canada* 28: 1437–1443.

Langerhans, P. (1884): Die Wurmfauna von Madeira. Part 4. *Zeitschrift für wissenschaftlich Zoologie Leipzig* 40: 247–285, plates 15–17.

Lanzavecchia, G., Eguileor, M. & Valvassori, R. (1988). Muscles. In: Westheide, W. & Hermans, C.O. (eds.) *The Ultrastructure of Polychaeta. Microfauna Marina* 4: 71–88.

Laubier, L. (1961): *Monticellina heterochaeta* n. g., n. sp., Cténodrilide (Polychètes Sèdentaires) des vases côtières de Banyuls-sur-Mer. *Vie et Milieu* 11: 601–604.

Laubier, L. (1966): Sur la position systèmatique de *Monticellina heterochaeta* Laubier, 1961. *Bulletin de la Société Zoologique de France* 91: 631–638.

Lechapt, J.-P. (1983a): Structure et dynamique d'une population de *Chaetozone setosa* (Polychaeta Cirratulidae) en Rance maritime. *Bulletin de la Société Scientifique de Bretagne* 55: 15–24.

Lechapt, J.-P. (1983b): *Chaetozone setosa* Malmgren, 1867 (Annelida Polychaeta Cirratulidae). Observations en Rance maritime. *Bulletin de la Société scientifique de Bretagne* 55: 25–33.

Lechapt, J.-P. (1994): *Tharyx retierei*, a new species of Cirratulidae (Annelida: Polychaeta) from the Atlantic coast of Morocco. *Journal of the Marine Biological Association of the United Kingdom* 74: 413–418.

Le Garrec, V., Grall, J., Chevalier, C., Guyonnet, B., Jourde, J., Lavesque, N., Bonifacio, P. & Blake, J.A. (2017): *Chaetozone corona* (Polychaeta, Cirratulidae) in the Bay of Biscay: a new alien species for the North-east Atlantic waters? *Journal of the Marine Biological Association of the United Kingdom* 97: 433–455. http://dx.doi.org/10.1017/S0025315416000540.

Lezzi, M., Çinar, M.E. & Giangrande, A. (2016): Two new species of Cirratulidae (Annelida: Polychaeta) from the southern coast of Italy. *Marine Biodiversity* 46: 681–686. http://dx.doi.org/10.1007/s12526-015-0418-5

Magalhães, W.F. (2015): *Reef and shore polychaetes of Hawaii and the western Pacific Islands*. University of Hawaii at Manoa. (ProQuest 10085604). Doctoral dissertation.

Magalhães, W.F. & Bailey-Brock, J.H. (2010): Redescription of *Cirriformia crassicollis* (Kinberg, 1866) and *Timarete hawaiiensis* (Hartman, 1956) new combination (Polychaeta: Cirratulidae), endemic polychaetes to the Hawaiian Islands. *Zootaxa* 2626: 53–62.

Magalhães, W.F. & Bailey-Brock, J.H. (2013a): Bitentaculate Cirratulidae (Annelida: Polychaeta) from the northwestern Pacific Islands with description of nine new species. *Zootaxa* 3630(1): 80–116.

Magalhães, W.F. & Bailey-Brock, J.H. (2013b): A new species of *Protocirrineris* (Polychaeta: Cirratulidae) from Hawaii including a redescription of the New Zealand *Protocirrineris nuchalis*. *New Zealand Journal of Zoology* 49(3): 196–204.

Magalhães, W.F. & Bailey-Brock, J.H. (2015): A new species and two new records of Cirratulidae (Annelida: Polychaeta) from Guam, Mariana Islands. *Journal of the Marine Biological Association of the United Kingdom* 95: 941–946.

Magalhães, W.F., Bailey-Brock, J.H. & Davenport, J.S. (2011): On the genus *Raphidrilus* Monticelli, 1910 (Polychaeta: Ctenodrilidae) with description of two new species. *Zootaxa* 2804: 1–14.

Magalhães, W.F., Seixas, V.C., Paiva, P.C. & Elias, R. (2014): The multitentaculate Cirratulidae of the genera *Cirriformia* and *Timarete* (Annelida: Polychaeta) from shallow waters of Brazil. *PlosOne* 9(11): 1–20.

Magalhães, W.F., Weidhase, M., Schulze, A. & Bailey-Brock, J.H. (2016): Taxonomic remarks on the genus *Ctenodrilus* (Annelida: Ctenodrilidae) including a description of a new species from the Pacific Ocean. *Zootaxa* 4103: 325–343.

Marcel, R. (1962): Sur quelques larves aberrantes de *Dodecaceria concharum* Oersted (Annélide Polychète). *Mémoires de la Societé Nationale des Sciences Naturelles et Mathématiques de Cherbourg* 50: 61–70.

Marcel, R. (1963): Contribution à l'étude de la vascularisation chez *Dodecaceria concharum* Oersted (Annélide Polychète). *Bulletin de la Société Zoologique de France* 88: 467–474.

Martin, E.A. (1933): Polymorphism and methods of asexual reproduction in the annelid, *Dodecaceria*, of Vineyard Sound. *Biological Bulletin* 65: 99–105.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Mastrodonato, M., Gherardi, M., Todisco, G., Sciscioli, M. & Lepore, E. (2006): The epidermis of *Timarete filigera* (Polychaeta, Cirratulidae): Histochemical and ultrastructural analysis of the gland cells. *Tissue and Cell* 38: 279–284.

McHugh, D. (2000): Molecular phylogeny of the Annelida. *Canadian Journal of Zoology* 78: 1873–1884.

McIntosh, C.C.A. (1915): *A monograph of the British Annelids. Polychaeta. Opheliidae to Ammocharidae*. Vol. 3 part 1, pp. i–vi + 1–368; part 2, plates 88–111. Ray Society, London.

Mead, A.D. (1898): The breeding of animals at Woods Holl during the month of April, 1898. *Science* 7(177): 702–703.

Meredith, T.L., Cowart, J.D., Henkel, T.P. & Pawlik, J.R. (2007): The polychaete *Cirriformia punctata* is chemically defended against generalist coral reef predators. *Journal of Experimental Marine Biology and Ecology* 353: 198–202.

Mesnil, F. & Caullery, M. (1897) Sur la position systématique du genre *Ctenodrilus* Clap.; ses affinités avec les Cirratuliens. *Comptes Rendus de l'Académie des Sciences Paris* CXXV: 542–544.

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

Michel, C. (1978): Étude histologique, histochimique et cytologique du stomodeum chez la polychète sédentaire, *Audouinia tentaculata* (Montagu). *Cahiers de Biologie Marine* 19: 433–446.

Milanovich, F.P., Spies, R., Guram, M.S. & Sykes, E.E. (1976): Uptake of copper by the polychaete *Cirriformia spirabrancha* in the presence of dissolved yellow organic matter of natural origin. *Estuarine and Coastal Marine Science* 4: 585–588.

Monro, C.C.A. (1930): Polychaete worms. *Discovery Reports* 2: 1–222, 91 figures.

Okuda, S. (1946): Studies on the development of the Annelida Polychaeta. I. *Journal of the Faculty of Sciences Hokkaido Imperial University* 9: 115–219, 17 plates.

Olive, P.J.W. (1970): Reproduction of a Northumberland population of the polychaete *Cirratulus cirratus*. *Marine Biology* 5: 259–273.

Olive, P.J.W. (1971): Ovary structure and oogenesis in *Cirratulus cirratus* (Polychaeta: Cirratulidae). *Marine Biology* 8: 243–259.

Olive, P.J.W. (1973): The regulation of ovary function in *Cirratulus cirratus* (Polychaeta). *General and Comparative Endocrinology* 20: 1–15.

Omena, E. & Creed, J.C. (2004): Polychaete fauna of seagrass beds (*Halodule wrightii* Ascherson) along the coast of Rio de Janeiro (southeast Brazil). *Marine Ecology* 25: 273–288.

Orrhage, L. (1964): Anatomische und morphologische studien über die polychaetenfamilien Spionidae, Disomidae und Poecilochaetidae. *Zoologiska bidrag från Uppsala* 36: 335–405.

Örsted, A.S. (1843): *Annulatorum danicorum conspectus. Fasc. 1 Maricolae (Quæstio ab universitate Hafniensi ad solvendum proposita et proemio ornata)*. Librariae Wahlianae, Hafniae, Copenhagen: 1–52. http://www.biodiversitylibrary.org/bibliography/11849.

Osborn, K.J. & Rouse, G.W. (2011): Phylogenetics of Acrocirridae and Flabelligeridae (Cirratuliformia, Annelida). *Zoologica Scripta* 40: 204–219.

Oyenekan, J.A. (1987): Population dynamics and secondary production in an estuarine population of *Caulleriella caputesocis* (Polychaeta: Cirratulidae). *Marine Biology* 95: 267–273.

Paiva, P.C., Seixas, V.C., Zanol, J. & Magalhães, W.F. (2016): Population genetic structure of a *Timarete punctata* complex species and their potential for biological invasion. *12th International Polychaete Conference*: 81 (Abstract).

Pardo, E.V. & Amaral, A.C.Z. (2004): Feeding behavior of the cirratulid *Cirriformia filigera* (Delle Chiaje, 1825) (Annelida: Polychaeta). *Brazilian Journal of Biology* 64: 283–288.

Penry, D.L. & Jumars, P.A. (1990): Gut architecture, digestive constraints and feeding ecology of deposit-feeding and carnivorous polychaetes. *Oecologia* 82: 1–11.

Petersen, M.E. (1991): A review of asexual reproduction in the Cirratulidae (Annelida: Polychaeta), with redescription of *Cirratulus gayheadius* (Hartman, 1965), new combination, and emendation or reinstatement of some cirratulid genera. *Bulletin of Marine Science* 48: 592 (Abstract).

Petersen, M.E. (1999): Reproduction and development in Cirratulidae (Annelida: Polychaeta). *Hydrobiologia* 402: 107–128.

Petersen, M.E. & George, J.D. (1991): A new species of *Raricirrus* from northern Europe, with notes on its biology and a discussion of the affinities of the genus (Polychaeta: Ctenodrilidae). *Ophelia* Supplement 5: 185–208.

Picton, L.J. (1899): On the heart-body and coelomic fluid of certain Polychaeta. *Quarterly Journal of Microscopical Science, London* 41: 263–302.

Reish, D.J. (1952): Discussion of the colonial tube-building polychaetous annelid *Dodecaceria fistulicola* Ehlers. *Bulletin of the Southern California Academy of Sciences* 51: 103–107.

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

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

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

Rouse, G.W. & Pleijel, F. (2003): Problems in polychaete systematics. *Hydrobiologia* 496: 175–189.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007): A molecular phylogeny of annelids. *Cladistics* 22: 1–23.

Salazar-Vallejo, S.I., Carrera-Parra, L.F. & Fauchald, K. (2008): Phylogenetic affinities of the Flabelligeridae (Annelida, Polychaeta). *Journal of Zoological Systematics and Evolutionary Research* 46: 203–215.

de Saint-Joseph, A. (1894): Les Annélides polychètes des côtes de Dinard. Pt. 3. *Annales des Sciences naturelles, Zoologie Paris* série 7: 1–395.

Schroeder, P.C. & Hermans, C.O. (1975): Annelida Polychaeta. In: Giese, A.C. & Pearse, J.S. (eds.) *Reproduction of Marine Invertebrates. III. Annelids and Echiurans*. Vol. 3. Academic Press, New York: 1–213.

Scott, J.W. (1911): Preliminary account of the early development of *Cirratulus grandis* Verrill. *Science* 33(842): 271.

Shull, D.H. & Yasuda, M. (2001): Size-selective downward particle transport by cirratulid polychaetes. *Journal of Marine Research* 59: 453–473.

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Simboura, N., Kurt Sahin, G., Panagoulia, A. & Katsiaras, N. (2010): Four new alien species on the coasts of Greece (Eastern Mediterranean). *Mediterranean Marine Science* 11: 341–352.

Smith, P.R. (1992): Chapter 2.4. Polychaeta: Excretory System. In: Harrison, F.W. & Gardiner, S.L. (eds.) *Microscopic Anatomy of Invertebrates* Volume 7: *Annelida*. Wiley-Liss, New York: 71–108.

Southern, R. (1914): Claire Island Survey Part 47. Archiannelida and Polychaeta. *Proceedings of the Royal Irish Academy* 31: 1–160, plates 1–15.

Stephenson, W. (1950a): The development of *Cirratulus cirratus* (O.F. Müller). *Report of the Dove Marine Laboratory for 1948:* 7–20.

Stephenson, W. (1950b): An epitokous cirratulid occurring in the Cullercoats tanks. *Report of the Dove Marine Laboratory for 1948*: 21–28, Plate 1.

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

Storch, V. & Schlötzer-Schrehardt, U. (1988): Sensory Structures. In: Westheide, W. & Hermanns, C.O. (eds.) *The Ultrastructure of the Polychaeta. Microfauna Marina* 4: 121–133. Gustav Fischer Verlag, Stuttgart & New York.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Struck, T., Hessling, R. & Purschke, G. (2002): The phylogenetic position of the Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of the 'Polychaeta', based on molecular data from 18S rDNA sequences. *Journal of Zoological Systematics and Evolutionary Research* 40: 155–163.

Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hosel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. (2011). Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.

Struck, T., Purschke, G. & Halanych, K.M. (2006): Phylogeny of Eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA) approach. *Systematic Biology* 55(1): 1–20.

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

Swaney, J.B. & Klotz, I.M. (1971): Properties of erythrocruorin from *Cirriformia grandis*. *Archives of Biochemistry and Biophysics* 147: 475–486.

Taboada, S., Doner, S., Blake, J.A. & Avila, C. (2012): A new species of Cirratulidae (Annelida: Polychaeta) described from a shallow-water whale bone in Antarctica. *Zootaxa* 3340: 59–68.

Vinn, O. (2009): The ultrastructure of calcareous cirratulid (Polychaeta: Annelida) tubes. *Estonian Journal of Earth Sciences* 58: 153–156.

Warren, L.M. (1981): Respiratory adaptations to temporary hypoxia by the polychaete *Cirriformia tentaculata*. *Comparative Biochemistry and Physiology* 69: 321–324.

Warren, L.M., Wells, R.M.G. & Weber, R.E. (1981): Erythrocruorins (extracellular haemoglobins) from the cirratulid polychaetes *Cirriformia tentaculata* (Montagu) and *Cirratulus cirratus* (Müller) with special reference to saturation dependent characteristics of the oxygen equilibria. *Journal of Experimental Marine Biology and Ecology* 55: 11–24.

Webster, H.E. & Benedict, J.E. (1887): The Annelida Chaetopoda from Eastport, Maine. *Reports of the U.S. Fish Commission for 1885:* 707–755, 8 plates.

Weidhase, M., Bleidorn, C. & Helm, C. (2014a): Structure and anterior regeneration of musculature and nervous system in *Cirratulus* cf. *cirratus* (Cirratulidae, Annelida). *Journal of Morphology* 275: 1418–1430.

Weidhase, M., Müller, J. & Bleidorn, C. (2014b): *Starting to eliminate chaos – Phylogeny of Cirratulidae (Annelida) based on molecular data.* Abstract presented at the BioDivEvo Conference.

Weidhase, M., Helm, C. & Bleidorn, C. (2015): Morphological investigations of posttraumatic regeneration in *Timarete* cf. *punctata* (Annelida: Cirratulidae). *Zoological Letters* 1: 20 DOI: http://dx.doi/10.1186/s40851-015-0023-2.

Weidhase, M., Bleidorn, C. & Simon, C.A. (2016): On the taxonomy and phylogeny of *Ctenodrilus* (Annelida: Cirratulidae) with a first report from South Africa. *Marine Biodiversity* 46: 243–252.

Weigert, A. & Bleidorn, C. (2016): Current status of annelid phylogeny. *Organisms Diversity & Evolution* 16: 345–362.

Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. (2014): Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution* 31: 1391–1401.

Whitlatch, R.B. (1980): Patterns of resource utilization and coexistence in marine intertidal deposit feeders. *Journal of Marine Research* 38: 743–765.

Wilson, D.P. (1936): The development of *Audouinia tentaculata* (Montagu). *Journal of the Marine Biological Association of the United Kingdom* 20: 567–579.

Winnepenninckx, B.M.H., Van de Peer, Y. & Backeljau, T. (1998): Metazoan relationships on the basis of 18S rRNA sequences: a few years later. *American Zoologist* 38: 888–906.

Woodham, A. & Chambers, S. (1994): A new species of *Chaetozone* (Polychaeta, Cirratulidae) from Europe, with a redescription of *Caulleriella zetlandica* (McIntosh). In: Dauvin, J.-C., Laubier, L. &. Reish, D.J. (eds). *Actes de la 4ème Conférence Internationale de Polychètes. Mémoires du Muséum National d'Histoire Naturelle (Zoologie)* 162: 307–316.

Worthington, D. (1989): Role of regeneration in respiration of the marine polychaete *Cirriformia* sp. *Pacific Science* 43: 206 (Abstract).

Yoshiyama, R.M. & Darling, J.D.S. (1982): Grazing by the intertidal fish *Anoplarchus purpurescens* upon a distasteful polychaete worm. *Environmental Biology Fisheries* 7: 39–45.

Zrzavý, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189.

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Sergio I. Salazar-Vallejo

### 7.3.1.6 Flabelligeridae Saint-Joseph, 1894

In memory of Dr. Carl Støp-Bowitz 1913–1997

#### Introduction

Flabelligerid polychaetes were called bristle-cage worms by Hartman (1961) and cage-worms by Hartman and Fauchald (1971). The name of the family is based on *Flabelligera* Sars, 1829; this name was built by combining the Latin words for fan (*flabell-*), with the one denoting to carry or to take (*ger-*). The fan is formed by the almost continuous array of chaetae of the first chaetiger, but this long series is limited to a few genera (Figs. 7.3.1.6.1 D, E and 7.3.1.6.2 B) and most have chaetae arranged in fascicles (Figs. 7.3.1.6.1 B, C, F and 7.3.1.6.3 A, B). Furthermore, the anterior end that includes the prostomium, the peristomium, and one or two anterior achaetous segments is retractile, being rarely exposed during preservation (Figs. 7.3.1.6.1 A, B and 7.3.1.6.3 C–E) and has been little studied, which explains the great confusion that has prevailed in the taxonomy within the family. The taxon Flabelligeridae contains about 130 species. The adults of the species of the family can be 10–100 mm long, but the organisms are often overlooked because they have cryptic or burrowing habits. Most genera have been recently illustrated (Salazar-Vallejo 2009), and some additional features are herein presented.

Besides the cephalic cage, flabelligerids are notable because of the thick coating usually with foreign particles adhering to the body papillae in certain species (Figs. 7.3.1.6.1 A and 7.3.1.6.3 C), or the thick, transparent layer or tunic enveloping the body in others (Figs. 7.3.1.6.1 D, E and 7.3.1.6.4 B, C), and especially because their chaetae are multiarticulated (Mesnil 1899), although they are fragile and often lost (Fig. 7.3.1.6.3 D). Furthermore, the members

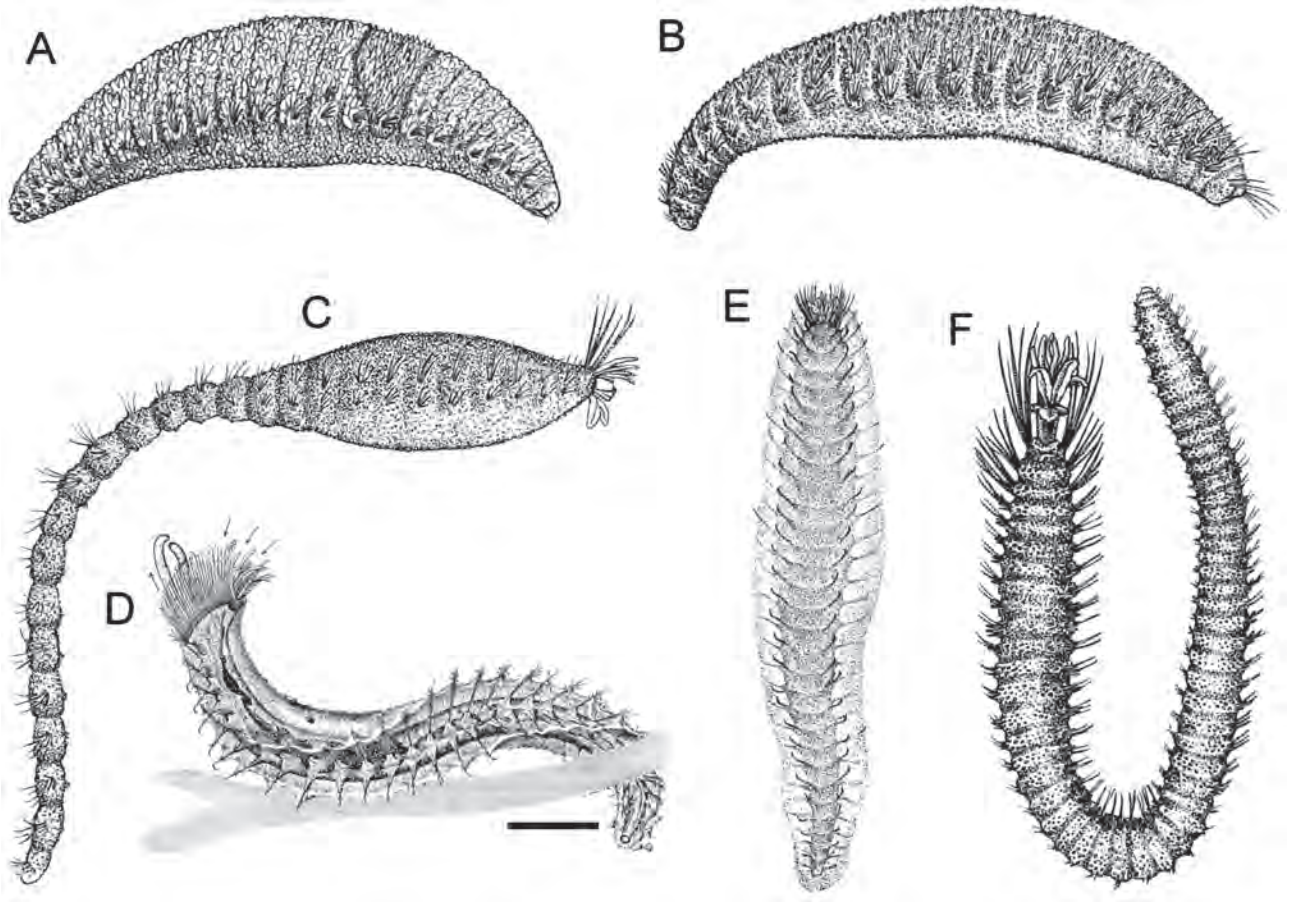


**Fig. 7.3.1.6.1:** Body shape in flabelligerids. A, *Brada granulosa*, lateral view. B. *Brada villosa*, lateral view. C. *Diplocirrus glaucus*, lateral view. D, *Flabelligera affinis* on seaweed. E. Same, ventral view. F. *Pherusa plumosa*, ventral view. Scale bar: D, 1.5 mm. All reproduced with permission. A–C, E, F, From Støp-Bowitz (1948a), © Univ. Oslo; D, from Rasmussen (1973) Ophelia.

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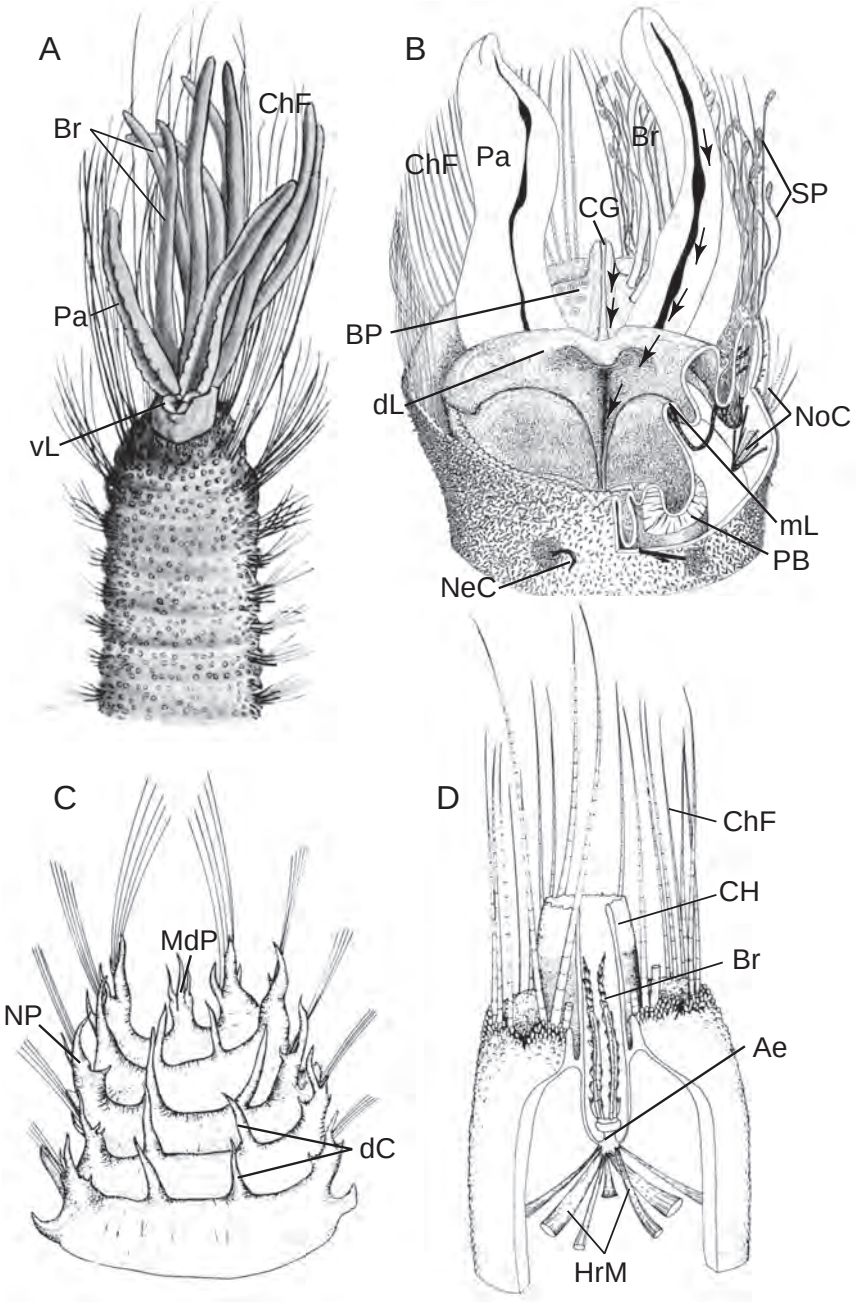


**Fig. 7.3.1.6.2:** Anterior ends of flabelligerids. A, *Pherusa plumosa*. Ventral view, chaetal fan (Chf) surrounding branchiae (Br) and grooved palps (Pa). B, *Flabelliderma commensalis*. Head with the ventral portion of the left removed to show musculature; branchiae and sensory paillae not shown on the right side, arrows indicate currents generated by the ciliation. C, *Piromis capulata*, ventral view, tunic removed showing modified anterior segments. D, *Stylarioides longisetosa*. Ventral part of body wall removed to show withdrawn head. Ae, anterior end (head); BP, branchial plate; Br branchia; CG, ciliary groove; CH, cephalic hood; ChF, chaetal fan; dC, dorsal cirrus; dL, dorsal lip; HrM, head retractor muscle; MdP, middorsal protuberance; mL, median lip; NeC, neurochaeta; NoC, notochaeta; NP, notopodium; Pa, Grooved palp; PB, Pharyngeal bulb; SP, sensory papilla; vL, ventral lip. A, Modified from Schlieper (1927); B–D, modified from Spies (1975), with permission of J. Wiley & Sons Inc.

of the family show several outstanding, unique features in comparison to the remaining polychaete families. For example, flabelligerids possess the longest chaetae compared to their body size, especially in some abyssal forms of the genus *Ilyphagus*, where they can be as long as the entire body (Fig. 7.3.1.6.3 E). The species belonging to *Piromis*, *Pycnoderma*, and *Trophoniella* have the thickest cuticle among the polychaetes (Fig. 7.3.1.6.4 B, C), which has been called a tunic (Salazar-Vallejo *et al*. 2008, Salazar-Vallejo 2009). The nephridia are restricted to a single pair formed by two long, longitudinal sacks that extend along at least the anterior body region, and the nephridiopores are present between the branchial plate and the caruncle (Fig. 7.3.1.6.5 D and 7.3.1.6.6 A, C). The gonads are permanent, and in several genera, they converge in one or two pairs of gonopodial papillae, present as two ventrolateral outgrowths in one or two anterior chaetigers.

Despite these unique features, the family has been little studied in terms of their biology or physiology, and besides the need for more studies dealing with taxonomy, further efforts are needed to better understand the ecology of the group. In fact, the diagnostic chaetal pattern for the family was recently redefined to smooth, multiarticulated

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chaetae, and this resulted in the transfer to Acrocirridae of several genera provided with chaetae having an often detachable cortex and made by a series of rings of tiny spines (Salazar-Vallejo *et al*. 2007, 2008).

## Morphology

### External Morphology

**Body shape and regions.** The body shape of the members of the family is quite variable; it could be basically described as fusiform, tapering toward both ends (Figs. 7.3.1.6.1 A, B and 7.3.1.6.3 D), as cylindrical with blunt anterior ends (Figs. 7.3.1.6.1 D, E and 7.3.1.6.3 E), or as having an anterior swollen region (Figs. 7.3.1.6.1 C and 7.3.1.6.3 A) and a tapering posterior region, without any further remarks. However, the body shape is sometimes modified by parapodial lobes (Fig. 7.3.1.6.3 C), while in others, there is a notorious differentiation in a trunk followed by a marked attenuation in the posterior region, or cauda (Fig. 7.3.1.6.4 A).

**Chaetae.** Most genera have very long chaetae in the first chaetigers, forming a cephalic cage (Fig. 7.3.1.6.2 A, B, D). As stated earlier, only in a few genera such as *Flabelligera* or *Flabelliderma* are the lengthened chaetae restricted to the first chaetiger. In other genera, the anterior long chaetae are arranged in fascicles along a few anterior chaetigers.

**Segmentation.** Species of *Semiodera* have a dorsal shield made up of cemented sediment particles (Fig. 7.3.1.6.3 A). The segments carrying the shield are modified so that the combination of structures functions as a kind of operculum sealing the tube when the animal retracts. The shield may either be well developed and relatively high, although in some cases, the margins are not well defined or even the sediment particles might be very scarce. In this case, the segments are still modified. In *Semiodera* and in *Stylarioides*, there is a relatively long cauda (Fig. 7.3.1.6.4 A), very delicate, that might have a similar role as the corresponding one in Sabellariidae. The cauda, however, is very fragile and might be easily lost during collecting or manipulation, and since the body contracts heavily after fracturing, the broken part might resemble a normal posterior end, and the presence of the cauda might not be recognized.

In the members of most flabelligerid genera, the relative length of the anterior chaetigers varies gradually and slightly, but there are some variations. Thus, in *Diplocirrus*, the anterior segments are very long, and often, several of them might be swollen (Fig. 7.3.1.6.1 C), while in *Semiodera*, the first segments are ventrally reduced. On the other hand, in *Therochaeta* Chamberlin, 1919, the second chaetiger is markedly longer that the neighboring ones, and it is sometimes thinner than the third chaetiger, indicating strongly contracted circular muscle bands with a denser arrangement toward its posterior margin.

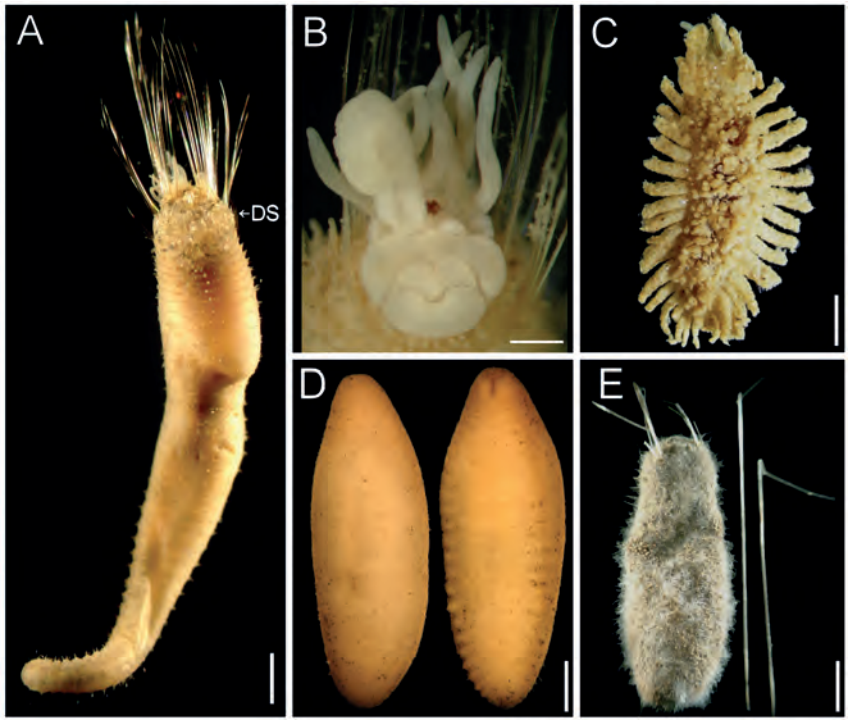


**Fig. 7.3.1.6.3:** A, *Semiodera inflata*, off Los Angeles, dorsal view (DS, dorsal shield). B, *Pherusa* sp, off Santa Barbara, anterior end exposed, ventral view, left palp removed. C, *Flabelliderma papillosa*, same locality, dorsal view. D, *Brada* sp., Alaska, dorsal and ventral views. E, *Ilyphagus bythincola*, off Western Mexico, dorsal view, long chaetae from chaetiger 1. Scale bars: A, 1.3 mm; B, 0.8 mm; C, 1.5 mm; D, 3.7 mm; E, 4 mm. C, From Leslie Harris; others, from SISV.

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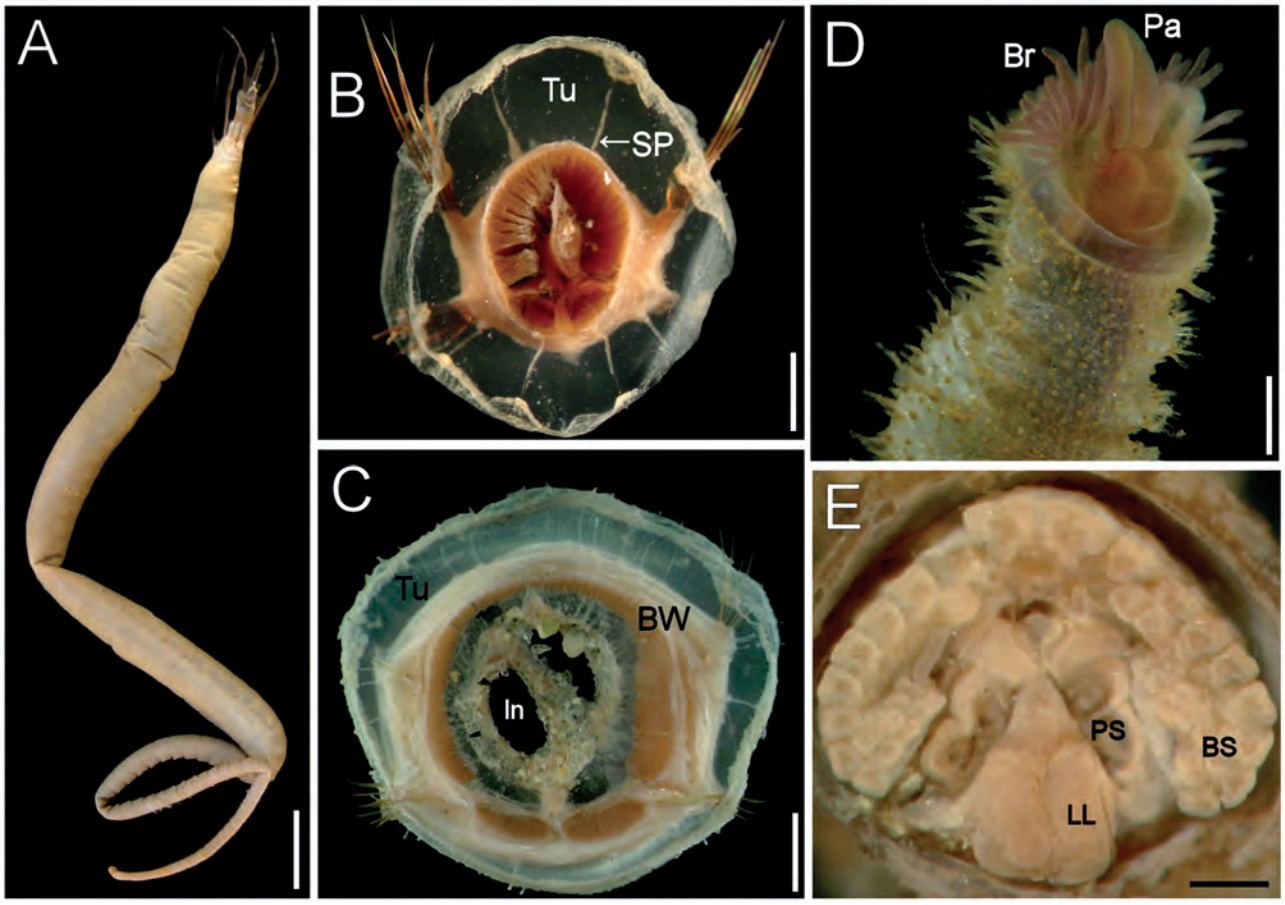


**Fig. 7.3.1.6.4:** A, *Stylarioides monilifer*, Naples, ventral view. B, *Trophoniella* sp., NW Atlantic Ocean, cross-section of anterior chaetiger (SP, sensory papillae; Tu, tunic). C, *Trophoniella* sp., Western Mexico, cross-section of a median chaetiger (BW, body wall; In, intestine; Tu, tunic). D, *Bradabyssa* sp., off Los Angeles, anterior end exposed, ventral view (Br, branchiae; Pa, Palp). E, *Semiodera* sp., same locality, anterior end dissected, branchiae and palps removed (BS, branchial scars; LL, lateral lip; PS, palp scar). Scale bars: A, 7 mm; B, 1.3 mm; C, 1.8 mm; D, 1 mm; E, 0.3 mm. D, From Leslie Harris; others, from SISV.

**Anterior segments.** The structure of the anterior end of flabelligerids is quite consistent (Fig. 7.3.1.6.2 A–D), with the exception of *Buskiella*, which lacks palps and branchiae (Salazar-Vallejo and Zhadan 2007). To distinguish it from the retractile anterior end in sipunculans called an introvert, some century. century zoologists called this eversible tube in Flabelligeridae an oral siphon. Furthermore, the anterior opening of the body is visible ventrally when the anterior end is invaginated (Fig. 7.3.1.6.3 D). The eversible portion was termed "siphon"; thus, Haase (1915: 12) used "vorstreckbarer Sipho" (eversible siphon) in his family diagnosis, and together with McIntosh (1915), he gave special attention to its relative development. Fauvel (1927: 112) used "tube cylindrique retractile" in the family diagnosis, and then used "siphon buccal" in every species diagnosis. The main similarity with the introvert or involucrum in sipunculans is that this eversible portion rolls over itself, while the oral siphon is not rolled, with the sole exception of those genera provided with a long cephalic hood like that present in *Stylarioides* (Fig. 7.3.1.6.2 D). This resemblance was noticed long time ago, prompting Otto (1821) to propose *Siphostoma* (which would become *Siphonostoma* or other orthographic spellings) to indicate the presence of an anterior oral tube or siphon. Others used an alternative word; Sars (1829: 32), for example, used "involucrum" to refer the retractable head. Rioja-LoBianco (1931) used the term "sifón oral," and Milligan (1984: 47.20) referred to it as oral tube.

It must be stressed that this eversible portion includes a nonchaetose, mostly feebly papillated tube; this eversible portion does not include chaetigers. However, it was rather surprising that Filippova *et al*. (2003: 1) concluded that there is no name previously employed for this structure, which is not the case, and that it further includes a chaetigerous segment. This apparent confusion stems

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from the fact that there are changes in the chaetal lobe in relation to its position in each successive segment. Thus, the first few chaetigers have the chaetal lobes anteriorly displaced, so that the first one is in the border line of the segment and, thereafter, the chaetal lobe displaces toward the median region of each segment. This can be noticed when any specimen is observed in lateral view.

In general, the term "head" (prostomium, peristomium and branchial plate) should be preferred to other terms because it is not only the mouth that is included in the eversible part. For its eversion, the head slips along a tube of variable length, the cephalic hood, that when it extends completely, it shows two rings. This tube or siphon is reduced in *Flabelligera* and can be very long in other genera since it could be half as long as the cephalic cage chaetae.

**Prostomium and Peristomium.** The prostomium is a rounded, small lobe, often with four dark eyes (Figs. 7.3.1.6.3 B and 7.3.1.6.4 D, E). However, the eyes are of different size and orientation (Fig. 7.3.1.6.5 A–F); the anterior eyes are often larger and directed anteriorly, whereas the posterior eyes are smaller and directed upward (Spies 1975, Vodopyanov and Purschke 2017). The prostomium posteriorly projects into a caruncle. It consists of a central, elevated fleshy lobe, more or less enlarged basally, tapering distally, often extending beyond the branchial plate and carrying one pair of lateral ciliated ridges. Lateral to the caruncle, a pair of nephridial lobes can often be seen (Fig. 7.3.1.6.5 D), but they are fragile and are easily detached when the branchial filaments are pulled off. The peristomium surrounds the mouth and bears the palps. The palp bases or palpophores have a ciliated, oblique slit, which include the nuchal organs. The mouth consists of a dorsal or superior lip, two often wide lateral lips, and the ventral lip. The latter might be reduced, and sometimes, the anterior pharyngeal lobe can be exposed. These features are better observed once the branchiae and palps have been carefully removed, but the relative distortion modifies their overall pattern (Figs. 7.3.1.6.2 A, B and 7.3.1.6.5 A–F).

**Branchiae.** The branchial pattern is a very important diagnostic feature (Fig. 7.3.1.6.2 A, B, and D). The branchiae are formed in the first two body segments, but they have migrated anteriorly. The direct evidence for this process is that in the genera possessing only a few filaments such as *Pherusa* (Figs. 7.3.1.6.3 B, 7.3.1.6.4 A, and 7.3.1.6.5 A) or *Diplocirrus* (Fig. 7.3.1.6.5 B), two groups of branchial filaments can be distinguished: one distal made up of four filaments and a proximal one with two filaments per side. Each group is associated with a segment and often separated by the nephridial lobes; the indirect evidence comes from the irrigation pattern, as clearly shown by Spies (1973). The two diagnostic features involving branchiae are their number and the relative development of the branchial plate.

A) **Taxa with a few branchial filaments.** The genera having a few branchial filaments have two basic patterns; sometimes, the filaments can be separated by the caruncle in two bilateral arranged groups. Thus, in *Pherusa* or in *Diplocirrus*, there are four distal filaments, while the four proximal ones are separated into two lateral groups, each with two branchiae per side (Figs. 7.3.1.6.2 A, 7.3.1.6.3 B, and 7.3.1.6.5 A, B). In *Poeobius* or in *Ilyphagus*, branchial filaments are arranged in two parallel lines, with filaments alternating in position, although in the former, this organization deserves some further studies (Salazar-Vallejo 2008).

B) **Taxa with many branchial filaments.** Other genera, exhibiting many branchial filaments, could be separated in three basic patters. In the first, the filaments are sessile on a flat branchial plate, either fixed in a single somehow spiral row per side (Fig. 7.3.1.6.4 E), as occurring in *Semiodera* or *Therochaeta*; fixed in a series of concentric rows, like in *Bradabyssa* (Figs. 7.3.1.6.4 B and 7.3.1.6.7 C); or lacking any distinct pattern, like in *Flabelliderma* or *Flabelligera* (Figs. 7.3.1.6.2 B and 7.3.1.6.5 C, D). In the second, the branchial filaments are placed on a tongue-shaped branchial plate often projecting from the rest of the anterior end (Figs. 7.3.1.6.5 E and 7.3.1.6.7 B). Here, the filaments are fixed in two lateral groups separated by the caruncle, as present in *Piromis, Pycnoderma*, or *Trophoniella*. In the third pattern, the branchial filaments are placed over two lateral branchial peduncles, like in *Stylarioides*, where each lateral peduncle bears many filaments, which are arranged in a spiral resembling the pattern of the tentacular crown in serpulids (Figs. 7.3.1.6.2 D, 7.3.1.6.5 F, and 7.3.1.6.7 D).

**Chaetae.** The notochaetae in flabelligerids are multiarticulate, although sometimes, the feature is restricted to their distal regions. The chaetal surface is smooth, while the successive articles might differ in their relative length. On the other hand, the neurochaetae are much more variable; those present in the first few chaetigers are similar to notochaetae being mostly multiarticulate, but most genera have several modifications in subsequent chaetigers. The only exception is *Diplocirrus* because their neurochaetae are all multiarticulate, resembling notochaetae, although being slightly thicker than the latter (Fig. 7.3.1.6.7 E).

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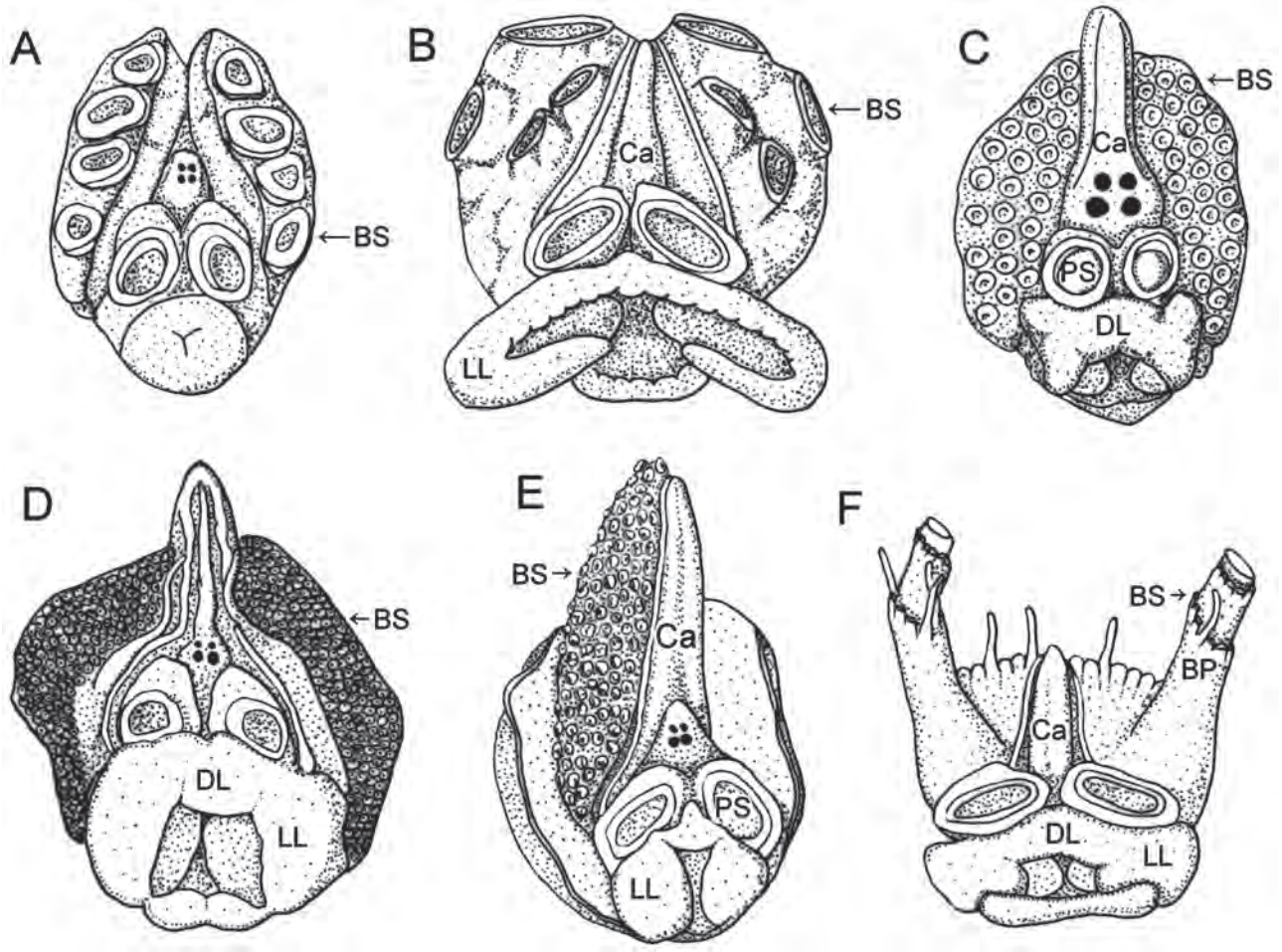


**Fig. 7.3.1.6.5:** Flabelligerid head in frontal view, palps and branchial filaments removed showing different patterns. A, *Pherusa*. B, *Diplocirrus*. C. *Flabelliderma*. D, *Flabelligera*. E, *Piromis*. F. *Stylarioides*. BP, branchial peduncle; BS, branchial scars; Ca, caruncle; DL, dorsal lip; LL, lateral lip; PS, palp scar. Redrawn after Spies (1975) with permission of J. Wiley & Sons Inc.

The neurochaetae can be classified according to their articulation. Thus, they would be multiarticulate if, through most of their length, it has notorious and numerous articles (>10). In case there are only a few articles (<5), they could be called oligo-articulate (Fig. 7.3.1.6.7 F). In some genera like *Flabelligera*, the articulation is mixed, having few, long articles in the handle and ankylosed small articles in the rest of the chaetae with a solid crest (Fig. 7.3.1.6.7 G). They could also be pseudocompound if there is an oblique notch that resembles a true articulation, as, for instance, is found in the chaetae of nereidids or hesionids, but in Flabelligeridae, they lack the articulation membrane and the hinge. It is frequently found that articulations are reduced or markedly reduced throughout the chaetae, such that the articulation is atrophied or anchylosed. In these cases, the anchylosed articles might be medium sized (Fig. 7.3.1.6.7 H). They are usually very short, but they can be noticed throughout the chaetae or at least in their basal and medial parts. In some cases, the articulation has been reduced so much that is noticed only in the nonemergent chaetal portion, while the exposed part is rather homogeneously solid and often with less pigmentation than the rest of the chaeta. Anchylosed neurochaetae are usually tapered, even if falcate, such that they could be regarded as having a cylindrical cross-section (Fig. 7.3.1.6.7 H, I). However, sometimes, they may have a depressed distal region, such that they resemble thin flat blades. They could be called lamispines because they combine a cylindrical basal region with a laminated distal region.

Another means to distinguish neurochaetae is by their tips. Thus, neurochaetal tips may be entire (Fig. 7.3.1.6.7 G, I), they may be aristate if they have a very fine, sharpened projection (Fig. 7.3.1.6.7 J), or they may be bidentate, with a primary tooth and another accessory one. Although it has been already mentioned that the surface of the chaetae is

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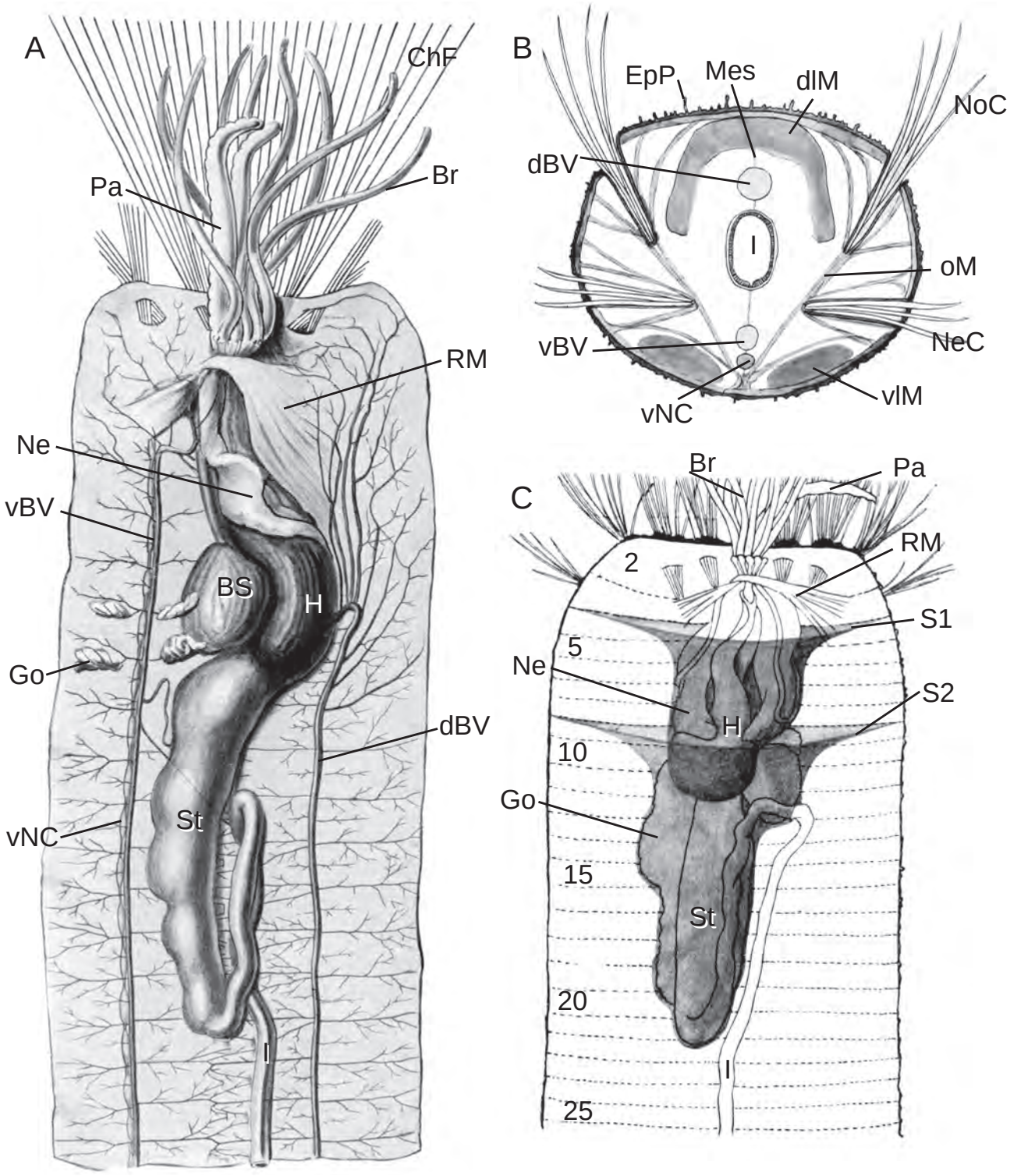


**Fig. 7.3.1.6.6:** Anatomy of *Pherusa plumosa*. A, Dissection of anterior part showing coiled gut (i) with stomach (St), heart (H), nephridium (Ne), gonads (Go), and blood vascular system. B, Cross-section through posterior segment; musculature of the body wall mainly comprised of four strong bundles, chaetal musculature only shown in part. C, Situs of a female individual showing the first two strong septa bulging posteriorly; numerals refer to segment numbers. Br, branchiae; ChF, chaetal fan; dBV, dorsal blood vessel; dlM, dorsal longitudinal musculature; EpP, epidermal papilla; Mes, mesenterium; NeC, neurochaeta; NoC, notochaeta; oM, oblique muscle; Pa, palp; RM, retractor muscle of the head; S1, first septum; S2, second septum; vBV ventral blood vessel; vlM ventral longitudinal musculature; vNC ventral nerve cord. Modified from Schlieper (1927).

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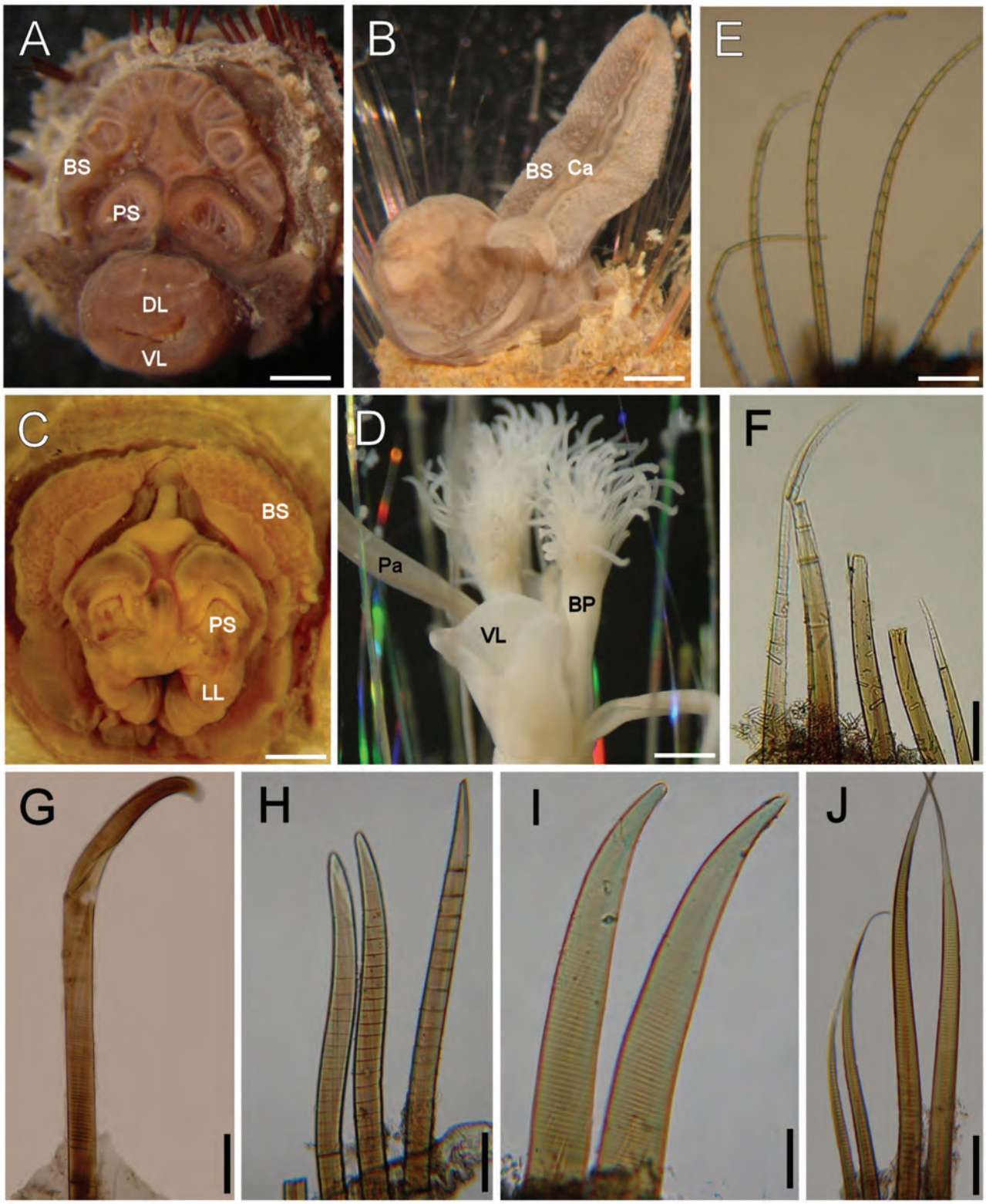


**Fig. 7.3.1.6.7:** A, *Pherusa* sp., frontal view, branchiae and palps removed (BS, branchial scar; DL, dorsal lip; PS, palp scar; VL, ventral lip). B, *Trophoniella* sp., ventrofrontal view, branchiae removed, left palp on site, pharynx everted, slightly damaged (BS, branchial scars; Ca, caruncle). C, *Bradabyssa* sp., frontal view, branchiae and palps removed, nuchal organs border the base of palps (BS, branchial scars; LL, lateral lip; PS, palp scars). D, *Stylarioides* sp., ventral view, palps and branchiae on site (BP, branchial peduncle; Pa, palp; VL, ventral lip). E, Multiarticulate chaetae. F, Oligo-articulate chaetae. G, Oligo-articulate and crested chaeta. H, Medium-sized ankylosed articles. I, Small ankylosed articles. J, Aristate, articles small. Scale bars: A, 0.4 mm; B, 0.9 mm; C, 0.7 mm; D, 1.2 mm; E, 45 µm; F; J, 180 µm; G, 25 µm; H, 120 µm; I, 40 µm. All photos from SISV.

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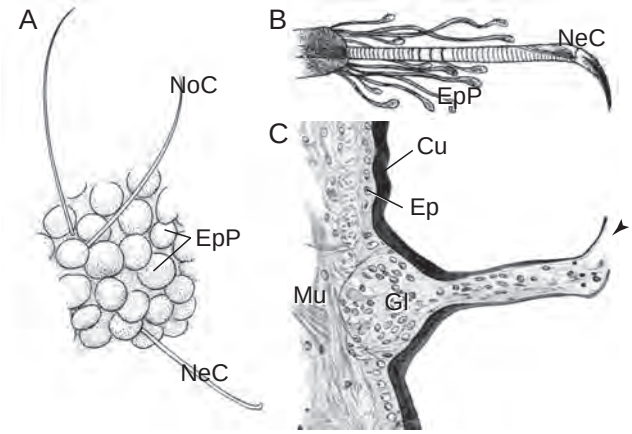


**Fig. 7.3.1.6.8:** Chaetae and epidermal papillae. A, *Diplocirrus* sp. chaetiger 15 with notochaetae (NoC), neurochaetae (NeC), and spherical epidermal papillae (EpP). B, *Flabelligera affinis*. Elongated club-shaped parapodial papillae (EpP) surrounding a neurochaeta (NeC). C, *Pherusa plumosa*. Longitudinal section of epidermal papilla; anterior segment; the basal group of cells is regarded to represent gland cells (Gl) sending and discharging their secretion at the distal end (arrowhead). Cu, cuticle; Ep, epidermis; EpP, epidermal papilla; Gl, gland cell; Mu, musculature; Nec, Neurochaeta; Noc notochaeta. A, Modified from Hutchings (2000); B, from Støp-Bowitz (1948a); C, from Schlieper (1927).

smooth, in some neurochaetae, their fibrilles can break up subdistally, making the chaetae look hirsute.

### Anatomy

**Tunic and papillae.** A distinctive feature among flabelligerids is their capacity to stick sediment particles to their tunic. This adhesion happens either directly on the individual papillae or on the tunic itself. In turn, the particles may be small, fixing themselves directly to each papilla or they can somehow penetrate into the tunic; likewise, they can be of larger size and adhere individually to the papillae or they are fixed on the tunic and standing out of it. On the other hand, the extension of the particle cover on the body has two basic patterns: it either might cover the body entirely or could be restricted to the dorsal and lateral surfaces.

Flabelligerid body papillae may be glandular or sensorial (Charrier 1924, Borodin 1929) and sorted out in four basic groups: piliform, tapering, capitate, and spherical, although the latter sometimes can be basally hypertrophied forming tubercles (Fig. 7.3.1.6.8 A–C). Piliform papillae are cylindrical, slightly swollen basally, and are the most delicate and often the longest of all; they are especially abundant, giving a pilose appearance in *Ilyphagus* (Fig. 7.3.1.6.3 E) and in some species of *Bradabyssa* (Fig. 7.3.1.6.4 D). Tapering papillae are frequent in the species of *Pherusa*, and they give the body a rough appearance. The capitate papillae have a distal or subdistal swollen portion, as in *Flabelligera*, where they have been referred to as lageniform because of their resemblance to a Roman urn or jar. Spherical papillae are short, rounded, rarely elongated, and often arranged in more or less transverse rows, at least along the anterior chaetigers (Fig. 7.3.1.6.3 A); their presence is limited to some species capable of boring in calcareous substrates or consolidated muds, especially among *Semiodera*. The hypertrophied papillae, which could rather be called tubercles, are limited to some species of *Bradabyssa*.

Sensory papillae are exposed beyond the tunic; they might form longitudinal series, being basically two dorsal and four ventral rows (*Piromis, Trophoniella*, Fig. 7.3.1.6.4 B), or become notoriously longer in the vicinity of the chaetael lobes, and as such, they can be found in most genera. However, most papillae are not exposed to the exterior being encased within the tunic and thus precluding any potential sensory role. However, it is probable that they have a rather supportive function anchoring the tunic (Fig. 7.3.1.6.4 C), somehow resembling the role of support filaments in the tunic of some ascidians, where they are regarded as playing a skeletal function.

**Digestive system.** As in most polychaetes, the gut is a continuous tube with a mouth and an anus. However, in flabelligerids, there are some interesting differences because the gut twists over itself, resembling other deposit-feeding tubicolous polychaetes like pectinariids or terebellids (Figs. 7.3.1.6.6 A, C and 7.3.1.6.9 A, B). Due to the transparency of the tunic, one of the first species descriptions (Otto 1821: 629–633) already provided many details on the internal anatomy, including the scarcity of segmental septa, and even resulted in the erroneous perception that they have a duplicated mouth (p. 629: "Oscula duo in eo apparent…"). This finding sparkled a lot of interest on their anatomy because of this unusual condition and because they were regarded as an intermediate stage between Errantia (by having compound neurochaetae) and Sedentaria (by their digestive tract). Thus, most following papers dealt with anatomical details and were frequently pointing out missing details or mistakes made by the others. Rathke (1842), who paid particular attention to anatomical structures and especially to the gut and circulatory system, rejected the supposed double mouth.

Claparède (1869: 98–104) described the anatomy of *Stylarioides monilifer*. The mouth has a lower nonciliated bilobed lip and within it three ciliated lobes, which can be everted and help in gathering food particles. Flabelligeridae are provided with a muscular ventral pharynx bulb (Figs. 7.3.1.6.2 B and 7.3.1.6.3 B),

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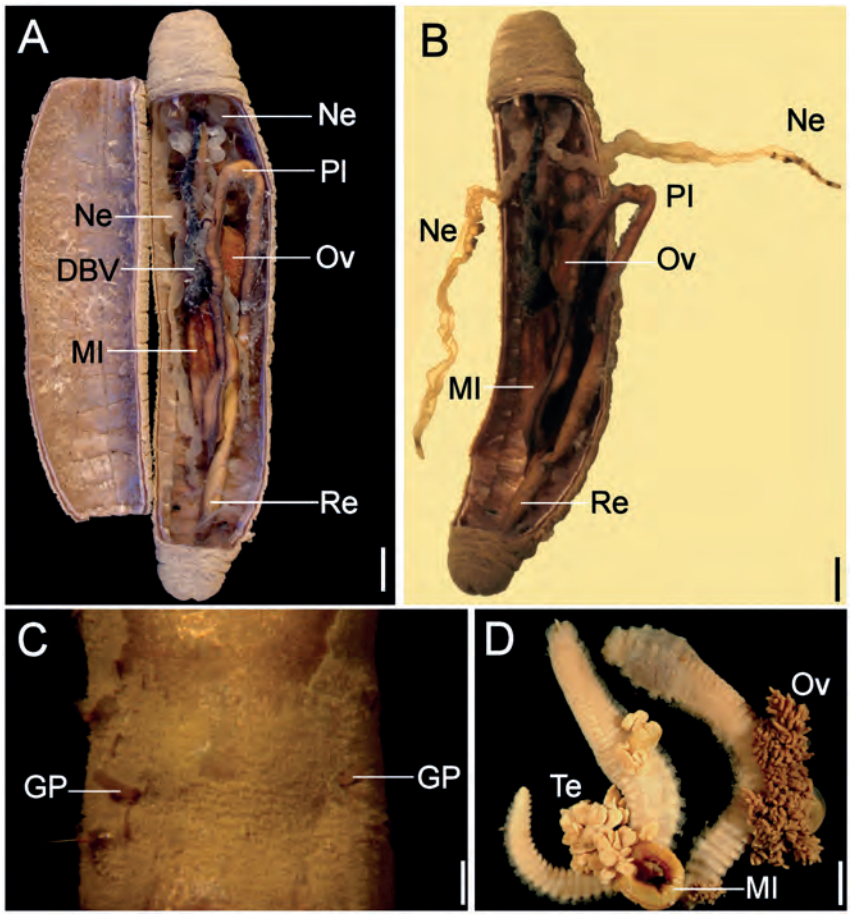


**Fig. 7.3.1.6.9:** A, *Brada inhabilis*, dorsal body wall removed. B, Same, 1 year later and inner organs pulled out to facilitate their observation. C. *Bradabyssa* sp., ventral view of chaetigers 4 and 5 showing gonopodial lobes. D, *Flabelligera commensalis*, preserved male (left) and female (right), with gonads exposed by fracture of the body wall. DBV, dorsal blood vessel; GP, gonopodial papilla; MI, median intestine; Ne, nephridium; Ov, ovary; PI, posterior intestine; Re, rectum; Te, testis. Scale bars: A, B, 3.4 mm; C, 1.7 mm; D, 2 mm. All photos from SISV.

as has been shown by Schlieper (1927), Orrhage (1973), and Wilfert (1975). The esophagus drives to a stomach with a large caecum and is followed by an intestine that proceeds anteriorly and then loops itself posteriorly toward the anus (Figs. 7.3.1.6.6 A, C and 7.3.1.6.9 A, B). Claparède (1869: 106–107) noticed that the digestive system is similar in *Piromis eruca*, but the stomach is red-brown with a longer anterior caecum. In *Flabelligera diplochaitus*, Bles (1892) found that the septum between chaetigers 9 and 10 includes the stomach, the intestine, the posterior parts of the nephridia, and ovaries in females but that nephridia extend posteriorly to chaetigers 16–20 and that it was the only complete septum in the body. Bles (1892: 374) also noticed that there was another complete septum between chaetigers 5 and 6 in *Pherusa*.

Penry and Jumars (1990) made an interesting analysis of gut architecture in carnivorous and deposit-feeding polychaetes. They found that large-sized opheliids and terebellids (780–22,000 $mm^3$) have four to five anatomically distinct gut compartments. Although they did not include flabelligerids, they may belong to this group as well because of their complex gut. They included fauveliopsids and sternaspids. The former have a simple tubular gut, as cirratulids and spionids, while the latter possess a three-compartment gut, as some ampharetids, arenicolids, and scalibregmatids. What appears to be unusual in other polychaetes is that in some abyssal flabelligerids, the gut loops around itself more than once. For instance, in *Ilyphagus wyvillei*, the gut may be about four times as long as the body length and makes two complete loops in the body cavity (McIntosh 1885: 368, Pl. 36A; Fig. 7.3.1.6.5).

**Blood vascular system.** The circulatory system is closed (Fig. 7.3.1.6.6 A, B) and carries the green respiratory pigment chlorocruorin, which was named as such by Lankester (1868: 115). The blood is moved by the muscular contraction of the dorsal vessel, which is placed anteriorly and dorsal to the stomach (Figs. 7.3.1.6.6 A and 7.3.1.6.9 A, B). According to Claparède (1869: 102), it is a large cylindrical tube, which has two layers; the external one is muscular and colorless, while the internal is thin and black. Its function was first pointed out by Dujardin (1839: 288), who also noticed the green blood, and proposed *Chloraema* by Costa (1841: 273) and

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Rathke (1842: 90), although its distinctive role was not confirmed until the studies by Horst (1885) and Cunningham and Ramage (1888: 674). The former studied some *Brada* specimens and confirmed a heart structure for it; he also noticed the formation of large blood lacunae around the stomach, concluding that its circulatory system resembled the one present in enchytraeid oligochaetes. The latter authors studied *Pherusa plumosa* and noticed that the dorsal and ventral vessels are connected by a pair of lateral vessels in each segment and that the posterior intestine is irrigated by the ventral vessel, while its backward loop receives the blood from two ventral vessels stemming from about segments 9 and 10 (Fig. 7.3.1.6.6 A). From these, the blood progresses into a series of lacunae in the gut wall and then moves forward through the dorsal vessel to the heart, receiving it as a vessel about half its length and is placed over the esophagus. This heart is enlarged posteriorly and tapers anteriorly, where it divides behind the brain to drive the blood to the branchiae.

In *Flabelligera*, there is a striking difference regarding the internal volume available in comparison with *Pherusa*. Again, Cunningham and Ramage (1888: 677) noticed several differences between them; for example, the dorsal vessel is not so large and is restricted to the anterior body portion, and they found no dorsal vessel toward the posterior end.

After the very careful and detailed study by Schlieper (1927) on *P. plumosa* (Fig. 7.3.1.6.6 A, B) the most detailed study on circulatory system in flabelligerids was made by Spies (1973) on the symbiotic *Flabesymbios commensalis* (as *Flabelliderma commensalis*). This polychaete lives on some species of intertidal and subtidal sea urchins in Southern California. This polychaete lacks a tunic but has a large number of branchiae. The circulatory system includes a long heart and a successive series of rings per segment, with some additional complications. The heart is placed anteriorly, and its fore end irrigates the anterior end, while the posterior end forms the blood sinus over the stomach. From its middle part extends a large vessel connected with the longitudinal dorsal vessel. Thus, the blood is oxygenated in the branchiae and runs ventrally toward the body at each segment, continuing to the posterior end, and from it then flows anteriorly through the dorsal vessel.

Spies (1973) found that in *F. commensalis*, the branchial branching pattern was less complicated than in *Pherusa plumosa*. He explained this difference as follows: in such species living buried in the sediment, all gas interchange must be achieved through the branchiae, while in *F. commensalis*, which is provided with little mucus cover and lives on other organisms, some interchange can be performed through the integument.

**Excretory system.** There is a single pair of nephridia in flabelligerids (Figs. 7.3.1.6.6 A, C and 7.3.1.6.9 A, B), which Goodrich (1945: 188) has regarded as mixonephridia. They were first observed by Otto (1821), who, however, confused them as a duplicate esophagus, and later noticed by Delle Chiaje (1841) and Costa (1841), but their excretory role was not clarified, even though there were some indications on salt regulation due to the presence of tiny, uric-acid crystals.

The nephridia form very long sacs and drive toward the branchial plate or lobe in some genera like *Flabelligera*, as illustrated by Claparède (1869, Pl. 25, Fig. 7.3.1.6.3). Formerly they either were regarded as tubular glands (Jourdan 1887: 36) or as salivary glands (de Quatrefages 1849: 297; Mueller 1852, Pl. 2, Fig. 16; Quatrefages 1866: 471; Günther 1912: 19, Figs. 1a, 2 Speicheldrüse). However, the latter role as salivary glands was already rejected by Claparède (1869: 110), and about its exit point, he stated: "...ces organs ne s'ouvrent point dans la bouche, mais se prolongent au dela du cerveau, jusqu'a la base des branchies." This translates as "these organs do not exit inside the mouth, but are prolonged beyond the brain right in the branchial bases."

Cunningham and Ramage (1888: 675) noticed that in *P. plumosa*, the nephridia can reach chaetigers 6–8 but are not open to the coelom. They converge in the anterior end and have a nephridial pore close to the branchial plate (Fig. 7.3.1.6.6 A, C). In *Flabelligera diplochaitos*, there is also a single pair of nephridia, and it has been said that in their simplicity and structure, they resemble the thoracic nephridia present in Serpulidae, with the important difference that there are no abdominal nephridia in Flabelligeridae (Bles 1892). In *Brada*, the nephridia are soft, slightly convoluted, and run throughout most of the body (Fig. 7.3.1.6.9 A, B). There is a single pair of nephridial lobes in certain Flabelligeridae, and they are situated in the branchial plate as, for example, shown in *Pherusa* by Amor (1994: 343, Fig. 3a) or implicitly in Fauvel (1930: 545, Fig. 8a). They are soft often with a basal dilatation and a long peduncle but can easily be torn apart while removing the branchial filaments.

Often, a pair of ventral lobes is present in some anterior chaetigers (Fig. 7.3.1.6.9 C), chaetigers 4 or 5 in *Brada*. They have been called nephridial lobes or nephridial papillae. These are usually digitate or cirriform, although in some genera, they have a transverse slit instead of a projecting lobe. However, there is no connection between the long nephridia and the gonads. Instead, the gonads

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are connected to the outside only via these lobes, and consequently, these lobes should be referred to as gonopodial lobes. This, however, stresses the need to clarify the structure and function of the flabelligerid nephridia to evaluate if they really are mixonephridia (Goodrich 1945).

**Nervous system.** Orrhage (1966, 1990, 2001) has dealt with the nervous system in flabelligerids, mainly in connection with his comprehensive studies including certain different polychaete families. His main findings on *Brada villosa* indicate that the brain is anterior, placed in the prostomium, and extends a double lateral branch to become fused ventrally, making the circumesophageal connective. Before they fuse, there are four ganglia along each connective: the nuchal ganglion, placed over the anterior branch; the dorsal ganglion, located over the posterior branch; and posteriorly two additional ones named buccal ganglia 1 and 2. The fusion includes another buccal ganglion (number 3 in his terminology). Thereafter, the double ventral nerve cord includes typical segmental ganglia. The palps are innervated by three branches, one from the brain and two others, one stemming from the anterior and the other from the posterior root of the connective. This pattern resembles the palp nerve root organization in Spionidae and Poecilochaetidae (Orrhage 1966: 108–109, 1990: 52–53), being quite different from what is found in other sedentary groups with anterior branchiae-like Ampharetidae, Pectinariidae, or Terebellidae. In fact, these groups do not possess palps altogether, and their feeding appendages should rather be called oral or buccal tentacles and are not homologous with either palps or antennae (Orrhage 2001: 69).

The nuchal organs of sedentary polychaetes were studied by Rullier (1951); he detailed and illustrated their histological structure in *P. plumosa* and *S. monilifer*. In both cases, he noticed that the nuchal organs are ciliated depressions running posteriorly from the middle of the prostomium and include the bases of the palps. Laterally, they become a deep cavity densely covered by cilia, which represent a continuation of the exposed ciliated series of the head. However, this interpretation mixed some ciliated regions of the head probably because the anterior ends available for his study were not fully everted.

**Reproductive organs and gametes.** Sexes are separate in Flabelligeridae. The presence of permanent gonads is another unique feature of the family (Fig. 7.3.1.6.6 A). Their number varies among different genera and sometimes in the same genus. There are four ovaries arranged as ventrolateral pairs; during reproduction, Claparède (1869: 104) noticed that they enlarge to cover the stomach and the intestine. Furthermore, he clarified that *S. monilifer* is not hermaphrodite but gonochoristic; testes in males are placed in the same position as the ovaries in the females, but there is a single pair that is a long tubular organ with a central blood vessel. This same condition is also present in *P. plumosa*, where Cunningham and Ramage (1888: 676) found that the gonads are closely packed with the intestinal loop and that are located in chaetigers 7–8; the ovaries are bright green, while the testes are pale yellow. In this species, males are larger than females. However, in *Flabelligera*, the authors found six pairs of gonads, although most features are just like those found elsewhere. In *Flabesymbios commensalis*, however, the gonads are more abundant and may occupy most of coelomic space; the testes are depressed, yellowish to whitish, while the ovaries are darker, with abundant lobes resembling grapes, and they are usually exposed during preservation (Fig. 7.3.1.6.9 D).

In *Brada*, the ovaries (and probably the testis) are placed in chaetigers 6–8, behind the ventral gonopodial lobes (McIntosh 1922: 103). In *Semiodera inflata*, the gonads fuse to make up a single longitudinal mass between chaetigers 6 and 21; thus, females, being 21 mm long, have ovaries along chaetigers 7–21, whereas males of 19 mm length have testis along chaetigers 6–17).

### Reproduction and development

**Sexual reproduction.** Swarming has been recorded at least four times in *Flabelligera*. The first record was made by Sorby (1906: 437); he found that many *Flabelligera affinis* were swimming abundantly during several years and that this abundance lasted for a few years. Sorby (1906) thought that while swimming, the adults may release their gametes. The second record was made by Gravier and Dantan (1928: 159–160); they collected with a light trap some specimens in February and June in the Mediterranean, but they were small, probably juvenile specimens. In the third report, Herpin (1929: 86–87) noticed many small specimens without gametes, but in July, he found large males releasing sperm when placed in flasks with sea water. He concluded that swarming may be made by just a few specimens. The fourth record was made by Berkeley and Berkeley (1960: 792–793); they noticed five specimens collected with a light trap in Friday Harbor. The specimens were sexually mature and spawning; with respect to their species identity, the authors found it closer to *F. affinis* than to *Flabelligera infundibularis*,

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which is common in the region. However, the differences described might be linked to reproductive transformation or epitoky. These findings have not been repeated, and it would be very useful to study whether such morphological changes occur in Flabelligeridae. By contrast, Pettibone (1954: 289) noticed that when the specimens appear in the water column, they lack any transparent tunic. These specimens were found to belong to an undescribed species, which was named after the Berkeleys as *Flabelliderma berkeleyorum* (Salazar-Vallejo 2007).

Thorson (1946: 106–107) noticed that a mature female *Diplocirrus glaucus* spawned after being stirred, through a rupture in the body wall. Ova were small (140 µm) and had a distinct zona pellucida, and because he had not found pelagic larvae, he regarded it as having nonpelagic development. He also included three other flabelligerd species (*B. villosa, F. affinis, P. plumosa*), for which he had not found any pelagic larvae. On the other hand, Spies (1977) indicated that *Flabesymbios roberti* has lecitotrophic larvae and recruits on the same echinoid host.

It has been shown that in some subantarctic flabelligerids like *Flabelligera pennigera* Ehlers, 1908, the embryos are incubated in the tunic of females (Bhaud and Duchêne 1987). Their eggs are large (500 µm), and as it seems to be the rule in the subantarctic province, the development is direct and holobenthic, implying a quite reduced dispersal capacity. Brooding has been recorded in *Flabegraviera mundata* by Gravier (1907: 37, 1911: 37, 1923a: 193–194); he found that the cephalic cage cavity was full of spherical, yellow eggs that were more or less agglutinated between themselves. The synthesis by Wilson (1991) only detailed a single record for a flabelligerid; it was the record by Gravier (1923a) on *Flabegraviera mundata*, which Wilson (1991) included in the reproductive mode Br-Ext-Dir, to indicate it has brooding, external to the body, and direct development.

### Life cycles

There are almost no records of pelagic larvae among flabelligerids. Early development has been little studied, and it would be useful to understand how many anterior segments migrate anteriorly to form the complex head. Spies (1977) illustrated the early development with larvae with three segments (Fig. 7.3.1.6.10 A); with seven segments or three chaetigers (Fig. 7.3.1.6.10 B), which show some long anterior chaetae, eight segments or four chaetigers (Fig. 7.3.1.6.10 C); with 11 segments or 9 chaetigers (Fig. 7.3.1.6.10 D) with the brain lobes well defined, but the cephalic cage chaetae not surrounding the anterior end; and with 15 segments or 13 chaetigers (Fig. 7.3.1.6.10 E), with the cephalic cage chaetae surrounding the anterior end.

## Biology and ecology

### Distribution

The family is cosmopolitan. Some genera are apparently restricted to cold waters or to abyssal depths, such as *Brada* or *Ilyphagus*, and some others are especially abundant in tropical or temperate environments like *Pherusa* or *Trophoniella*, but most species have a restricted distribution. Some earlier records for cosmopolitan or bipolar species have been based on little detailed studies, often disregarding the strict comparison of specimens. It is true that some of the boring species might have been displaced together with some aquaculture mollusks, but those would be exceptional records. Estuarine species have been less extensively studied, and some publications listed unidentified flabelligerids (Li and Gao 1989, Cortelezzi *et al*. 2007). However, some species of *Diplocirrus* are common in temperate environments in Australia (Stephenson *et al*. 1970) or in California (Dexter and Crooks 2000), whereas some species of *Flabelligera* or *Stylarioides* have been recorded for South Africa (Day 1955) or India (Khan and Murugesan 2005). Some species of *Pherusa* are common in the Western North Atlantic estuaries (Kennish 2001), whereas in the Mediterranean Sea, *Piromis* has been reported (Martinelli *et al*. 1997). There are no records of flabelligerids for surface, cave, or underground freshwater systems (Glasby *et al*. 2009).

### Ecology

Our knowledge about the ecology of flabelligerids is very limited. Most flabelligerids are found in sandy or muddy bottoms, a few can be found living in mud pockets in rocky environments, while some species bore into calcareous

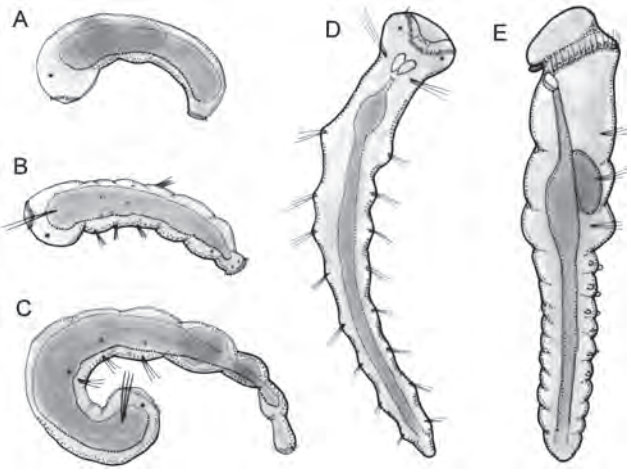


**Fig. 7.3.1.6.10:** *Flabesymbios roberti*, larval development. A, Three-segment larva. B, Seven-segment or three-chaetiger larva. C, Eight-segment or four-chaetiger larva. D, 11-segment or nine-chaetiger larva. E, 15-segment or 13-chaetiger larva. Redrawn after Spies (1977).

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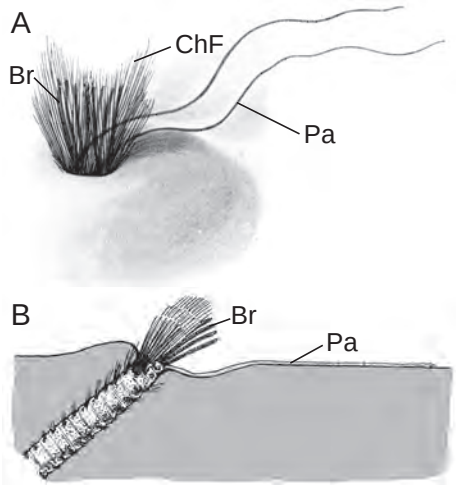


**Fig. 7.3.1.6.11:** *Pherusa plumosa*. Position of living animals within the sediment. A, View from above with capillary chaetae forming cephalic cage (ChF), branchiae (Br) and palps (Pa) emerging above the surface. B, Feeding position within the substrate; palps (Pa) extend over the sediment surface but their relative length deserves confirmation. Modified from Schlieper (1927).

substrates. Benthic flabelligerids are slow movers, if they move at all. Recorded depths range from the intertidal to the abyssal. Flabelligerids are seldom abundant, in general, but under certain conditions, they may become the dominant or one of the dominant species. *Diplocirrus* sp. occurs in densities of several thousand per square meter (L. Harris 2002, unpublished observation). On the other hand, Harrington and Griffin (1897) found that in muddy bottoms in Puget Sound, an area half an acre in extent yielded several bushels of a jelly-mass polychaete, what was later described as *Flabelligera infundibularis* Johnson, 1901. More recent studies failed to document this abundance in nearby areas, and it was even not included in the top abundant invertebrates (Lie and Kisker 1970).

Flabelligeridae have been regarded as deposit feeders (Day 1967, Fauchald and Jumars 1979), which use their anterior appendages, palps, and branchiae for gathering food; however, there may be some differences in their relative role depending on the development of the cephalic cage (Fig. 7.3.1.6.11 A, B). The early work by Hunt (1925) included two unspecified species of flabelligerids; he regarded them, together with other polychaetes provided with canaliculated palps, as deposit feeders; the gut analysis resulted in detritus, sediment, diatoms, algal cysts and spores, foraminiferans, tintinids, as well as larvae of other benthic invertebrates including polychaetes.

The long anterior chaetae forming the cephalic cage have defensive connotations. However, it has been observed that some species are able to spread mucous filaments among the chaetae of the cephalic cage, and after a while, these filaments are ingested, rendering them as passive filter feeders. This mechanism, which implies a stiff, radiating structure and the use of mucous to collect drifting particles, has elsewhere been documented by McDaniel and Banse (1979) for a subtidal maldanid, *Praxillura maculata*. The maldanid, however, has no palps and apparently salivates from one radiating filament to the next, later ingesting the mucous net.

The species with a well-developed cephalic cage usually project their palps beyond the cage to gather some fine sediment particles, and this is supplemented by some fine particles brought to the mouth by the activities of their ciliated structures, branchiae and lips (Figs. 7.3.1.6.2 A, B and 7.3.1.6.11 A, B; see Lindroth 1941). In *Pherusa papillata*, a deposit feeder, it has been observed that once the animal consumes the available particles in a certain area, it moves backward in the sediment and emerges at a certain distance to restart feeding (Abbott and Reish 1980). Thus, the gut contents (Chamberlin 1919: 396) include sediment particles, diatoms, radiolarians and foraminferans, spines of sea-biscuits, sponge spicules, algae fragments, and other organic debris. *Flabelligera affinis* crawls over the bottom, uses its palps to detect and collect detritus, and carry them to the mouth (Rasmussen 1973: 114).

Most species are benthic and just a few are holopelagic (*Poeobius meseres*), feeding on marine snow. The benthic forms live in the water-sediment interface in an oblique (*Bradabyssa*) or vertical position (Fig. 7.3.1.6.11 A, B; *Pherusa*), while others are able to remain inside the sediment (*Piromis* and *Trophoniella*). Some species live in rock interstices in mixed beaches (*Trophoniella*), while others can perforate consolidated calcareous or rocky substrates, where they expose only the cephalic cage (*Semiodera*). Those species having a feebly developed cephalic cage might rely more on direct deposit feeding, but it has not been studied yet. Likewise, less motile flabelligerids may depend more on a passive suspension feeding mechanism than the more active worms. Thus, palps may form a mucous web using the cephalic cage chaetae as a framework, while in less sedentary worms like in *Flabelligera*, palps can gather sediment particles individually having little or no use of any mucous web.

Stimpson (1856: 391) made the first record of a flabelligerid boring in calcareous substrates; he noticed that his *Siphonostomum laeve*, described from the Cape of Good Hope, was "found in holes which it forms in fragments of corals, in the coralline zone." However, this property was not taken seriously into account, and most other records of apparently boring flabelligerids were assigned to other species, probably because Stimpson (1856) did not include illustrations. Thus, there have been references to several

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flabelligerids resembling *Stylarioides parmatus*, originally described from the Philippine Islands, because they have a dorsal shield. For example, this same name has been recorded for New Zealand (Augener 1926: 180, 1927: 354) or from Madeira (Augener 1933: 199). Nevertheless, Haswell (1892: 334) indicated that there were dorsal shields in several species besides *S. parmatus*, such as *Stylarioides cariboum*, *Stylarioides cingulatus*, or *Stylarioides cinctus*. Hartman (1951: 98, 1952: 74) noticed that *S.* (olim *Trophonia) inflata* inhabits U-shaped burrows in shale rocks and other materials like sponge or shell masses. Scott and Cope (1986) found a flabelligerid boring into living corals; they did not identify the species but studied some 40 coral species The flabelligerid was the third most widespread because it was found in 17 different coral species, just behind sabellids (probably *Notaulax*) and *Lithophaga* bivalves.

As stated previously, some flabelligerids take a vertical position for living. They can feed by enlarging the palps and then mopping adjacent sediments for gathering food particles. Whenever the sediment is deprived of food, the animal can displace to the sediment-water interface and migrate by moving backward to another feeding site. If the site is rich or stable with regard to the availability of food particles, the animal can have a more permanent residence. In these circumstances, they can have some problems getting rid of fecal pellets. Thus, they can migrate and rest obliquely in another place, but some flabelligerids are provided with a long thin cauda resembling sabellariids, which would facilitate fecal pellets expulsion. This is clearly seen in *S. monilifer* living in soft substrates, and it is also found in *Semiodera*, which bores in calcareous substrates. The upright living position is inferred from the fact that worms collected with a trawl are often transversely cut. On the other hand, the sabellariid-like role for the posterior cauda most likely is a convergent feature.

The dorsal or nuchal shield has been regarded as the equivalent of an operculum (Fauvel 1919: 435), resembling those present in sabellariids or serpulids. But it was not clear if the animal could bore to make its own gallery or if it could just occupy an empty hole. The fine mechanism was not detailed until Amor (1994) made an extensive study on one of these species, which is now known as *Daylithos amorae*. She found that the dorsal shield actually works as an operculum; further, she found that the animal has the capacity to bore sedimentary rocks by a combination of chemical and mechanical means and that it can also produce an inner coverage of aragonite. The gallery is a blind hole and the animal lives having the thinner distal portion or cauda bent over itself and it is employed to get rid of feces. Further, the chemical activity was indirectly demonstrated by a special staining indicating the presence of acidic muco-polysaccharids while the ventral chaetae might be responsible for the mechanical means. This would explain why these chaetae have eroded tips.

**Predators.** Since most flabelligerids live inside or on the bottom, they may be important food items for some marine mammals or demersal fishes. Thus, in the Canadian Arctic, Chamberlin (1920: 21B) found that some flabelligerids like *Flabelligera affinis* are preyed upon by bearded seals, *Erignathus barbatus*. On the other hand, Amaral and Migotto (1980) noticed that in the Southwestern Atlantic, flabelligerids are especially frequent in the stomachs of fishes such as *Etropus intermedius* and *Paralonochrus brasiliensis*.

**Symbiotic associations**

Some gregarines (*Lecudina pherusae* and *Lecudina zimmeri*) have been found in *Piromis capulata* in Southern California (Abbott and Reish 1980). *Selenidium pennatum* Simdyanov, 1992, an archigregarine, has been found in *Flabelligera affinis* (Kuvardina and Simdyanov 2002). However, the best documented parasites of flabelligerids are copepods.

Levinsen (1878: 371) described a parasitic copepod (*Bradophila pygmaea*) from the gut of *Brada villosa*, and the record was referred by Chamberlin (1919: 396). The parasite morphology has inspired Marchenkov (2002) to propose an independent family to include this species. McIntosh (1885: 368) described *Trophoniphila bradii* from the branchial region of *I.* (olim *Trophonia*) *wyvillei*.

The best detailed studies on a copepod parasite living on flagelligerids were made by Gravier, who described and studied the copepod *Flabellicola neapolitana* infesting *Flabelligera diplochaitus* in a series of papers. Following the description of the parasite (Gravier 1918a) and a general study (Gravier 1918b), he made a couple of papers on the habitat (Gravier 1923b), the frequency of infestation (Gravier 1923c), and his last contribution dealt with the ontogeny of the parasite (Gravier 1924).

Symbiotic relationships involving flabelligerids have been also documented. Thus, other polychaetes can build their tubes on some flabelligerids, especially on those provided with a thick tunic and living on the bottom. Gravier (1911: 33, 137, 138) found the terebellids *Laenaea wandelensis* Gravier and *Thelepides kohleri* Gravier building their tubes on the tunic of *Flabegraviera mundata*. On the other hand, there are some species, especially in *Flabelligera*, that have been recorded associated to other invertebrates. Thus, *Flabelligera diplochaitos* (as *Chloraema dujardini*) has been recorded as living on sea urchins and there may be up to 12 specimens per echinoderm individual (de Quatrefages 1849: 284–285, 1866: 474). These two names have been regarded as synonyms, but there are differences in numbers of cephalic cage chaetae and branchial filaments. Moreover, ventral

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papillae were not seen in the symbiont form (de Saint-Joseph 1894: 100). In Southern California, the symbiotic *Flabesymbios commensalis* (Moore, 1909) has been recorded in the intertidal sea urchin *Strongylocentrotus purpuratus*, and it would be interesting to make a detailed study on speciation following some recent findings on these echinoderms (Biermann *et al*. 2003).

Further, some flabelligerids may be especially common in the nests of a swimming bivalve, *Lima hians*. Newbigin (1900: 190) thought there was no indication of any biological interaction, but this deserves a further analysis. Rasmussen (1973: 113–114) noticed that *Flabelligera affinis* is rather an epifaunal species, especially abundant among mussels, sponges, and macroalgae. On the contrary, Amouroux (1974) found that the same species lives in dark sites not exposed to sunlight and that it moves like aphroditids, but they can move fast as well. There seems to be at least two different morphs involved in the same name: one has a transparent (smooth) outer cuticle with some fine sediment attached, while the other has a greenish (rough), opaque tunic. If they are different species, this may explain why some authors have recorded it from rocky, well-lit bottoms, while others have recorded it from deeper, soft, or mixed bottoms under poorly lit or dim environments (Salazar-Vallejo 2012a).

## Phylogeny and taxonomy

### History

**Fossil record.** There is a good record of several polychaete families with fossils from the Middle Cambrian, especially in the famous Burgess Shale fauna. However, the records of worms that could belong to Flabelligeridae are rather scarce. Howell (1962) indicated that the fossil record of the family spans from the Ordovician, but the two genera that he included (*Eotrophonia* and *Siphonostomites*), apparently had a body shape that does not seem to fit into those of current genera. Nevertheless, Hay (2002) has recently established a new genus and species (*Mazopherusa prinosi*) with some fossils found in the Francis Creek Shale, Illinois. The body resembles a typical *Pherusa* or *Piromis*, but there were no clear chaetae in his materials. However, the similarity to contemporary worms is striking, although these fossils proceed from a horizon belonging to the Carbondale Formation, Desmoinesian Series, from the Middle Pennsylvanian of the United States or equivalent to the European Westphalian D. This means that the layer is about 295 million years old and that these polychaetes were already present some time before Pangaea.

**Classification.** The taxonomic history of Flabelligeridae has been complicated. Some species were already named by Müller (1776), but their affinities were rather obscure and the forthcoming named taxa were placed in different families. For example, Blainville (1828), following Savigny (1822), placed *Aristenia* among amphinomids (p. 453), then *Pherusa* after sabellids, but before spionids (p. 440), and *Siphostoma* among oligochaetes (p. 494). Its independent position as a distinct family was briefly recognized by Otto (1821) and by Blanchard (*in* Gay 1849) and simultaneously but in a monographic fashion by Quatrefages (1849), who included historical aspects. He recognized two genera: *Flabelligera* (*olim Chlorhaema*) and *Pherusa* provided diagnoses and ecological data for all known species as well as detailed anatomical accounts on *Flabelligera*.

Later, the family was briefly recognized again, now as Pherusea by Grube (1850), and revisited by Quatrefages (1866); the latter recognized eight genera, including the apparently uniramous *Lophiocephala*, but three genera were regarded as *incertae sedis* (*Spinther, Fleminiga*, and *Stylarioides*), and again as Pherusea by Claparède (1869). However, it was Saint-Joseph (1894) who, as part of a major faunistic study, employed *Flabelligera* Sars, 1829 as the type genus for Flabelligeridae. Later, he recognized *Stylarioides* over *Pherusa*, *Trophonia*, and *Lophiocephala*. He indicated that the included species should be separated using the type of both chaetae and branchiae (de Saint-Joseph 1898), and these groups became independent genera afterward.

The name for the family has promoted some debate in the Annelida discussion group. Following the Principle of Priority (International Commission on Zoological Nomenclature [ICZN] 1999, Art. 23.1 and 23.1.1) the valid name for the family should be the oldest available name. The chronological list is as follows:

Siphonostomae Otto, 1821, with *Siphonostoma* Otto, 1821, as type genus.

Siphostomacea Blanchard *in* Gay, 1849 (Siphostomidae Blanchard *in* Gay, 1849), with *Siphostoma* as type genus,

Chloraemea Quatrefages, 1849 (Chloraemidae Quatrefages, 1849), with *Chloraema* Dujardin, 1839, as type genus,

Pherusea Grube, 1850 (Pherusidae Grube, 1850), with *Pherusa* Oken, 1807, as type genus, and

Flabelligeridae Saint-Joseph, 1894, with *Flabelligera* Sars, 1829, as type genus.

However, if any of these names were introduced by any change, and these changes in name happened before 1961, as is the case here, Article 40 (ICZN 1999, Synonymy of the type genus) has to be followed. The first section (40.1) indicates that the original name of the family should not be changed, despite having a type genus that is recognized

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as a junior synonym. However, since the replacement took place before 1961 (Art. 40.2), the substitute name is to be maintained if it is in prevailing use. Flabelligeridae is in prevailing use and its full name should be Flabelligeridae Saint-Joseph, 1894 (1849).

However, *Pherusa* Oken, 1807 is a valid name and Pherusidae Grube, 1850 might be employed if one regards Flabelligeridae as invalid by following Art. 23.3.5, because it states "...if a name in use...is found to be unavailable or invalid it must be replaced by the next oldest available name from among its synonyms." However, both *Flabelligera* and Flabelligeridae are valid. Further, *Flabelligera* was originally proposed as a replacement name for *Pherusa* Oken, 1815, which was apparently preoccupied although the original publication was overlooked, indeed. Thus, Grube (1877: 63) changed his mind and preferred to use Chloraeminae instead of his own Pherusea.

Støp-Bowitz (1948a) also revised the use of the family name and employed Flabelligeridae on the basis of the then ruling International Rules of Zoological Nomenclature (Art. 5), which stated: "The name of a family or subfamily is to be changed when the name of its type genus is changed" and concluded (Støp-Bowitz 1948a: 6): "...le nom correct de la famille doit donc être Flabelligeridae quand le nom du genre *Chloraema* est changé à *Flabelligera* Sars, 1829, quoique les noms génériques *Stylarioides* et *Pherusa* sont plus anciens." Nevertheless, if, after being aware of this, we read article 41 of the code (ICZN 1999) and think that "...stability and continuity in the meaning of a family-group name are threatened by the discovery that the type genus of the taxon is misidentified (which is not the case)...", we must see Art. 65.2 dealing with the misidentification of, or the altered concept of, the type genus. We then should reject any further change or attempt to look for a ruling of the commission because the type genus was not misidentified (65.2.1, 65.2.3) and the fixation of its type species was not overlooked (65.2). Therefore, there is no indication that the current usage of both *Flabelligera* Sars, 1829 and Flabelligeridae Saint-Joseph, 1894 is threatened. No further action is needed. On the other hand, Poeobiidae Heath, 1930 has been included in Flabelligeridae on the basis of molecular and morphological data; the only representative genus, *Poeobius* Heath, 1930, has been dealt with some detail elsewhere (Salazar-Vallejo 2008).

**Taxonomy**

There has never been a comprehensive study for the whole family (Blake 2000). Some regional studies have been published, like those for Arctic and boreal species (Haase 1915; Støp-Bowitz 1948a, b), Great Britain (McIntosh 1915), France (Fauvel 1927), California (Hartman 1961, Blake 2000), the northern Gulf of Mexico (Milligan 1984), the North Sea and the Baltic Sea (Hartmann-Schröder, 1971, 1996), South Africa (Day 1961, 1967), the Arctic (Jirkov and Filippova 2001), or the Antarctic Oceans (Hartman 1966, 1967, 1978).

There are three systematic efforts dealing with the entire family and three additional faunistic studies deserving special mention because of their high level of improvements. Among the systematic papers the first was by Grube (1877); following Quatrefages (1866), he revised the family, defined the five genera then known (rejecting four others that had been included by Quatrefages), and listed all known species. To separate the genera, he made a key using the presence of the cephalic cage and then the development of the papillae over the body. He further used (but not in a key format) the chaetal types and branchial development to separate closely allied genera. The second large scale effort was made by Chamberlin (1919); he developed a key and used the differentiation of the branchiae, the presence of anterior appendages, and finally the types of chaetae and papillae. On these grounds, he recognized 14 genera and provided six new genera names to allocate the already known species or to place some others being newly described by him. He pointed out that there was a heterogeneous group of species in *Stylarioides*. The third attempt to deal with all the family was done by Fauchald (1977); he prepared a key for the 14 then-known genera in the family and used the body shape, followed by the type of chaetae, the branchial development, the development of the cephalic cage, and the presence of a long oral tube. Further, for all genera, he added the type species, the number of species, and a brief diagnosis. Thus, after his proposal, the family had five monotypic genera: *Bradabyssa*, *Coppingeria*, *Flabelliderma*, *Pantoithrix*, and *Therochaetella*, while there were three genera with some 20 species or more: *Brada*, *Flabelligera*, and *Pherusa*. *Pherusa* comprised almost half of the total number of species in the whole family.

The first of the faunistic investigations was carried out by Støp-Bowitz (1948a); he showed that the use of *Pherusa* Oken, 1807 should be retained and regarded as senior synonym of some other names that were proposed as replacement names. He further tried to clarify the faunistic composition of the Norwegian species and provided some detailed descriptions for most of his included species. Day (1967) made the second relevant faunistic work, mainly following the previous author. In his key, he introduced the presence of a tunic, then the type of chaetae and branchial arrangement, and then the abundance and type of papillae. He especially clarified the differences between *Pherusa* and *Piromis*. However, he refined this issue later (Day 1973), concluding that those species provided with bidentate hooks belong into the second genus. The third faunistic work was presented by Fauchald (1972) as part of a major effort

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to group similar species in different families. He listed the species in *Pherusa*, arranged after their number of branchial pairs being either four (including the type species) or many pairs, and then used the presence of a dorsal shield. Further, he noticed (Fauchald 1972: 225–226) that the type species of *Stylarioides* would belong to a different group. However, he added in a rather modest self-evaluation that his groupings were only for practical purposes lacking any systematic meaning.

As stated earlier, Flabelligeridae as a whole has not been revised after Grube (1877). However, some useful contributions were made by several authors: Chamberlin (1919) standardized the delimitation of genera and proposed several new ones. Støp-Bowitz (1948a), when studying the Scandinavian flabelligerids, redefined several genera and species. Day (1961, 1967, 1973) emphasized some aspects of the chaetal patterns and the development of the appendages of the anterior end. Fauchald (1972, 1977) proposed a standardization of the development of the gills and of some morphological modifications, such as the presence of dorsal shields to define genera. In the Pink Book (Fauchald 1977), he included a key for all genera. However, in these studies, there have been no attempts to revise the type material and to characterize in a standardized way the appendices of the anterior end. In this sense, the papers by Day (1961, 1967, 1973) deserve to be mentioned, which might have driven the publication by Spies (1975), who carried out a detailed morphological study and provided a series of comparative illustrations of the anterior ends of several flabelligerid genera. An updated key to genera has been presented by Salazar-Vallejo (2009). Several genera have been recently revised (e.g., Salazar-Vallejo and Zhadan 2007, Salazar-Vallejo 2011, 2012a,b,c,d, Salazar-Vallejo and Buzhinskaja 2011).There are still some genera needing revision, and the phylogenetic analysis available (Salazar-Vallejo *et al.* 2008) may deserve some improvements before clear subfamiliar affinities and generic diagnoses are provided.

Until now, subfamilies within Flabelligeridae have not been recognized; Fauchald (1972) grouped the known species within large genera. As described earlier, individuals of most genera expose only the anterior end. Thus, this is the most important body part for gathering food, breathing, and avoiding predation. Consequently, the anterior end and especially the branchial pattern should be selected to guide the grouping of genera. Furthermore, since the neurochaetae are the most useful tool for locomotion and for anchoring the body within the sediment, they should also be taken into consideration for any further grouping.

Following these lines, and by using the branchial pattern, the genera can be grouped in four clades: The first clade is characterized by branchial filaments sessile on a flat branchial plate. This group comprises the genera *Daylithos, Diplocirrus, Ilyphagus, Pherusa*, *Brada, Poeobius, Semiodera, Therochaeta, Flabelliderma*, *Annenkova*, *Flabegraviera, Flabehlersia, Flabesymbios*, and *Flabelligera*. The second group bears branchial filaments on a tongue-shaped branchial plate and consists of *Piromis, Pycnoderma*, and *Trophoniella*. Members of the third taxon possess branchial filaments on two distinct peduncles as present in *Stylarioides* and *Treadwellius*. In the last group, only represented by *Buskiella*, the branchiae are transformed into a trifid organ.

### List of genera

#### *Annenkova* Salazar-Vallejo, 2012

**Type species:** *Flabelligera mastigophora* Annenkova, 1952 Monotypic

**Diagnosis:** Body clavate to cigar shaped. Tunic thick, often without sediment particles or papillae adhering sediment particles dorsally. No dorsal or lateral lobes made by papillae and sediment. Branchiae abundant, thin filaments, sessile on branchial plate. Notochaetae shorter than body width, inside dorsal lobes or exposed. Neuropodia ventrolateral, neurochaetae multiarticulated hooks with a tapering, apparently articulated crest. Benthic; free-living.

#### *Brada* Stimpson, 1854

**Type species:** *Brada granosa* Stimpson, 1854, by subsequent designation (Hartman 1959: 413)

The number of species for *Brada* and *Bradabyssa* will be settled once these genera are revised.

**Diagnosis**: Body fusiform to cigar shaped. Tunic thin without sediment particles or thicker forming sediment tubercles or crust. Branchiae eight filaments, thick, smooth, free from each other, sessile on branchial plate. Neuropodia ventrolateral; neurochaetae ankylosed, falcate, blunt neurohooks. Benthic; free-living (Figs. 7.3.1.6.1 A, B, 7.3.1.6.3 D, and 7.3.1.6.9 A, B).

#### *Bradabyssa* Hartman, 1967

**Type species:** *Bradabyssa papillata* Hartman, 1967, by original designation, monotypic

**Diagnosis:** Body fusiform to cigar shaped. Tunic thin without sediment, or thicker forming sediment tubercles or crust. Branchiae many filaments, thin, free from each other, sessile on branchial plate. Neuropodia ventrolateral; neurochaetae ankylosed, straight or curved, aristate neurospines. Benthic; free-living (Figs. 7.3.1.6.4 D, 7.3.1.6.7 C, and 7.3.1.6.9 C).

#### *Buskiella* McIntosh, 1885

**Type species:** *Buskiella abyssorum* McIntosh, 1885 (including *Flota* Hartman, 1967; *fide* Salazar-Vallejo and Zhadan 2007)

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Two species
**Diagnosis:** Body fusiform to cigar shaped. Tunic thick, without sediment particles. Branchiae and palps modified into a trifid organ. Neuropodia ventrolateral; neurochaetae multiarticulate spines, articles very long. Pelagic or bathypelagic; free-living.

***Daylithos* Salazar-Vallejo, 2012**
**Type species:** *Stylarioides parmata* Grube, 1877, by original designation
Six species
**Diagnosis:** Body clavate to tapering, with a nuchal shield and a posterior depressed cauda. Tunic thin, rarely with sediment particles. Branchiae 10 or more filaments, sessile on branchial plate. Neuropodia ventrolateral; neurochaetae very short, anchylosed, falcate neurohooks; posterior chaetigers with neurohooks in longitudinal series. Benthic, boring calcareous or consolidated substrates.

***Diplocirrus* Haase, 1915**
**Type species:** *Trophonia glauca* Malmgren, 1867, by original designation (includes *Bradiella* Rullier, 1965 and *Diversibranchus* Buzhinskaja, 1994; *fide* Salazar-Vallejo and Buzhinskaja 2011).
13 species
**Diagnosis:** Body clavate to cigar shaped. Tunic thin without sediment particles, sometimes with mud or sand grains, rarely forming a crust. Branchiae eight filaments, sessile on branchial plate; filaments basally annulated, dorsally corrugated, or smooth. Posterior branchial four filaments fused laterally; anterior branchiae free from each other. Neuropodia ventrolateral; neurochaetae multiarticulated spines. Benthic; free-living (Figs. 7.3.1.6.1 C, 7.3.1.6.5 B, and 7.3.1.6.8 A).

***Flabegraviera* Salazar-Vallejo, 2012**
**Type species:** *Flabelligera mundata* Gravier, 1906, by original designation
Two species
**Diagnosis:** Body clavate to cigar shaped. Tunic thick, without sediment particles or papillae adhering sediment particles dorsally. No dorsal or lateral lobes made by papillae and sediment. Branchiae abundant, thin filaments, sessile on branchial plate. Notochaetae much larger than body width, exposed. Neuropodia ventrolateral, neurochaetae multiarticulated hooks or ankylosed hooks, crest or tips blunt. Benthic; free-living.

***Flabehlersia* Salazar-Vallejo, 2012**
**Type species**: *Flabelligera induta* Ehlers, 1897, by original designation
Two species
**Diagnosis:** Body tapering in both ends. Tunic thick, covering dorsal papillae, without sediment particles. No dorsal or lateral lobes made by papillae and sediment. Branchiae abundant, thin filaments, sessile on branchial plate. Notopodia directed ventrally, at least anteriorly. Notochaetae shorter than body width, exposed or inside a lobe. Neuropodia ventrolateral; neurochaetae multiarticulated hooks with a bent, blunt crest. Benthic; free-living.

***Flabelliderma* Hartman, 1969**
**Type species**: *Stylarioides papillosa* Essenberg, 1922, reinstated (Salazar-Vallejo 2007: 2039)
Eight species
**Diagnosis:** Body clavate to cigar shaped. Tunic thin without sediment particles or papillae forming dorsal tubercles and lateral lobes, often incorporating sediment. Branchiae abundant, thin filaments, sessile on branchial plate. Notochaetae shorter than body width, inside dorsal lobes. Neuropodia ventrolateral; neurochaetae multiarticulated hooks with a bent, blunt crest. Benthic; free-living (Figs. 7.3.1.6.2 B, 7.3.1.6.3 C, 7.3.1.6.5 C, and 7.3.1.6.9 D).

***Flabelligera* Sars, 1829**
**Type species:** *Flabelligera affinis* Sars, 1829, by monotypy
16 species
**Diagnosis:** Body clavate to cigar shaped. Tunic thick, covering dorsal papillae, often without sediment particles or with sediment particles dorsally. No dorsal or lateral lobes made by papillae and sediment. Branchiae abundant, thin filaments, sessile on branchial plate. Notochaetae shorter than body width, inside dorsal lobes or exposed. Neuropodia ventrolateral, neurochaetae multiarticulated hooks with a bent, blunt crest. Benthic; free-living (Figs. 7.3.1.6.1 D, E, 7.3.1.6.5 D, and 7.3.1.6.8 B).

***Flabesymbios* Salazar-Vallejo, 2012**
**Type species:** *Flabelligera commensalis* Moore, 1909
Two species
**Diagnosis:** Body clavate to cigar shaped. Tunic thin, not covering dorsal papillae, without sediment particles. No dorsal or lateral lobes made by papillae and sediment. Branchiae abundant, thin filaments, sessile on branchial plate. Notochaetae shorter than body width, exposed, forming lateral fans. Neuropodia displaced ventrally; neurochaetae multiarticulated hooks with a bent, blunt crest. Benthic; living on sea-urchins (Fig. 7.3.1.6.10 A–E).

***Ilyphagus* Chamberlin, 1919**
**Type species:** *Ilyphagus bythincola* Chamberlin, 1919, by original designation
Four species

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**Diagnosis:** Body cigar shaped to clavate. Tunic very thin, with mud particles, at least basally on each papilla. Branchiae abundant, thick filaments, sessile on branchial plate, arranged in a horseshoe pattern. Neuropodia ventrolateral; neurochaetae ankylosed, straight or curved, aristate neurospines. Benthic; free-living (Fig. 7.3.1.6.3 E).

***Pherusa* Oken, 1807**

**Type species:** *Amphitrite plumosa* Müller, 1776, by original designation

The number of species will be settled once the genus is revised.

**Diagnosis:** Body clavate to tapering. Tunic thin, with mud particles, sometimes with sand particles, not forming sediment crusts. Branchiae eight filaments, thick, sessile on branchial plate. Posterior branchial four filaments smooth, free from each other. Neuropodia ventrolateral; neurochaetae shorter than body width, ankylosed, falcate neurohooks. Benthic; free-living (Figs. 7.3.1.6.1 F, 7.3.1.6.2 A, 7.3.1.6.3 B, 7.3.1.6.5 A, 7.3.1.6.6 A–C, 7.3.1.6.7 A, 7.3.1.6.8 C, and 7.3.1.6.11 A, B).

***Piromis* Kinberg, 1867**

**Type species:** *Piromis arenosus* Kinberg, 1867, by monotypy

12 species

**Diagnosis:** Body clavate to tapering. Tunic thick, with mud particles or sand particles, sometimes forming sediment crusts, rarely without sediment. Branchiae many thin filaments, sessile on a tongue-shaped branchial plate. Neuropodia ventrolateral; neurochaetae multiarticulate neurohooks, entire or bidentate. Benthic; free-living (Figs. 7.3.1.6.2 C and 7.3.1.6.5 E).

***Poeobius* Heath, 1930**

**Type species:** *Peobius meseres* Heath, 1930 by monotypy

Monotypic.

**Diagnosis:** Body oval to clavate. Tunic thin, without sediment particles. Branchiae 10 or more filaments, sessile on branchial plate. Parapodia or chaetae missing. Pelagic; free-living.

***Pycnoderma* Grube, 1877**

**Type species:** *Pycnoderma congoense* Grube, 1877, by monotypy

Eight species.

**Diagnosis:** Body clavate to tapering. Tunic thick or thin, with little mud particles, often without sediment. Branchiae many thin filaments, sessile on a tongue-shaped branchial plate. Neuropodia ventrolateral; neurochaetae oligo-articulate neurohooks, blunt or aristate. Benthic; free-living.

***Semiodera* Chamberlin, 1919**

**Type species:** *Siphonostomum cariboum* Grube & Ørsted *in* Grube, 1859, by original designation

14 species

**Diagnosis**: Body clavate to tapering, often with a nuchal shield and a posterior cylindrical cauda. Tunic thin, rarely with sediment particles. Branchiae 10 or more filaments, sessile on branchial plate. Neuropodia ventrolateral; neurochaetae very short, ankylosed, falcate neurohooks; posterior chaetigers with neurohooks in a transverse line. Benthic; boring calcareous or consolidated substrates (Figs. 7.3.1.6.3 A and 7.3.1.6.6 E).

***Stylarioides* Delle Chiaje, 1831**

(includes *Coppingeria* Haswell, 1892; *fide* Salazar-Vallejo 2011)

**Type species:** *Stylarioides monilifer* Delle Chiaje, 1831, by monotypy

11 species

**Diagnosis:** Body clavate to tapering. Tunic thin, with mud particles, rarely with sand particles, not forming sediment crusts. Branchiae two lateral, cylindrical, tapering peduncles, each with filaments arranged in spiral. Neuropodia ventrolateral; neurochaetae shorter than body width, ankylosed, falcate neurohooks. Benthic; free-living (Figs. 7.3.1.6.2 D, 7.3.1.6.4 A, 7.3.1.6.5 F, and 7.3.1.6.7 D).

***Therochaeta* Chamberlin, 1919**

**Type species:** *Stylarioides collarifer* Ehlers, 1887, by original designation.

The number of species will be defined in an upcoming revision.

**Diagnosis:** Body clavate to tapering. Tunic thin, often with sand particles, forming prominent, sediment tubercles over few anterior chaetigers. Branchiae 10 or more filaments, sessile on branchial plate. Neuropodia ventrolateral; neurochaetae shorter than body width, pseudocompound hooks in some anterior chaetigers, ankylosed, falcate neurohooks in posterior chaetigers. Benthic; free-living.

***Treadwellius* Salazar-Vallejo, 2011**

**Type species:** *Stylarioides atentaculata* Hoagland, 1920

Three species

**Diagnosis:** Body clavate to tapering. Tunic thin, with mud particles, forming a thin sediment crust over anterior chaetigers. Branchiae two lateral, racket-like peduncles, each with filaments arranged in transverse lines, leaving a longitudinal, smooth region. Neuropodia ventrolateral; neurochaetae shorter than body width, ankylosed, falcate neurohooks. Benthic; free-living.

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***Trophoniella* Hartman, 1959 (includes *Therochaetella* Hartman, 1967; *fide* Salazar-Vallejo 2012b)**

**Type species:** *Trophoniella avicularia* Caullery, 1944, by subsequent designation (Hartman 1959: 423).

27 species

**Diagnosis:** Body clavate to tapering. Tunic thick, with mud or sand particles, often forming sediment crusts, rarely without sediment. Branchiae many thin filaments, sessile on a tongue-shaped branchial plate. Neuropodia ventrolateral; neurochaetae ankylosed neurohooks, entire or bidentate. Benthic; free-living (Figs. 7.3.1.6.4 B, C and 7.3.1.6.7 B).

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## References

Abbott, D.P. & Reish, D.J. (1980): Polychaeta: The marine annelid worms. In: Morris, R.H., Abbott, D.P. & Haderlie, E.C. (eds.) *Intertidal Invertebrates of California*. Stanford Univ. Press, Stanford: 448–449.

Amaral, A.C.Z. & Migotto, A.E. (1980): Importáncia dos anelídeos poliquetas na alimentação da macrofauna demersal e epibentónica da região de Ubatuba. *Boletim do Instituto oceanográfico, São Paulo* 29: 31–35

Amor, A. (1994): Ecology of *Pherusa* sp. (Polychaeta, Flabelligeridae). In: Dauvin, J.C., Laubier, L. & Reish, D.J. (eds) *Actes de la 4ème Conference Internationale des Polychètes*. Memoires du Museum National d'Histoire Naturelle, Paris 162: 339–346.

Amouroux, J.M. (1974): Sur la présence de *Flabelligera affinis* Sars (annélide polychète Flabelligeridae). *Vie et Milieu, séries A* 24: 179–180.

Augener, H. (1926): Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16, 34. Polychaeta 3. Polychaeta von Neuseeland, 2. Sedentaria. *Videnskabelige Meddelelser fra Dank naturhistorik Forening i Kobenhavn* 81: 157–294.

Augener, H. (1927): Die Polychaeten der Sammlung Thilenius von Neuseeland und Samoa. *Mitteilungen aus dem Zoologischen Museum in Berlin* 13: 338–363.

Augener, H. (1933): Polychaeten und Hirudineen aus dem zoologischen Museum in Buitenzorg. *Treubia* 14: 173–206.

Berkeley, E. & Berkeley, C. (1960): Some further records of pelagic Polychaeta from the Northeast Pacific north of latitude 40° N and East of longitude 175° W, together with records of Siphonophora, Mollusca, and Tunicata from the same region. *Canadian Journal of Zoology* 38: 787–799.

Bhaud, M. & Duchêne, J.-C. (1987): Biologie larvaire et stratégie de reproduction des annélides polychètes en province Subantarctique. *Actes du Colloque sur la Recherche Française dans les Terres Australes, Strasbourg 1987, C.N.F.R.A. Paris:* 145–152.

Biermann, C.H., Kessing, B.D. & Palumbi, S.R. (2003): Phylogeny and development of marine model species: strongylocentrotid sea urchins. *Evolution & Development* 5: 360–371.

de Blainville, H.M.D. (1828): Vers (Entomoz.). *Dictionnaire des Sciences Naturelles* 57: 365–625.

Blake, J.A. (2000): Family Flabelligeridae Saint-Joseph, 1894. Blake, J.A., Hilbig, B. & Scott, P.V. (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel. The Annelida 4, Polychaeta: Flabelligeridae to Sternaspidae*. Santa Barbara Museum of Natural History, Santa Barbara: 1–23.

Bles, E.J. (1892): Report on the occupation of the Table (at the Zoological Station of Naples: the study of the adult anatomy of the Chlorhaemidae, a family of polychaete worms). Report of the Sixty-First Meeting of the British Association for the Advancement of Science, Cardiff, August 1891, 372–376.

Borodin, D.N. (1929): Vergleichende Histologie der Hautorgane bei den Chloraemiden (Polychaeta). *Zeitschrift für Morphologie und Ökologie der Tiere* 16: 26–48.

Chamberlin, R.V. (1919): The Annelida Polychaeta of the Albatross Tropical Pacific Expedition, 1891–1905. *Memoirs of the Museum of Comparative Zoology, Harvard College* 48: 1–514.

Chamberlin, R.V. (1920): The polychaetes collected by the Canadian Arctic Expedition, 1913–18. Reports of the Canadian Arctic Expedition, 1913–18, 9. *Annelids, Parasitic Worms, Protozoans, etc., B. Polychaeta, Southern Party* 1913–16: 1B–41B.

Charrier, H. (1924): Les papilles du *Stylarioides moniliferus* (D. Ch.). Compte-Rendu de l'Association Française pour l'Advancement des Sciences, Paris 47: 536–537.

Claparède, E. (1869): Les Annélides Chétopodes du Golfe de Naples. Seconde Partie. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 20(1): 1–225.

Cortelezzi, A., Rodrígues-Capítulo, A., Boccardi, L. & Arocena, R. (2007): Benthic assemblages of a temperate estuarine system in South America: Transition from a freshwater to an estuarine zone. Journal of Marine Systems 68: 569–580.

Costa, O.G. (1841): Description des quelques annélides nouvelles du golfe de Naples. *Annales des Sciences Naturelles (Zoologie), Série 2* 16: 267–280.

Cunningham, J.T. & Ramage, G.A. (1888): The Polychaeta Sedentaria of the Firth of Forth. *Transactions of the Royal Society of Edinburgh* 33: 635–684.

Day, J.H. (1955): The Polychaeta of South Africa, 3. Sedentary species from Cape shores and estuaries. *Journal of the Linnean Society, London* 42: 407–452.

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

Day, J.H. (1967): A Monograph on the Polychaeta of Southern Africa. *British Museum (Natural History) Publications* 656: 38 + 878 pp.

Day, J.H. (1973): New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *National Oceanographic and Atmospheric Administration, Technical Report of the National Marine Fisheries Service, Circular* 375: 1–153.

Delle Chiaje, S. (1841). Animali senza Vertebre del Regno di Napoli. Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi negli anni 1822–1830: 1. Molluschi Cefalopedi e Pteropedi; 2. Molluschi Gasteropedi; 3. Molluschi Acefali, Bracciopedi, Cirropedi, Crostacei, Anellosi. *Batelli e Comp., Napoli,* 1: 19+98, 2: 1–146; 3: 1–142, 6: Plates 1–180.

Dexter, D.M. & Crooks, J.A. (2000): Benthic communities and the invasion of an exotic mussel in Mission Bay, San Diego. *Bulletin of the Southern California Academy of Sciences* 99: 128–146.

Dujardin, F. (1839): Observations sur quelques annelids marines. *Annals de Sciences Naturelles, Paris, série 2* 11: 287–294.

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

Fauchald, K. (1977): The polychaete worms: Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1–190.

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

Fauvel, P. (1919): Annélides polychètes de Madagascar, de Djibouti et du Golfe Persique. *Archives de Zoologie Expérimentale et Générale Paris* 58: 315–473.

Fauvel, P. (1927): Polychètes sédentaires & addenda aux polychètes errantes. *Faune de France* 16: 1–494.

Fauvel, P. (1930): Annélides polychètes de Nouvelle Caledonie recueillies par Mme A. Pruvot-Fol en 1928. *Archives de Zoologie Expérimentale et Générale Paris* 69: 501–562.

Filippova, A.V., Tzetlin, A.B. & Purschke, G. (2003): Morphology and ultrastructure of the anterior end of *Diplocirrus longisetosus* Marenzeller, 1890 (Flabelligeridae, Polychaeta, Annelida). Sigvaldadóttir, E, Mackie, A.S.Y., Helgason, G.V., Reish, D.J., Svavarsson, J., Steingrímsson, S.A. & Gudmundsson, G. (eds.) Advances in Polychaete Research, Proceedings of the 7th International Polychaete Conference held in Reykjavik, Iceland, 2–6 July 2001. Developments in Hydrobiology 170, series editor H.J. Dumont, Hydrobiologia 496: 215–223.

Gay, C. (1849): *Historia Física y Política de Chile*. Museo de Historia Natural, Santiago, 3 vols.

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

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

Gravier, C. (1907): Annélides polychètes. Expédition Antarctique Française (1903–1905) commandée par le Dr. Jean Charcot. *Sciences Naturelles, Vers* 12: 1–75.

Gravier, C. (1911): Annélides polychètes. Deuxième Expédition Antarctique Française (1908–1910) commandée par le Dr Jean Charcot. *Sciences Naturelles. Masson et Cie., Paris* 1: 1–165.

Gravier, C. (1918a): Sur un nouveau copépode (*Flabellicola* n.g. *neapolitana* n. sp.) parasite d'un annélide polychète [*Flabelligera diplochaitos* (Otto)]. *Comptes Rendus de l'Académie des Science, Paris* 166: 502–506.

Gravier, C. (1918b): Contribution à l'étude d'un copépode (*Flabellicola neapolitana* Gravier) parasite d'un annélide polychète [*Flabelligera (Siphonostoma) diplochaitos* (Otto)]. *Publicazioni della Stazione Zoologica di Napoli* 2: 209–222.

Gravier, C. (1923a): La ponte et l'incubation chez les annélides polychètes. *Annales des Sciences Naturelles (Zoologie), Série 10* 6: 153–247.

Gravier, C. (1923b): Sur l'habitat du *Flabellicola neapolitana* Gravier. *Bulletin du Muséum National d'Histoire Naturelle* 39: 503–505.

Gravier, C. (1923c): Sur un crustacé parasite (*Flabellicola neapolitana* Gravier) et sur sa fréquence chez un annélide polychète [*Flabelligera (Siphonostoma) diplochaitos* (Otto)]. *Bulletin du Muséum National d'Histoire Naturelle* 29: 560–562.

Gravier, C. (1924): Sur l'évolution d'un crustacé parasite (*Flabellicola neapolitana* Gravier). *Comptes Rendus de l'Académie des Science, Paris* 178: 163–168.

Gravier, C. & Dantan, J.-L. (1928): Pêches nocturnes a la lumière dans la Baie d'Alger. *Annales de l'Institut Océanographique, Paris* 5(1): 1–185.

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

Grube, A.E. (1877): Mittheilungen über die Familie der Chlorhaeminen. Jahresberichte der Schlesischen Gesellschaft fur Vaterlandische Cultur: 60–73.

Günther, K. (1912): Beiträge zur Systematik der Gattung *Flabelligera* und Studien über den Bau von *Flabelligera (Siphonostoma) diplochaitus*, Otto. *Jenaische Zeitschrift für Naturwissenschaft herausgegeben von der Medizinisch-naturwissenschaftlichen Gesellschaft zu Jena 48, Neue Folge* 41: 93–186.

Haase, P. (1915): Boreale und arktisch Chloraemiden. Wissenschaftliche Meeresuntersuchungen der Kommission zur Wissenschaftlichen *Untersuchung der Deutschen Meere, Neue Folge, Kiel* 17: 169–228.

Harrington, N.R. & Griffin, B.B. (1897): Notes upon the distribution and habits of some Puget Sound invertebrates. *Transactions of the New York Academy of Sciences* 16: 152–165.

Hartman, O. (1951): The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science, Texas University* 2: 7–124.

Hartman, O. (1952): On the identity of *Stylarioides inflata* (Treadwell) and its extended distribution. *Pacific Science* 6: 71–74.

Hartman, O. (1959): Catalogue of the Polychaetous Annelids of the World, 2. *Allan Hancock Foundation Occasional Papers* 23(2): 355–628.

Hartman, O. (1961): Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* 25: 1–226.

Hartman, O. (1966): Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarctic Research Series* 7: 1–158.

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

Hartman, O. (1978): Polychaeta from the Weddell Sea Quadrant, Antarctica. *Antarctic Research Series* 26: 125–222.

Hartman, O. & Fauchald, K. (1971): Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas, 2. *Allan Hancock Monographs in Marine Biology* 6: 1–327.

Hartmann-Schröder, G. (1971): *Annelida, Borstenwürmer, Polychaeta. Die Tierwelt Deutschlands Vol. 58.*. Fischer, Jena.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Hartmann-Schröder, G. (1996): *Annelida, Borstenwürmer, Polychaeta. Die Tierwelt Deutschlands Vol. 58.* 2nd ed. Fischer, Jena.

Haswell, W.A. (1892): Observations on the Chloraemidae, with special reference to certain Australian forms. *Proceedings of the Linnean Society of New South Wales, series 2* 6: 329–356.

Hay, A.A. (2002): Flabelligerida (sic) from the Francis Creek shale of Illinois. *Journal of Paleontology* 76: 764–766.

Herpin, R. (1929): Essaimages des annélides polychètes (note complementaire). *Bulletin Biologique de la France et de la Belgique* 63(1): 85–92.

Horst, R. (1885): Über ein räthselhaftes Organ bei den Chloraemiden Qfg. (Pherusea Gr.). *Zoologischer Anzeiger* 8: 12–15.

Howell, B.F. (1962): Worms. In: Moore, E.D. (ed.) *Treatise on Invertebrate Paleontology Part W., Miscellanea.* Geological Society of America, New York, and University of Kansas Press, Lawrence: 144–177.

Hunt, O.D. (1925): The food of the bottom fauna of the Plymouth fishing grounds. *Journal of the Marine Biological Association of the United Kingdom* 13: 560–599.

Hutchings, P.A. (2000): Family Flabelligeridae. In: Beesley, P.L., Ross, G.J.B., & Glasby, C.J. (eds.) *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia Vol 4ª. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne: 215–218.

ICZN (International Commission on Zoological Nomenclature). (1999): *International Code of Zoological Nomenclature*. 4th ed. Trust for Zoological Nomenclature (The Natural History Museum), London. www.iczn.org/iczn/index.jsp.

Jirkov, I.A. & Filippova, A.V. (2001): Flabelligeridae Saint-Joseph, 1894. Jirkov, I.A. *Polikhety Severnogo Ledovitogo Okeana*. Yanus-K, Moskva: 348–363.

Jourdan, E. (1887): Étude anatomique sur le *Siphonostoma diplochaetos*, Otto. *Annales du Musée d'Histoire Naturelle de Marseille, Zoologie* 3(2): 1–43.

Kennish, M.J. (2001): Benthic communities of the Barnegat Bay – Little Egg harbor estuary. *Journal of Coastal Research* SI(32): 167–177.

Khan, S.A. & Murugesan, P. (2005): Polychaete diversity in Indian estuaries. *Indian Journal of Marine Sciences* 34: 114–119.

Kuvardina, O.N. & Simdyanov, T.G. (2002): Fine structure of syzygy in *Selenidium pennatum* (Sporozoa, Archigregarinida). *Protistology* 2: 169–177.

Lankester, E.R. (1868): Preliminary notice on some observations with the spectroscope of animal substances. *Journal of Anatomy and Physiology* 2: 114–116.

Levinsen, G.M.R. (1878): Om nogle parasitiske Krebsdyr der snylte hos Annelider. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 1877: 351–380.

Li, F. & Gao, S. (1989): The relationship between environment and benthic diversity in the Changjiang estuary and adjacent areas. *Asian Marine Biology* 6: 19–29.

Lie, U. & Kisker, D.S. (1970): Species composition and structure of benthic infauna communities off the coast of Washington. *Journal of the Fisheries Research Board, Canada* 27: 2273–2285.

Lindroth, A. (1941): Atmungsventilation der Polychaeten. *Zeitschrift für vergleichende Physiologie, Berlin* 28: 485–532.

Marchenkov, A.V. (2002): Bradophilidae fam. nov. – Novoe semeistvo mezoparazitischeskikh veslonogikh (Copepoda: Poecilostomatida) naidennykh na *Brada villosa* v Belom More. *Parazitologiya* 36: 514–517.

Martinelli, M., Santoni, M. & Castelli, A. (1997): Distibuzione dei policheti nello stagno di Calich (Sardegna nord-occidentale): evoluzione a medio termine (1988–1995). *Bollettno della Società Sarda di Scienzi Naturali* 31: 45–59.

McDaniel, N. & Banse, K. (1979): A novel method of suspension feeding by the maldanid polychaete *Praxillura maculata*. *Marine Biology* 55: 129–132.

McIntosh, W.C. (1885): Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873–76. *Challenger Reports* 12: 1–554.

McIntosh, W.C. (1915): *A Monograph of the British Annelids, 3. Polychaeta: Opheliidae to Ammocharidae*. Ray Society, London.

McIntosh, W.C. (1922): Notes from the Gatty Marine Laboratory, St. Andrews, 44: 1. On new and rare Polychaeta, Gephyrea, etc., from various regions; 2. Recent additions to the British marine Polychaeta (continued). *Annals and Magazine of Natural History, series 9* 9: 1–30.

Mesnil, F. (1899): La position systématique des Flabelligériens St. Joseph (Chlorémiens Quatrefages) et des Sternaspiens. *Zoologischen Anzeiger* 22: 81–85.

Milligan, M.R. (1984): Family Flabelligeridae Saint Joseph, 1894. In: Uebelacker, J.M. & Johnson, P.G. (eds.) *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico*. Barry A. Vittor, Mobile: 47.1–47.20.

Mueller, M. (1852): *Observationes anatomicae de Vermibus quibusdam maritimis. Dissertatio inauguralis comparator-anatomica quam consensus et auctoritate Gratiosi Medicorum ordinis in Alma Litteratum Universitate Friderica Guilelma ut Summi in Medicina et Chirugia honores*. Univ. Friedrick Wilhem, Berolini.

Müller, O.F. (1776): *Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum. Characteres, nomina et synonyma imprimis popularium*. Hallageriis, Havniae.

Newbigin, M.I. (1900): On British species of *Siphonostoma*. *Annals and Magazine of Natural History, series 7* 5: 190–195.

Orrhage, L. (1966): Über die Anatomie des zentralen Nervensystems der sedentären Polychaeten: Ein Beitrag zur Diskussion über die Architektur des Polychaeten-Gehirns und über den Begriff Palpen bei den Borstenwürmen. *Arkiv för Zoologi Serie 2* 19: 99–133.

Orrhage, L. (1973): Two fundamental requirements for phylogenetic-scientific works as a background for an analysis of Dales's (1962) and Webb's (1969) theories. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 11(3): 161–173.

Orrhage, L. (1990): On the microanatomy of the supraoesophageal ganglion of some amphinomids (Polychaeta. Errantia), with further discussion of the innervation and homologues of the polychaete palps. *Acta Zoologica (Stockholm)* 71: 45–59.

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

Otto, A.G. (1821): Animalium maritorum nondum editorum, Genera duo. *Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher* 10(2): 617–634.

Penry, D.L. & Jumars, P.A. (1990): Gut architecture, digestive constraints and feeding ecology of deposit-feeding and carnivorous polychaetes. *Oecologia* 82: 1–11.

Pettibone, M.H. (1954): Marine polychaete worms from Point Barrow, Alaska, with additional records from the North Atlantic and North Pacific. *Proceedings of the United States National Museum* 108: 203–356.

de Quatrefages, A. (1849). Études sur les types inférieurs de l'embranchment des Annelés. Mémoire sur la Famille des

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Chlorèmiens, *Chloraemea*, Nob. *Annales des Sciences Naturelles, troisième série, Zoologie* 12: 277–306, Pl. 9–10.

de Quatrefages, A. (1866 (1865)): *Histoire Naturelle des Annelés Marins et d'Eau Douce: Annélides et Géphyriens. Tome Premier. Collection des Suites a Buffon formant avec les Oeuvres de cet auteur un Cours Complet d'Histoire Naturelle*. Librairie Encyclopédique de Roret, Paris (Wright, E.P. 1866. Annelida. Zoological Record, Section 6 (Annelida, etc.): 578–600).

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

Rathke, H. (1842): Beiträge zur vergleichenden Anatomie und Physiologie, Reisbemerkungen aus Skandinavien, nebst einem Anhange über die rückschreitenden Metamorphose der Thiere, 4. *Siphonostoma plumosum* (*Amphitrite plumosa* Müll., *Pherusa mülleri* Blainville). *Neuste Schriften der naturforschenden Gesellschaft in Danzig* 3(4): 84–92.

Rioja-LoBianco, E. (1931): Estudio de los poliquetos de la península Ibérica. *Memorias de la Academia de Ciencias Físicas, Exactas y Naturales, Madrid* 2: 1–471.

Rullier, F. (1951): Étude morphologique, histologique et physiologique de l'organ nucal chez les annélides polychètes sédentaires. *Annales de l'Institut Océanographique* 25: 207–341.

de Saint-Joseph, A. (1894): Les annélides polychètes des côtes de Dinard, troisième partie (Nephtydiens – Serpuliens). *Annales des Sciences Naturelles, Zoologie, 7ème série* 17: 1–395.

de Saint-Joseph, A. (1898). Les annélides polychètes des côtes de France (Manche et Océan). *Annales des Sciences Naturelles, Zoologie, 8ème série*, 5: 209–464.

Salazar-Vallejo, S.I. (2007): Revision of *Flabelliderma* Hartman, 1969 (Polychaeta: Flabelligeridae). *Journal of Natural History* 41: 2037–2061.

Salazar-Vallejo, S.I. (2008): Review of *Poeobius* Heath, 1930 (Polychaeta: Flabelligeridae). *Cahiers de Biologie Marine* 49: 191–200.

Salazar-Vallejo, S.I. (2009): Flabelligeridae de Saint-Joseph, 1894. In: León-González, J.A. de, Bastida-Zavala, J.R., Carrera-Parra, L.F., García-Garza, M.E., Peña-Rivera, A., Salazar-Vallejo, S.I. & Solís-Weiss, V. (eds.) *Poliquetos (Annelida: Polychaeta) de México y América Tropical*. Universidad Autónoma de Nuevo León, Monterrey, México: 195–206.

Salazar-Vallejo, S.I. (2011): Revision of *Stylarioides* delle Chiaje, 1831 (Annelida: Flabelligeridae). *Italian Journal of Zoology* 78 Supplement 1: 163–200.

Salazar-Vallejo, S.I. (2012a): Revision of *Flabelligera* Sars, 1829 (Polychaeta: Flabelligeridae). *Zootaxa* 3203: 1–64.

Salazar-Vallejo, S.I. (2012b): Revision of *Trophoniella* Hartman, 1959 (Polychaeta: Flabelligeridae). *Zoosystema* 34(3): 453–519.

Salazar-Vallejo, S.I. (2012c): Revision of *Ilyphagus* Chamberlain, 1919 (Polychaeta, Flabelligeridae). *Zookeys* 190: 1–19.

Salazar-Vallejo, S.I. (2012d): Revision of *Flabelligera* Sars, 1829 (Polychaeta: Flabelligeridae). *Zootaxa* 3203: 1–64.

Salazar-Vallejo, S.I. & Buzhinskaja, G. (2011): Revision of *Diplocirrus* Haase, 1915, including *Bradiella* Rullier, 1965, and *Diversibranchus* Buzhinskaja, 1993 (Polychaeta, Flabelligeridae). *Zookeys* 106: 1–45.

Salazar-Vallejo, S.I., Carrera-Parra, L.F. & Fauchald, K. (2008): Phylogeny of Flabelligeridae (Annelida: Polychaeta). *Journal of Systematic Zoology and Evolutionary Research* 46: 203–215.

Salazar-Vallejo, S.I., Gillet, P. & Carrera-Parra, L.F. (2007): Revision of *Chauvinelia*, redescriptions of *Flabelliseta incrusta* and *Helmetophorus rankini*, and their recognition as acrocirrids (Polychaeta: Acrocirridae). *Journal of the Marine Biological Association of the United Kingdom* 87: 465–477.

Salazar-Vallejo, S.I. & Zhadan, A.E. (2007): Revision of *Buskiella* McIntosh, 1885 (including *Flota* Hartman, 1967), and description of its trifid organ (Polychaeta, Flotidae). *Invertebrate Zoology* 4: 65–82.

Sars, M. (1829): *Bidrag til Söedyrenes Naturhistorie; Förste Hæfte*. Dahl, Bergen.

Savigny, J.C. (1822): Système des Annélides, principalement de celles des cotes de l'Egypte et de la Syrie, offrant les caractères tant distinctifs que naturelles des ordres, familles et genres, avec la description des espèces. *Description de l'Egypte. Histoire naturelle, Paris* 21: 325–472 (publication date fixed after Sherborn, 1897, and after ICZN 1987, Op. 1461).

Schlieper, C. (1927): *Stylarioides plumosus*, eine Monographische Darstellung. *Zeitschrift für Morphologie und Ökologie der Tiere* 7: 320–383.

Scott, P.J.B. & Cope, M. (1986): Tolo revisited: a resurvey of the corals in Tolo Harbor and channel six years later and half a million people later. In: Morton, B. (ed.) *Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986*. Hong Kong Univ. Press, Hong Kong: 1203–1220.

Sorby, H.C. (1906): Notes on some species of Nereis in the district of the Thames Estuary. *Journal of the Linnean Society* 29: 434–439.

Spies, R.B. (1973): The blood system of the flabelligerid polychaete *Flabelliderma commensalis* (Moore). *Journal of Morphology* 139: 465–490.

Spies, R.B. (1975): Structure and function of the head in flabelligerid polychaetes. *Journal of Morphology* 147: 187–208.

Spies, R.B. (1977): Reproduction and larval development of *Flabelliderma commensalis* (Moore). In: Reish, D.J. & Fauchald, K. (eds.) *Essays on the Polychaetous Annelids in Memory of Dr Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles: 323–346.

Stephenson, W., Williams, W.T. & Lance, G.N. (1970): The macrobenthos of Moreton Bay. *Ecological Monographs* 40: 459–494.

Stimpson, W. (1856 (1855)): Descriptions of some new marine Invertebrata. *Proceedings of the Academy of Natural Sciences of Philadelphia* 7: 385–395.

Støp-Bowitz, C. (1948a): Les Flabelligériens Norvégiens. Bergens Museums Arbok 1946 og 1947(2): 1–59.

Støp-Bowitz, C. (1948b): Sur les polychaetes arctiques, des famillies des glicériens, des ophéliens, des scalibregmiens et des flabelligériens. *Tromsø Museums Årshefter* 66(2): 1–58.

Thorson, G. (1946): Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the Sound (Øresund). *Meddelelser fra Kommissionen for Danmarks Fiskeri – Og Havundersøgelser, Serie: Plankton* 4(1): 1–523.

Vodopyanov, S. & Purschke, G. (2017): Fine structure of the cerebral eyes in *Flabelligera affinis* (Annelida, Sedentaria, Cirratuliformia): new data prove the existence of typical converse annelid multicellular eyes in a sedentary polychaete. *Zoomorphology* 136: 307–325.

Wilfert, M. (1975): Nachweis eines Pharynxbulbus bei Polychaeten aus der Familie Flabelligeridae. *Helgoländer wissenschaftliche Meeresuntersuchungen* 27: 313–323.

Wilson, W.H. (1991): Sexual reproductive modes in polychaetes: Classification and diversity. *Bulletin of Marine Science* 48: 500–516.

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### 7.3.1.7 Acrocirridae Banse, 1968

#### Introduction

The family Acrocirridae is distributed worldwide and includes 43 formally described species, as well as a handful of undescribed species (Rouse and Pleijel 2001, Osborn and Rouse 2011). Despite this relatively small number of species, the family is morphologically highly diverse and exhibits a wide range of life strategies (Fig. 7.3.1.7.1 A–G). The family is represented both in the pelagic and benthic environment (Osborn *et al.* 2011a, Osborn and Rouse 2011), including marine and anchialine caves (Núñez *et al.* 1997,

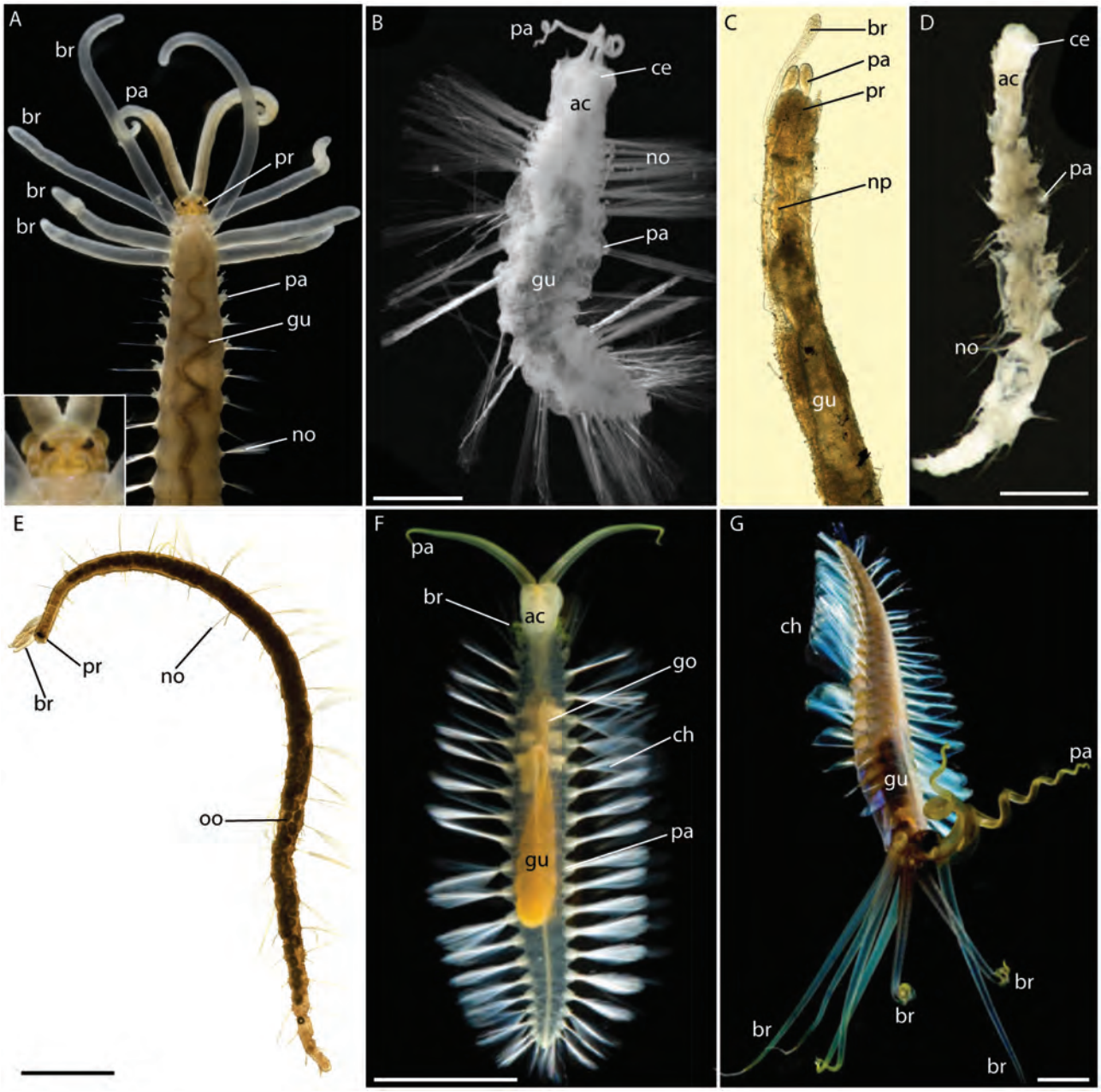


**Fig. 7.3.1.7.1:** General organization and habitus of Acrocirridae. Light microscopy of live and fixed animals. A, *Acrocirrus validus,* live individual, dorsal view. B, *Chauvinelia biscaensis,* dorsal view. C, *Flabelligena* sp., ventral view. D, *Helmetophorus rankini,* dorsal view. E, *Macrochaeta* sp., lateral view. F, *Swima bombiviridis,* dorsal view. G, *Teuthidodrilus samae,* live paratypes in ventral view. ac, anterior cephalic region; br, branchia; ce, cephalic hood; ch, chaetae; go, gonoducts; gu, gut; np, nephridium; no, notochaetae; oo, oocytes; pa, palp; pr, prostomium. A, Reproduced from Osborn *et al.* (2008); B, reproduced from Salazar-Vallejo *et al.* (2008); D, F, G, reproduced from Osborn and Rouse (2011), all with permission.

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Gonzalez *et al.* 2012). Some of these species exhibit quite unique adaptations, such as the luminescent deep-sea bombers of the genus *Swima* Osborn, Haddock, Pleijel, Madin & Rouse, 2009 or the very long palps and branchiae adapted for suspension feeding of the so-called squid worm *Teuthidodrilus samae* Osborn, Madin & Rouse, 2011 (see Osborn *et al.* 2009, 2011b).

Despite the *Macrochaeta clavicornis* (Sars, 1835) was described already in 1835, the family Acrocirridae was not formally erected until 1968, here comprising 14 species of *Macrochaeta* Grube, 1850 and *Acrocirrus* Grube, 1873. Prior to that, species of *Macrochaeta* and of the subsequently described genus *Acrocirrus* were placed within Cirratulidae. Since the family was established, it was pointed out that Acrocirridae was very closely related to Flabelligeridae, sharing many features but differing in the structure of the chaetae (Banse 1969). In fact, many species now included in Acrocirridae were first described as flabelligerids and only moved to Acrocirridae relatively recently (Salazar-Vallejo *et al.* 2007). Moreover, a sister-group relationship between these two families has been recovered in all phylogenetic studies, regardless whether they were based on morphological characters (Rouse and Fauchald 1997, Parry *et al.* 2016), few genetic markers (Rousset *et al.* 2007), or larger phylogenomic datasets (Struck *et al.* 2015). The clade Flabelligeridae-Acrocirridae is often placed next to Cirratulidae, forming Cirratuliformia, which might from a morphological perspective, and is related to Fauveliopsidae (Rouse and Pleijel 2001).

Their colonization of a wide range of habitats, the presence of distinct morphological features potentially correlated to the habitats, as well as the existence of well-documented fossil records (Osborn and Rouse 2011, Gonzalez *et al.* 2012, Parry *et al.* 2016) point at Acrocirridae as a group of potential interest for ecological and evolutionary studies. Unfortunately, the family has not received much attention historically, and information on the group is scattered. For example, details on the internal anatomy (i.e., nervous system, musculature) are missing for most species; many genera are defined by a combination of ambiguous or plesiomorphic character states (Banse 1969, Hartman 1978, Gillet 2001); and several species of potential ecological interest remain to be formally described (Núñez *et al.* 1997, Osborn *et al.* 2009, 2011a, Gonzalez *et al.* 2012).

## Morphology

### External morphology

**Head.** Acrocirridae typically have cylindrical bodies, with a distinct head and 10–200 segments depending on the group considered (Fig. 7.3.1.7.1) (Rouse and Pleijel 2001).

**Prostomium and Peristomium.** The prostomium normally lies dorsally to the peristomium but varies in size and shape depending on the species (Fig. 7.3.1.7.2). It is well developed and rounded or heart shaped in *Acrocirrus, Macrochaeta, Flabelligella,* and *Flabelligena* (Figs. 7.3.1.7.3 B, 7.3.1.7.4 A, 7.3.1.7.5 A, and 7.3.1.7.6 A) (Banse 1969, Rouse and Pleijel 2001); smaller and triangular in *Chauvinelia* and *Helmetophorus* (Figs. 7.3.1.7.7 A and 7.3.1.7.8 B) Glasby and Fauchald 2001, Salazar-Vallejo *et al.* 2007); or limited to the tissue surrounded the nuchal organs in *Swima* and *Teuthodrilus* (Fig. 7.3.1.7.1 F, G) (Osborn *et al.* 2011a,b). The prostomium can be retracted into the anterior segments in *Flabelligena* and *Flabelligella* (Fig. 7.3.1.7.6 A–C) (Orensanz 1974, Kolmer 1985, Aguirrezabalaga and Ceberio 2006, but see Osborn and Rouse 2011). The prostomium always possesses a pair of nuchal organs and can bear up to three pairs of eyes, as well as the so-called head branchiae depending on the species (Banse 1969, Rouse and Pleijel 2001). Nuchal organs are present on the posterior margin of the prostomium (Osborn and Rouse 2011). In *Macrochaeta* and most *Acrocirrus* species, the nuchal organs consist of more or less straight ciliated ridges extending dorsoventrally on each lateral side of the prostomium (Fig. 7.3.1.7.2 B–E) (Banse 1969, Kudenov 1976). In other species, they are fused as a w-shaped transverse ridge extending dorsally on the prostomium, as in *Acrocirrus validus* and *Chauvinelia arctica* (Fig. 7.3.1.7.1 A) (Salazar-Vallejo *et al.* 2007, Osborn and Rouse 2011). Very complex nuchal organs are found in the pelagic squid-worm *Teuthodrilus samae,* consisting of looped ciliary rings associated to branching appendages and spiral structures (Osborn *et al.* 2011b). One to three pairs of dark pigmented eyes are found in some species of *Macrochaeta* and *Acrocirrus* (Figs. 7.3.1.7.3 B and 7.3.1.7.4 A) but are mostly absent in *Flabelligella, Flabelliseta, Flabelligena*, as well as in the pelagic species (Banse 1969, Rouse and Pleijel 2001). Head branchiae are present in the genera *Chauvinelia*, *Swima*, and *Helmetophorus* (Figs. 7.3.1.7.7 A and 7.3.1.7.8 B) (Salazar-Vallejo *et al.* 2007, Osborn *et al.* 2011a) as two forms, sometimes co-occurring on the same individual: (1) one or few small, subulate appendices with a broad base and tapering toward the distal end and (2) numerous, short, digitiform structures projecting between the prostomium and the peristomium (Osborn and Rouse 2011). In contrast to the main branchiae, head branchiae are not easily lost in fixed individuals (Osborn and Rouse 2011).

Acrocirrids have a variable number of anterior achaetous segments (Fig. 7.3.1.7.2 D, E). They can be enlarged or exhibit a varying degree of fusion (Banse 1969, Aguirrezabalaga and Ceberio 2006). The first achaetous segment is considered as homologous to the peristomium, since it carries the mouth and the palps (Fig. 7.3.1.7.2 A–H) (Rouse

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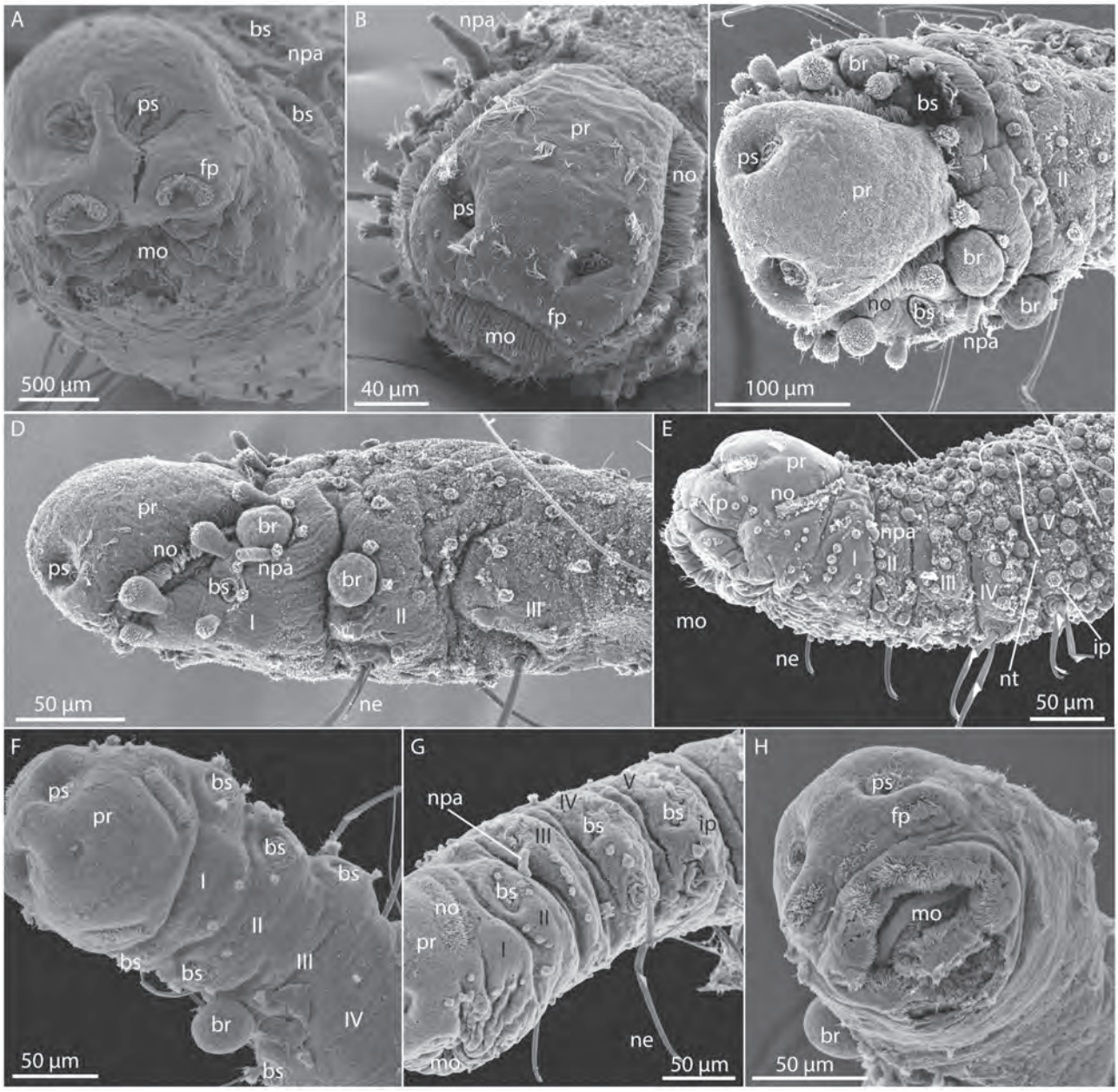


**Fig. 7.3.1.7.2:** Scanning electron micrographs of the head region. A, *Acrocirrus* sp., Quintana Roo (México), frontal view (author Brett C. Gonzalez). B, *Macrochaeta* cf. *clavicornis,* Roscoff (France), frontal view. C, *Flabelligena* sp., Tenerife (Canary Islands), dorsal view. D, Same specimen, lateral view. E, *Macrochaeta* cf. *westheidei,* Cuba, lateral view. F, *Macrochaeta* sp., Lanzarote (Canary Islands), dorsal view. G, Same specimen, lateral view. E, Ventral view. bs, branchia scar; fs, frontal sensory pit; ip, interramal papilla; mo, mouth; ne, neurochaeta; no, nuchal organ; npa, nephriodiopore papilla; nt, notochaeta; pr, prostomium; ps, palp scar.

and Pleijel 2001, Osborn and Rouse 2011). In species of *Macrochaeta* and *Acrocirrus*, the morphology of segment 1 is quite constant, consisting of a narrow ring, more or less visible dorsally, which projects ventro-anteriorly to the prostomium and surrounds the mouth opening (Fig. 7.3.1.7.2 D, E) (Banse 1969). In certain species, such as *Flabelligena*, the peristomium completely encircles the prostomium (Fig. 7.3.1.7.6 A–C) (Orensanz 1974, Aguirrezabalaga and Ceberio 2006), while in others such as *Swima* or *Teuthidodrilus*, it constitutes most of the head due to the reduction of the prostomium to the tissue around the nuchal organs (Osborn *et al*. 2011a,b).

Acrocirridae have grooved ventral palps, which arise from the anterior peristomium, normally immediately in front of the mouth (Fig. 7.3.1.7.2 A–H). Therefore, they are considered as peristomial, although this needs to be confirmed by developmental studies as well as innervation patterns (Rouse and Pleijel 2001, Osborn and Rouse

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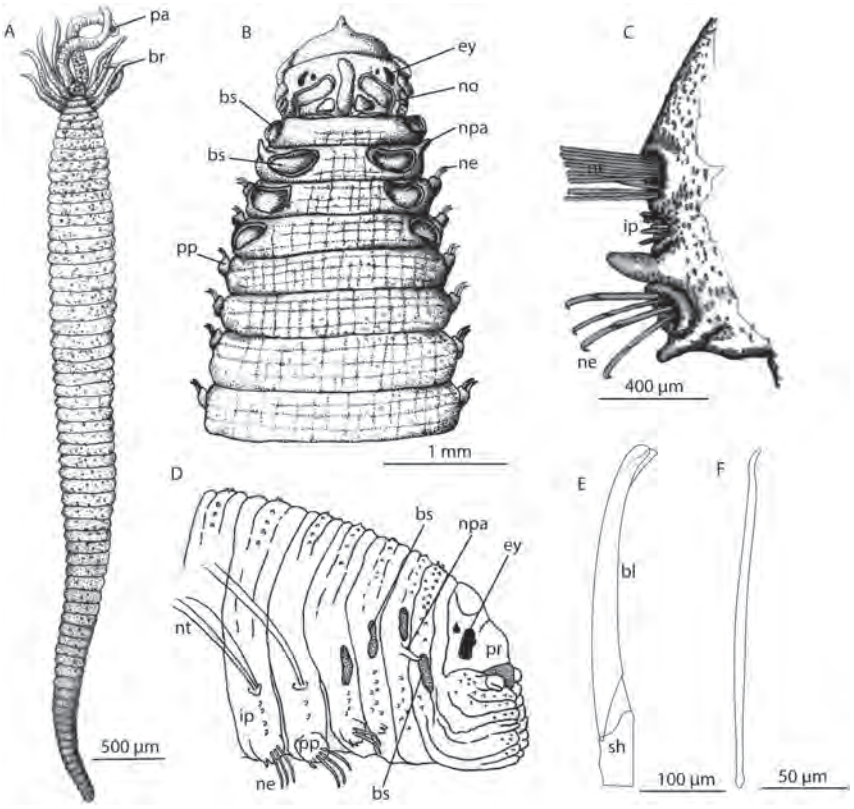


**Fig. 7.3.1.7.3:** Genus *Acrocirrus,* main diagnostic characters. A, *Acrocirrus uchidai,* dorsal view. B, *Acrocirrus validus*, anterior end, dorsal view. C, *Acrocirrus aciculigerus,* right parapodium of segment 9, anterior view. D, *Acrocirrus crassifilis,* anterior end, lateral view. E, *Acrocirrus aciculigerus,* acicular hook. F, Abdominal neurochaetae. Scale bar for D unknown. bl, blade; br, branchia; bs, branchia scar; ey, eye; ip, interramal papilla; ne, neurochaeta; no, nuchal organ; npa, nephridiopore papilla; nt, notochaeta; pa, pal; pp, parapodium; sh, shaft. A, B, Redrawn from Okuda (1934); C, E, F, Kudenov (1976); D, Banse (1969).

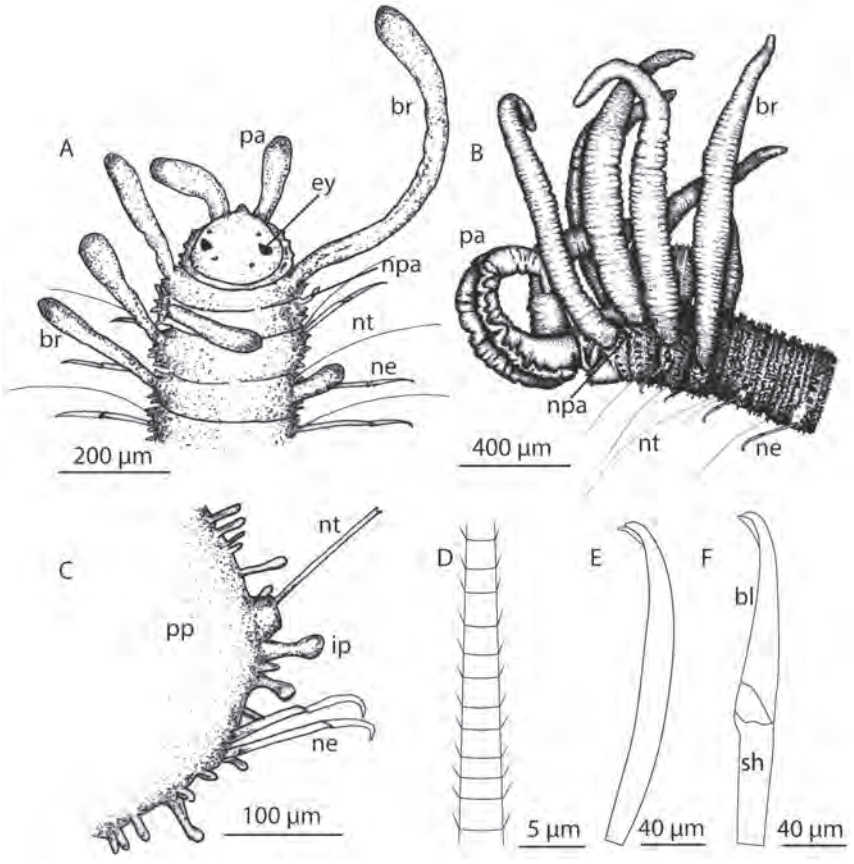


**Fig. 7.3.1.7.4:** Genus *Macrochaeta,* main diagnostic characters. A, *Macrochaeta clavicornis,* dorsal view of anterior end. *Macrochaeta australiensis.* B, Lateral view of anterior end. C, Right parapodium, segment 12. D, *Macrochaeta multipapillata,* notochaeta. E, *Macrochaeta helgolandica,* simple neurochaetae. F, Compound neurochaeta. bl, blade; br, branchia; ey, eye; ip interramal papilla; ne, neurochaetae; npa, nephridiopore papilla; nt, notochaeta; pa, palp; pp, parapodium; sh, shaft. A, E, F, Redrawn from Banse (1969); B, C, Kudenov (1976); D, Westheide (1981).

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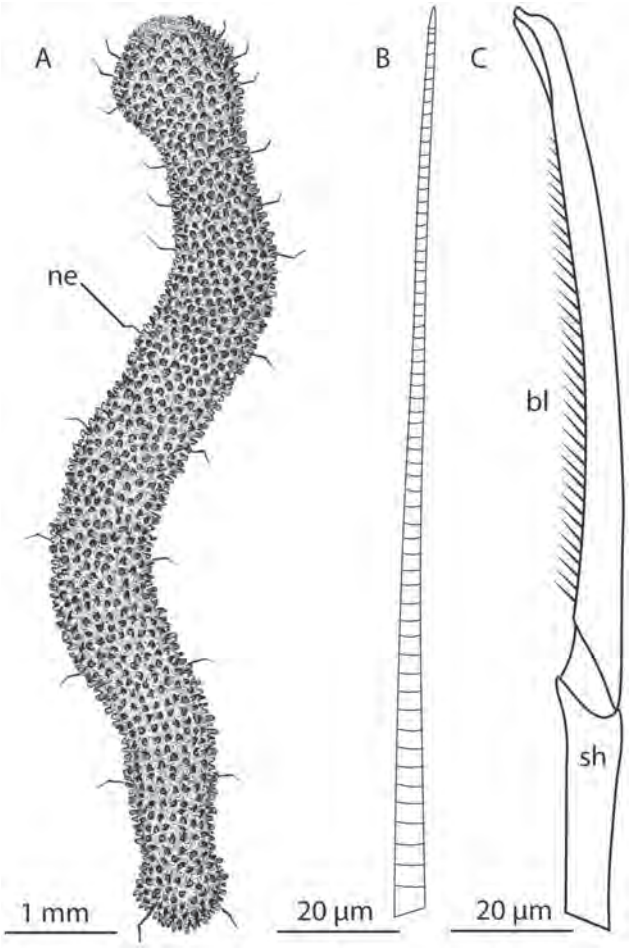


**Fig. 7.3.1.7.5:** Genus *Flabelligella*. A, *Flabelligella papillata,* dorsal view. B, *Flabelligella minuta,* notochaeta. C, *Flabelligella papillata,* neurochaetae. bl, blade; ne, neurochaeta; sh, shaft. Redrawn from Hartman (1965).

2011). Palps are long in pelagic suspension feeding species and in *Acrocirrus* (Fig. 7.3.1.7.1 A, B, F, G) (Osborn *et al.* 2011b) and shorter in *Macrochaeta* and *Flabelligella* (Fig. 7.3.1.7.1 C, E) (Aguirrezabalaga and Ceberio 2006). Palps were described as absent in the species of *Flabelligella,* but since palps are shed easily, this demands further confirmation (Gillet 2001, Osborn and Rouse 2011). A pair of crescent-shaped pits is found anteriorly on the peristomium in some *Macrochaeta* and *Acrocirrus* species (Fig. 7.3.1.7.2 A, H). These frontal pits often occur ventrally to the insertion of the palps, and presumably have a sensory function (Banse 1969, Kudenov 1976).

The subsequent anterior achaetous segments carry the branchiae and the nephridiopore papillae and show a wide variability in different species of acrocirrids. They might be fused, enlarged, or modified into the so-called cephalic hood. The cephalic hood has been described in *Chauvinelia arctica, Chauvinelia biscayensis*, and *Helmetophorus rankini* and is formed by the enlargements of segments 1–2, which fold over the head (Figs. 7.3.1.7.1 B, D, 7.3.1.7.7 A, D, and 7.3.1.7.8 A). In *Swima, Teuthidodrilus, Flabelligella,* and *Flabelligena,* the anterior segments are enlarged or fused in various degrees without forming a cephalic hood (Fig. 7.3.1.7.1 F). Live observations indicate that at least *C. biscayensis* and *Flabelligena erratica* can retract or evert the prostomium from the cephalic hood (Laubier 1974, Orensanz 1974). Following these observations, heads have been described as retractable in many of species of *Flabelligella* and *Flabelligena* based on the varying degree of contraction observed on fixed material (Aguirrezabalaga and Ceberio 2006, Osborn and Rouse 2010). *Swima* and *Teuthidodrilus* lack retractable heads (Osborn *et al.* 2011a,b). Since the anterior achaetous region carries the branchiae, it is sometimes referred to as "branchial membrane" in some pelagic species such as *Teuthidodrilus samae* and *H. rankini* (Glasby and Fauchald 1991, Osborn *et al.* 2011b).

The main branchiae consist of a variable number of filaments, which can be arranged segmentally (Fig. 7.3.1.7.2, 7.3.1.7.3 B, and 7.3.1.7.4 C) (i.e., *Acrocirrus* and *Macrochaeta*) or situated on the anterior fused segments (Figs. 7.3.1.7.1 A, 7.3.1.7.7 A, and 7.3.1.7.8 A, B) (i.e., *Flabelligena* and *Helmetophorus*) (Banse 1969, Aguirrezabalaga and Ceberio 2006). They have been referred to as main branchiae in order to distinguish them from the head branchiae arranged on the prostomium (Osborn and Rouse 2011). Four pairs of main branchiae are typically found in *Macrochaeta* and *Acrocirrus* (Figs. 7.3.1.7.3 A and 7.3.1.7.4 A, B) (Banse 1969), three in *Chauvinelia* (Fig. 7.3.1.7.8 B–D) (Salazar-Vallejo *et al.* 2007), and one to three pairs in *Flabelligena* (Fig. 7.3.1.7.6 A–C) (Aguirrezabalaga and Ceberio 2006). Main branchiae are absent in *Flabelligella*, although this might well be an artifact and needs to be confirmed (Gillet 2001). Branchiae are elongated structures, either tapering or slightly inflated toward the distal end in *Acrocirrus, Flabelligena,* and *Macrochaeta* (Figs. 7.3.1.7.3 A and 7.3.1.7.4 A, B) (Okuda 1934, Banse 1969, Kolmer 1985), or shorter and elliptical and modified as bioluminescent bombs at least in *Swima bombiviridis* and *Swima fulgida* (Fig. 7.3.1.7.1 F) (Osborn *et al.* 2011a). Main branchiae consist of extremely long filaments in the squid-worm *Teuthidodrilus samae*, almost as long as the full body length (Fig. 7.3.1.7.1 G) (Osborn *et al.* 2011b).

The nephidiopore papillae consist of a pair of enlarged papillae present on anterior segments of most acrocirrids, carrying the nephridiopores (Fig. 7.3.1.7.2). These papillae are situated below the second pair of branchiae in most Acrocirridae, and on segments 4–5 in *C. arctica* or on the achaetous anterior region of *Swima* and *Teuthidodrilus*

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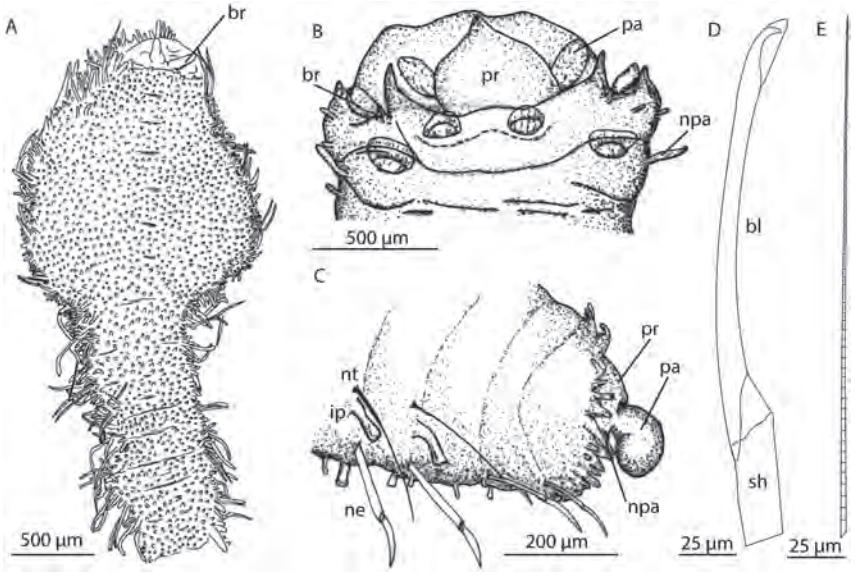


**Fig. 7.3.1.7.6:** Genus *Flabelligena,* main diagnostic characters. A, *Flabelligena biscayensis,* dorsal view. B, *Flabelligena gascognesis,* dorsal view of prostomium. C, *Flabelligena erratica,* lateral view of prostomium. D, *Flabelligena* cf. *cirrata,* neuro- and notochaeta. bl, blade; br, branchia; ip, interramal papilla; ne, neurochaeta; npa, nephridiopore papilla papilla; nt, notochaeta; pa, palp; pp, parapodium; pr, prostomium; sh, shaft. A, D, E, Redrawn from Kolmer (1985); B, redrawn from Aguirrezabalaga and Ceberio (2006); C, redrawn from Orensanz (1974).

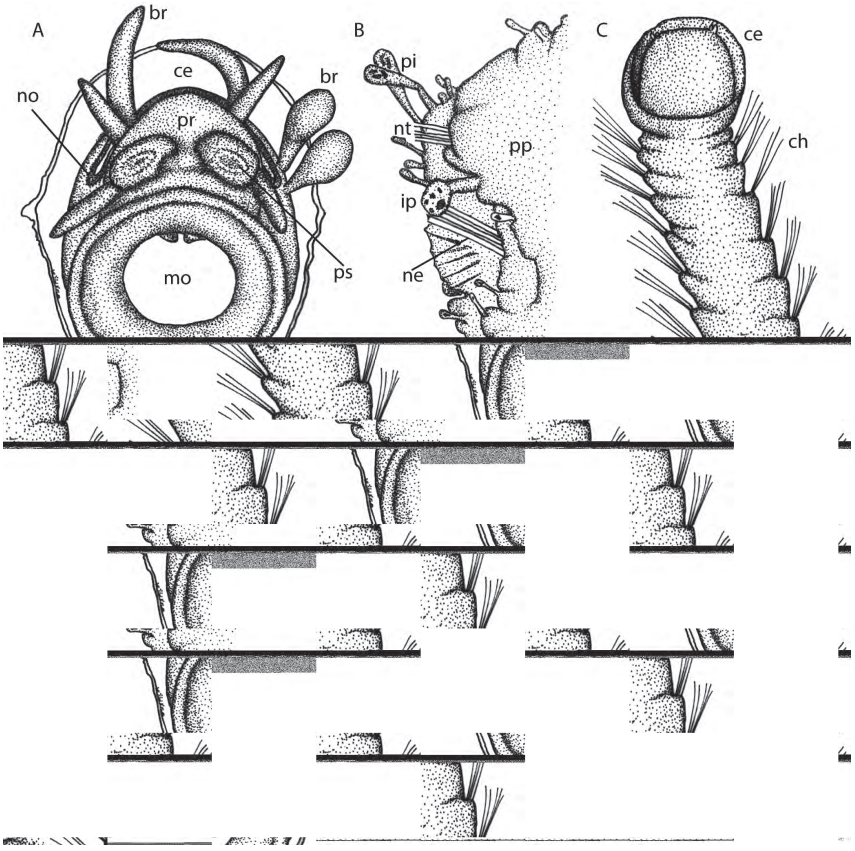


**Fig. 7.3.1.7.7:** Genus *Helmetophorus,* main diagnostic characters. *Helmetophorus rankini.* A, Frontal view of head. B, Lateral view of head. C, Dorsal view of holotype. D, Midbody parapodium. br, branchia; ce, cephalic hood; ch, chaetae; ip, interramal papilla; mo, mouth; ne, neurochaeta; no, nuchal organ; nt, notochaeta; pi, papilla; pr, prostomium; ps, palp scar. A, B, D, Redrawn from Glasby and Fauchald (2001); C, redrawn from Hartman (1971).

(Banse 1969, Osborn *et al.* 2011a,b). The nephridiopore papilla is inconspicuous and difficult to observe in some species of *Macrochaeta* (Fig. 7.3.1.7.2 E).

**Trunk.** The trunk is cylindrical and not regionalized, except for species of *Acrocirrus* and *Macrochaeta*, where a thoracic and an abdominal region can be distinguished based on the arrangement of the neurochaetae, which point backward in the thoracic regions and face forward in the abdominal region. The thoracic region extends along the first 11 chaetigers in *Acrocirrus*, while its extension varies in *Macrochaeta* (Banse 1969, Osborn an Rouse 2011).

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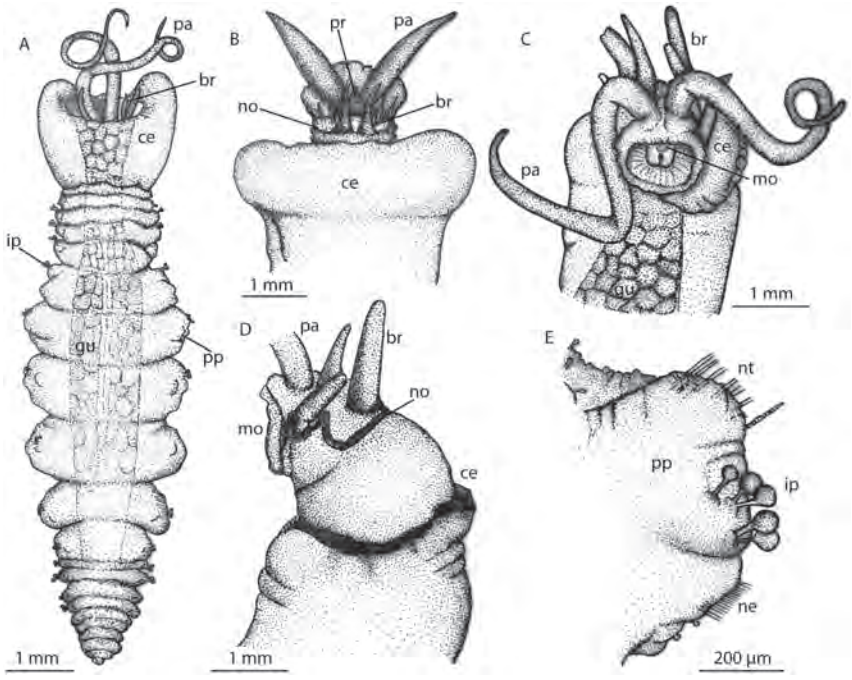


**Fig. 7.3.1.7.8:** Genus *Chauvinelia,* main diagnostic characters. A, Dorsal view of entire animal, chaetae are not drawn. B, Dorsal view of head. C, Ventral view of head. D, Lateral view of head. E. Parapodia. A, C–E, *Chauvinelia biscayensis,* redrawn from Laubier (1974). B, *Chauvinelia arctica,* redrawn from Jirkov (2001). br, branchia; ce, cephalic hood; gu, gut; ip, interramal papilla; mo, mouth; ne, neurochaetae; no, nuchal organ; nt, notochaetae; pa, palp; pp, parapodium.

The trunk is covered by a characteristically papillated epidermis (Fig. 7.3.1.7.2 D, E and 7.3.1.7.9 A). The papillae can cover the entire body (i.e., *Macrochaeta westheidei* and *Macrochaeta multipapillata*) or concentrate near the parapodia in discrete bands. Papillae can also appear between the noto- and neurochaetae as interramal papillae (Fig. 7.3.1.7.9 A) (i.e., *Helmetophorus*) or forming bands or discrete groups around the mouth, anus and nuchal organs (Fig. 7.3.1.7.9 B). Papillae vary from short or long and from tapering to clavate (Fig. 7.3.1.7.9 D–F). Species with clavate papillae often possess thick mucus covering the body, which suggests that the epidermal papillae might be involved in mucus production. Mucus adhere sand grains and detritus in benthic species such as *Macrochaeta*, *Flabelligena, Flabelligera,* and *Flabelliseta* (Fig. 7.3.1.7.9 A, B), and it forms gelatinous sheaths in pelagic species of the genus *Swima* (Salazar-Vallejo *et al.* 2007, Osborn and Rouse 2011).

**Parapodia.** Except for the anterior segments, each trunk segment carries a pair of lateral parapodia. Parapodia form protruding lobes in many species of *Acrocirrus*, *Chauvinelia, Swima,* and *Teuthidodrilus* (Figs. 7.3.1.7.1 A–G, 7.3.1.7.4 D, and 7.3.1.7.5 E) but are small in *Macrochaeta*, in which the chaetae emerge close to the body wall (Fig. 7.3.1.7.4 C). Parapodia are biramous, except for those on chaetigerous segments 1–2, which are typically uniramous (Figs. 7.3.1.7.2 D, E, G and 7.3.1.7.9 A). Generally, there are only a few chaetae per ramus (Banse 1969), except in the pelagic species were chaetae are more numerous, possibly linked to swimming (Osborn *et al.* 2011a,b). One or two needle-shaped neuroaciculae are described in most species (Fig. 7.3.1.7.9 C). Epidermal papillae are present between both rami in most species (Figs. 7.3.1.7.2 and 7.3.1.7.9). In most benthic species, these interramal papillae are larger and identical in shape to the remaining epidermal papillae (Figs. 7.3.1.7.3 C, 7.3.1.7.4 C, and 7.3.1.7.9 A) (Banse 1969), while they are often pedunculated and lollipop-shaped in pelagic *Swima, Chauvinelia*, and *Helmetophorus*, having a variably long stem and a terminal rounded tip (Figs. 7.3.1.7.7 E and 7.3.1.7.8 E) (Glasby and Fauchald 1991, Salazar-Vallejo *et al.* 2007, Osborn *et al.* 2009).

**Chaetae.** Acrocirrids chaetae are typically referred to as spinous, as they consist of successive rings of tiny denticles or spines over a smooth, nonannulated core (Fig. 7.3.1.7.9 G, H) (Salazar-Vallejo *et al.* 2007, 2008). Notochaetae are always simple, whereas neurochaetae can be simple, compound, or pseudocompound (Figs. 7.3.1.7.2 and 7.3.1.7.9). Pseudocompound chaetae morphologically resemble compound chaetae but possess a fold instead of a complete hinge. The shaft of the compound chaetae can be straight or curved or have a distinctly hooked tip. Stout, simple hooks are present on segment 14 of six species of *Acrocirrus,* including *Acrocirrus heterochaetus* and *Acrocirrus bansei*. The pelagic *Teuthidodrilus samae* and *Swima tawitawiensis* possess broad, flattened chaetae, presumably optimized for swimming (Osborn *et al.* 2011a,b). So-called swimming chaetae have been recorded in *Acrocirrus*, but their nature and function have only been poorly described (Banse 1969).

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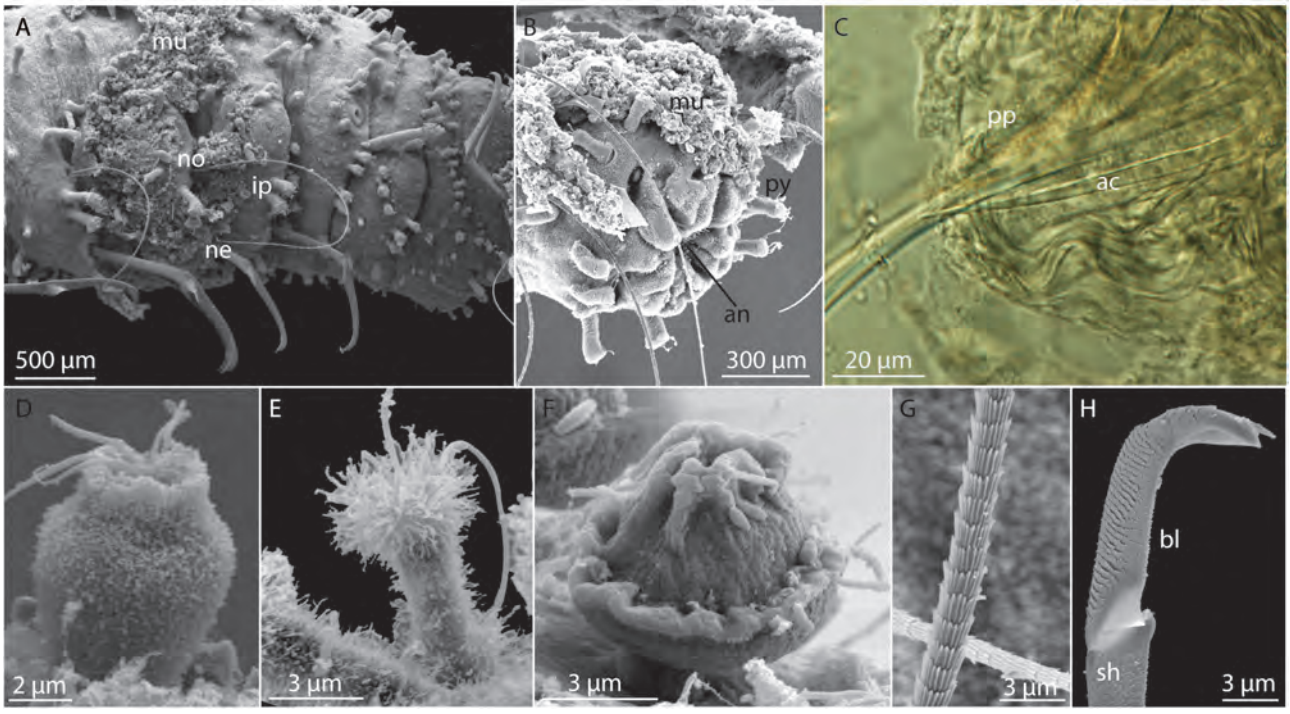


**Fig. 7.3.1.7.9:** Light and scanning electron micrographs of the trunk and pygidium. A, *Macrochaeta* cf. *clavicornis*, Fiskebäcskill (Sweden), lateral view, segment 10. B, Same specimen, pygidium in lateral view. C, *Macrochaeta* sp., Lanzarote (Canary Islands), detail of the acicula on segment 6. D, *Flabelligena* sp., Tenerife (Canary Islands), epidermal papilla. E, *Macrochaeta* sp., Lanzarote (Canary Islands), epidermal papilla. F, *Macrochaeta* cf. *westheidei* (Cuba), epidermal papilla. G, *Macrochaeta* sp., Lanzarote (Canary Islands), detail of the spinous notochaeta. H, *M.* cf. *westheidei* (Cuba), detail of the neuropodial hook. ac, aciculum; an, anus; bl, blade; ip, interramal papilla; mu, mucous sheath; ne, neurochaeta; nt, notochaeta; pp, parapodium; py, pygidium; sh, shaft.

**Pygidium.** The pygidium of all acrocirrids is small and forms a collar without pygidial cirri around the anus, which is terminal and opens toward its dorsal side, often surrounded by papillae (Fig. 7.3.1.7.9 B).

### Anatomy

Very few studies have specifically addressed the internal anatomy of Acrocirridae, with only very few investigations done using semithin sections and light microscopy (Okuda 1934). Despite that, the cuticle and epidermis in the Acrocirridae are more or less transparent, facilitating the observation of many details of the internal anatomy with conventional light microscopy (Fig. 7.3.1.7.1 A, F).

**Digestive system.** The intestinal system is the most conspicuous internal structure (Fig. 7.3.1.7.1 A–G). It consists of mouth and buccal cavity, pharynx, esophagus, foregut and hindgut (sometimes indistinguishable from each other), and anus. The mouth is situated in anterior-ventral position in most of species (Fig. 7.3.1.7.2 H and 7.3.1.7.9 B, D). It is relatively small, folded, and surrounded by a crown of epidermal papillae. The ventral buccal cavity is unarmed and forms eversible lips. In *Acrocirrus* and *Macrochaeta*, it is little more than a ventral lip when everted (Banse 1969), whereas it is larger and forming lateral lips in *Swima* (Osborn *et al.* 2011a). The gut is straight and not clearly regionalized in the species of *Acrocirrus*, *Macrochaeta*, and *Flabelligena*. In contrast, in species of *Swima*, the gut extends from the buccal organ straight along one-third of the body length corresponding to chaetigers 8–10 depending on the species (Fig. 7.3.1.7.1 F). After that point, the gut broadens and loops back along several segments, running anteriorly along several segments before folding rearward again and continuing straight to the anus. The region before the loops, corresponding with the foregut, is darkly pigmented and expandable to near body width. In *Teuthidodrilus samae*, the gut resembles that of *Swima*, forming three loops within segments 2–6 (Fig. 7.3.1.7.1 G).

The epithelium of the gut consists of small columnar cells, typically ciliated in the esophagus and intestine, as well as of different types of glandular cells (Fig. 7.3.1.7.10 B, D) (Okuda 1934). In three investigated species of *Acrocirrus*, glandular cells are absent in the mouth epithelium but abundant in the pharynx and esophagus. The number of glands seems to decrease again in the pygidium. The epithelium of the pharynx possesses characteristic spindle-shaped mucous gland cells in *Acrocirrus uchidai*. In transverse section, the gut epithelium is folded in

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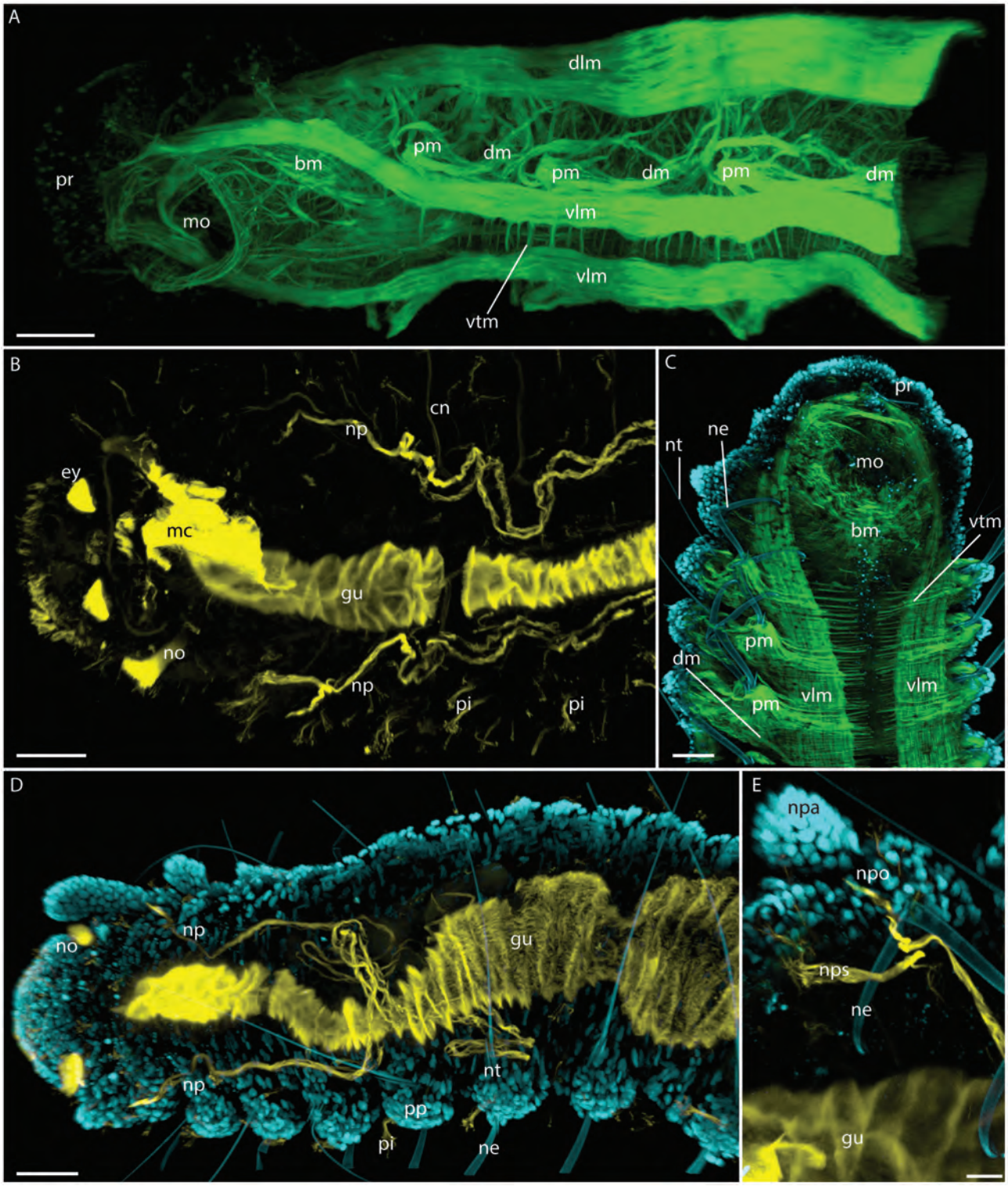


**Fig. 7.3.1.7.10:** Confocal laser scanning microscopy, maximum intensity projections of Z-stack of scans. A, *Flabelligena* sp., phalloidin stained musculature of the anterior end, ventrolateral view. B, *Macrochaeta* sp. from Italy, nerves, gut, and nephridia showing antiacetylated α-tubulin Immunoreactivity (yellow), ventral view. C, *Macrochaeta* sp. from Italy, phalloidin stained musculature (green) of the anterior end and cell nuclei stained with DAPI (cyan), ventral view. D, *Macrochaeta* sp. from Italy, nerves, gut, and nephridia showing antiacetylated α-tubulin immunoreactivity (yellow) and cell nuclei stained with DAPI (cyan), dorsal view. E, *Macrochaeta* sp. from Italy, detail of the nephridiopore and the nephrostome, showing acetylated α-tubulin immunoreactivity (yellow) and cell nuclei stained with DAPI (cyan). bm, buccal musculature; cn, circular nerve; dlm, dorsal longitudinal muscle; dm, diagonal muscle; ey, eye; gu, gut; mc, mouth ciliation; mo, mouth; no, nuchal organ; ne, neurochaetae; np, nephridium; npo, nephridiopore; nps, nephrostome; nt, notochaeta; pp, parapodium; pm, parapodial muscle; pi, papilla; pr, prostomium; vlm, ventral longitudinal muscle; vtm, ventral transverse muscle.

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*Acrocirrus*. In *Acrocirrus muroranensis,* dorsal and ventral folds are present near the esophagus, becoming subdivided in multiple folds toward the posterior end, where the intestine becomes a rosette. Also, in *Acrocirrus*, a distinct ventral groove, which consists of long ciliated cylindrical cells, has been described the posterior part of the intestine to the anus (Okuda 1934).

**Musculature.** Musculature consists of prominent longitudinal muscles, as well as transverse and parapodial muscles in each segment (Fig. 7.3.1.7.10 A, C). Longitudinal muscles consist of discrete pairs of ventro- and dorsolateral muscles running from the head to the pygidium (Fig. 7.3.1.7.10 A, C). The ventrolateral pair of longitudinal muscles diverges in the peristomium to surround the mouth musculature before inserting in the prostomium. Transverse muscles are present ventrally at least in *Macrochaeta* and *Flabelligena,* sometimes extending into the parapodia. Parapodial muscles comprise both longitudinal muscles, branching off from the main bundles and diagonal muscles, forming conspicuous neuropodial chaetal sacs and less well-defined bundles around the notopodial chaetae.

**Blood vascular system.** A circulatory system has been described in species of *Macrochaeta, Acrocirrus, Swima*, and *Teuthidodrilus*. This circulatory system consists of a heart body situated just posterior to the peristomium and several blood vessels (Marion 1874, Mesnil 1899, Okuda 1934, Banse 1969), which extend through the anterior part of the body (Osborn *et al*. 2011a). The heart in *Teuthidodrilus samae* connects to afferent and circular vessels, which supply the elongate branchiae and the nuchal organs being highly vascularized and appearing yellow in individuals alive because of blood visible through the body wall (Osborn *et al*. 2011b).

**Excretory system.** Acrocirridae possess a single pair of anterior nephridia, which form a U-shaped canal extending at each side of the gut along a variable a number of segments (Fig. 7.3.1.7.10 B–D) (Rouse and Pleijel 2001). In *Acrocirrus*, nephridia extend along segments 2–13 and are formed by a single layer of columnar ciliated cells (Okuda 1934). In this genus, the nephrostome opens in segment 3 and extends as a nonpigmented, thin-walled and rather wide upper canal posteriorly until segment 10–13, where it bends anteriorly, forming the lower canal. The lower canal is pigmented and more slender, opening as the nephridiopore on segment 2 (Marion and Bobretzky 1875, Okuda 1934). Similar nephridia are described in *Macrochaeta, Swima*, and *Teuthidodrilus*, lying ventrally in the body cavity (Fig. 7.3.1.7.10 B, D, E) (Banse 1969). Although this has not been demonstrated for all species, it is assumed that the nephridiopore opens as a papilla on the anterior segments (Fig. 7.3.1.7.2) (Gillet 2001, Aguirrezabalaga and Ceberio 2006, Salazar-Vallejo *et al*. 2007).

**Nervous system and sensory organs.** The organization of the nervous system in Acrocirridae has not been yet investigated. However, in species of *Swima* and *Teuthidodrilus*, the nerve cord is visible on the anterior part through the body wall, where it consists of two paired, segmentally arranged ganglia. The nerve cords are fused, but they diverge to surround the mouth and they fuse again just posterior to the insertion of the palp. In *Teuthidodrilus samae*, large nerves have been observed along each branchia.

## Reproduction and development

Acrocirridae are gonochoristic with separate sexes. Depending on the species, gonads occur in the mid or posterior part of the body, arranged segmentally in pairs with an element at each side of the gut. In *Acrocirrus* and *Macrochaeta*, there are 20–25 pairs of gonads in the abdominal region extending between segments 13–17 and 31–39 in *Acrocirrus* (see Okuda 1934) and from segment 13 to 33–38 in *Macrochaeta clavicornis* (see Banse 1969). Gonads are less numerous in other genera. There are five pairs on segments 5–9 observed in *Flabelligena gascognensis* (see Aguirrezabalaga and Ceberio 2006) and two to three pairs on segments 4–6 in *Swima* and segments 2–4 in *Teuthidodrilus samae*.

Gonopores have been described for some species. Gonopores open ventrally on segments 8–9 in *Chauvinelia* and on segments 4–6 in *Swima* (Salazar-Vallejo *et al*. 2007, Osborn *et al*. 2011a). In the species of these genera, gonopores open on swollen structures near the base of neuropodia, referred to as gonopodial lobes in *Chauvinelia* (see Salazar-Vallejo *et al*. 2007). Although this needs confirmation, the enlarged ventral papillae found in *Flabelligena gascognensis* and *Flabelligena erratica* (segments 7–8), as well as *Flabelligena mediterranea* (segments 5–6), might carry the gonopores in these species (Aguirrezabalaga and Ceberio 2006). Gonopores occur in numerous posterior segments in *Acrocirrus* and *Macrochaeta* but remain unknown in *Flabelligella* and *Flabelliseta*.

Details on the sperm transfer, fertilization, and development are still unknown in Acrocirridae.

## Biology and ecology

Acrocirridae exhibit wide range of life strategies. Benthic species are found among the genera *Acrocirrus, Macrochaeta, Flabelligella, Flabelligena*, and *Flabelliseta* (Rouse

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and Pleijel 2001). Species of *Acrocirrus* and *Macrochaeta* are common in shallow waters, typically above 100 m depth. Species of *Macrochaeta* prefer sandy bottoms, and some species such as *M. westheidei* or *M. multipapillata* are considered as interstitial (Westheide 1981, Santos and Silva 1993). Species of *Acrocirrus* are more versatile ecologically, although many Pacific species are common under rocks and pebbles on sandy bottoms in shallow water environments (Okuda 1934). In contrast, species of *Flabelligella* and *Flabelligena* are more common at greater depths and are often recorded below 1,000 m (Salazar-Vallejo *et al.* 2007, Osborn and Rouse 2011). Little information is available regarding habitat preference for the species of these two genera, although a few of them have been found in mud. Benthic acrocirrids crawl on or within the substratum using muscular movements of the body wall and the parapodia. Most benthic species are regarded as selective deposit feeders (Jumars *et al.* 2015) that select deposited food particles using the ventral palps and carry them toward the mouth using the ciliated longitudinal grooved (Marion and Bobretzky 1875, Banse 1969). Some benthic species of Acrocirridae have been exclusively found in anchialine caves in the Caribbean and the Canary Islands and may represent cave exclusive species (Núñez *et al.* 1997, Gonzalez *et al.* 2012). However, in contrast to other described cave-exclusive annelids, cave acrocirrids do not exhibit special adaptations to colonize the water column of these caves, as found in cave-dwelling Protodrilidae, Nerillidae, or Scalibregmatidae (Martínez *et al.* 2013, 2016, Worsaae *et al.* 2004), nor secondary troglomorphic traits such as loss of eyes or elongation of the sensory appendages as found in cave Phyllodocida (Gonzalez *et al.* 2017).

Several pelagic species have been described among the genera *Chauvinelia, Helmetophorus, Swima*, and *Teuthidodrilus*. Whereas the behavior of *Chauvinelia* and *Helmetophorus* remains unknown (Salazar-Vallejo *et al.* 2007), a comparatively large amount of behavioral information has been collected for *Swima* and *Teuthidodrilus* using remotely operated vehicles (ROVs) (Osborn *et al.* 2009, 2011b). Species of *Swima* and *Teuthidodrilus* are always found in the water column, sometimes several hundred meters from the bottom, hovering either in horizontal or oblique positions. The palps and branchiae are often extended and waving around the body and sometimes coiling toward the mouth (Osborn *et al.* 2009, 2011b). In *Teuthidodrilus,* swimming is produced by metachronal waves of the parapodia generated from the pygidium to the prostomium. These movements are improved by the presence of broad, paddle-like chaetae, which are more likely twisted during the recovery stroke to reduce drag. In contrast, in species of S*wima*, the lateral undulation of the body is coupled with an expansion on the power stroke and a contraction on the recovery stroke of the chaetal fans. Pelagic acrocirrids are probably suspension feeders, using the grooved palps to collect suspended food particles, such as marine snow or small, passively drifting prey. The efficiency of suspension feeding is probably favored by the increased palp length, which is longer than the body *Teuthidodrilus,* giving this species its popular squid-like external appearance (Fig. 7.3.1.7.1 G) (Osborn *et al.* 2011b).

At least the deep-sea pelagic species *Swima bombiviridis* can produce bioluminescence using its so-called "bioluminescent bombs," which actually represent the anterior modified branchiae. This probably is an escape reaction upon predators, serving a defensive function. The autotomization of these structures has been observed in response to stimulation both in situ using ROVs, as well as in the laboratory (Osborn *et al.* 2009).

## Phylogeny and taxonomy

The family Acrocirridae was erected to accommodate the genera *Acrocirrus* and *Macrochaeta* previously included in Cirratulidae (Banse 1969). Later on, Acrocirridae incorporated the genus *Flabelligella*, previously considered as a fauveliopsid (Orensanz 1974), subsequently split into *Flabelligella* and *Flabelligena* (Gillet 2001). *Chauvinelia biscayensis* was described as a Flabelligeridae (Laubier 1974) but was subsequently transferred to Acrocirridae upon the description of *Chauvinelia arctica* (see Averincev 1980b). *Helmetophorus rankini*, initially described as a monotypic family (Hartman 1978), was afterward transferred to Flabelligeridae by Glasby and Fauchald (1991) and finally placed in Acrocirridae along with the flabelligerid *Flabelliseta* (see Salazar-Vallejo *et al.* 2007). Most recently, bathypelagic species of acrocirrids were described from the Pacific Ocean. This includes three species of the genus *Swima*, as well as the squid-worm *Teuthidodrilus samae* (Osborn *et al.* 2009, 2011a,b).

Currently, Acrocirridae consists of nine genera: *Acrocirrus*, *Macrochaeta*, *Flabelligella*, *Flabelligena*, *Chauvinelia*, *Helmetophorus*, *Flabelliseta, Swima*, and *Teuthidodrilus,* with 43 described species. The formal diagnosis of each genus and the distribution of all valid species are presented in the following.

### Family Acrocirridae Banse, 1969

**Diagnosis:** Free-living annelids, benthic or pelagic, with cylindrical body and 20–200 trunk segments. Reduced prostomium dorsal on peristomium. Frontal grooved palps, easily lost but leave obvious scars. Mouth subterminal, proboscis unarmed with a buccal sac. With or without eyes. Nuchal organs straight, variously convoluted ciliated bands

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or extending onto free-standing, oppositely branched and spiral structures. Sometimes with one or more rows of subulate branchiae on the head. Achaetous anterior segments often present, sometimes fused, sometimes reduced, sometimes forming a cephalic hood. Transparent, gelatinous sheath sometimes present. One to four pairs of anterior branchiae, easily lost. One pair of large anterior nephridia, nephridiopores ventral, often as elongate papillae. Gonoducts in two or three anterior segments or in numerous abdominal segments. Epidermis with papillae, interramal papillae prominent. Gut straight or looped. Chaetae characteristically spinous, more obviously at distal tips. Notochaetae capillary, rarely lacking. Neurochaetae pseudocompound hooks or compound spinigers or hooks, rarely with posterior neurochaetae simple.

***Acrocirrus* Grube, 1873 (type genus)** (Fig. 7.3.1.7.3)
**Type species:** *Acrocirrus frontifilis* (Grube, 1860)
13 described species
**Diagnosis:** Benthic Acrocirridae. Body cylindrical with more than 50 segments. Prostomium rounded or heart shaped. Cephalic hood absent, head nonretractile. Peristomial palps originating closely together frontally, usually reaching at least segment 10. Four pairs of branchiae. Nephridiopore papillae on segment 3 below the branchiae. Trunk divided into thoracic and abdominal regions based on the chaetal arrangement. Thoracic region always includes segments 1–12. Body surface with few, small, epidermal papillae sometimes arranged as rows. Conspicuous parapodial lobes in some species. Parapodia 1–2 uniramous; biramous subsequently. Notochaetae spinous capillary; neurochaetae as compound or simple hooks. Neuropodial acicular hook on segment 14 in some species.
**Remarks:** Species of *Acrocirrus* are very similar to those of *Macrochaeta*, and both genera are only distinguished by a combination of a few characters. These include the insertion and length of the palps, the size of the body, the number of segments, the presence of only neuropodial compound hooks, and the presence of a constant number of thoracic segments. Because the definition of these characters is not always clear and several species might present intermediate states, a revision of the status of both genera is necessary.
**Distribution and habitat:** *Acrocirrus* consists of 13 described species. Except for *A. frontifilis*, all species are found in the Indo-Pacific, mainly in Japan and California. Species of the genus are more common in shallow waters, particularly under stones on sandy substrates.

***Acrocirrus aciculigens* Kudenov, 1976**
**Type locality:** Long Reef, Collaroy, Sydney, New South Wales (Australia) (Kudenov 1976)
**Habitat:** Intertidally, in sand under stones

***Acrocirrus bansei* Magalhães & Bailey-Brock, 2012**
**Type locality:** Coconut Island, Kaneohe Bay, Oahu, HI (USA) (Magalhães and Bailey-Brock 2012)
**Habitat:** Substratum not described, shallow subtidal waters

***Acrocirrus columbianus* Banse, 1979**
**Type locality:** Brochie Ledge, off Ogden Point breakwater, Victoria, British Columbia (Canada) (Banse 1979)
**Habitat:** Burrows at the base of a clump of *Balanus nubilus*, rocky bottoms, 4.5–7.5 m depth

***Acrocirrus crassifilis* Moore, 1923**
**Type locality:** R/V Albatross Sta. 4430, off Santa Cruz Island, Channel Islands, CA (USA) (Moore 1923)
**Additional localities:** Pacific Ocean (Hartman 1955, 1961, 1963)
**Habitat:** Black sand, pebbles, and rock at slope depths

***Acrocirrus frontifilis* (Grube, 1860)**
**Type locality:** Cres (Croatia) (Grube 1850)
**Additional records:** Mediterranean Sea (Grube 1861, Fauvel 1927, Peres 1954, Bellan 1963, Banse 1969), Atlantic Ocean (Banse 1969, Fauchald *et al*. 2009), and Indo-Pacific (Banse 1969)
**Habitat:** Soft bottom, subtidally

***Acrocirrus heterochaetus* Annenkova, 1934**
**Type locality:** Komandorski Islands, Bering Sea (Russia) (Annenkova 1934)
**Additional records:** Pacific Ocean (Hartman 1948, Uschakov 1955, Banse 1969, Blake 2000)

***Acrocirrus incisa* Kudenov, 1975**
**Type locality:** Puerto Peñasco, Sonora, Gulf of California (Mexico) (Kudenov 1975)
**Habitat:** Intertidal, attached to basalt boulders

***Acrocirrus muroranensis* Okuda, 1934**
**Type locality:** Muroran, Hokkaido (Japan) (Okuda 1934, Banse 1969)
**Habitat:** Intertidal, under stones

***Acrocirrus occipitalis* Banse, 1979**
**Type locality:** Mouth of Brundige Inlet, near Dundas Island, British Columbia (Canada) (Banse 1979).
**Habitat:** 29 m, rocky reef

***Acrocirrus okotensis* Imajima, 1963**
**Type locality:** Off Kamchatka Peninsula, Okhotsk Sea (Russia) (Imajima 1963)
**Habitat**: Not recorded (Banse 1969)

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***Acrocirrus trisectus* Banse, 1969**
**Type locality:** Portobello, Auckland Harbour, Takapuna (New Zealand) (Banse 1969)
**Habitat:** Intertidal, under stones in sand beach

***Acrocirrus uchidai* Okuda, 1934**
**Type locality:** Akkeshi, Hokkaido (Japan) (Okuda 1934)
**Habitat:** Gray mud, 9 m depth

***Acrocirrus validus* Marenzeller, 1879**
**Type locality:** Sagami Bay, east coast of Enoshima Island (Japan) (von Marenzeller 1879)
**Additional records:** Pacific Ocean (Grube 1873, Okuda 1934, Annenkova 1938, Imajima and Hartman 1964, Liu 2008)
**Habitat:** intertidal under stones

***Chauvinelia* Laubier, 1974** (Fig. 7.3.1.7.8)
**Type species:** *Chauvinelia biscayensis* Laubier, 1974
Two species
**Diagnosis:** Bathypelagic Acrocirridae. Body cylindrical, tapering posteriorly, with 20–30 segments. Prostomium small and triangular. Peristomial palps long, originating frontally. Nuchal organs convoluted. Cephalic hood well developed. Three pairs of cirriform branchiae on segment 1–2. Nephridiopore on lateral nephridial lobes on segments 3–4. Body surface with few epidermal papillae; interramal papillae well developed, long, and clavate. Gonopodial lobes on segments 4–5. Parapodia biramous. Notochaetae spinous capillary; neurochaetae as compound or simple spinigers.
**Distribution and habitat:** *Chauvinelia* consists of two described bathypelagic species known from the Arctic and Atlantic oceans at great depth and described from very few individuals.

***Chauvinelia arctica* Averincev, 1980**
**Type locality:** Canadian Slope (Canada) (Averincev 1980a)
**Additional localities**: Arctic Ocean (Kirkegaard 1982, Jirkov 2001, Salazar-Vallejo *et al.* 2007, Budaeva *et al.* 2014)
**Habitat**: Water column, 2,300–3,290 m

***Chauvinelia biscayensis* Laubier, 1974**
**Type locality:** Bay of Biscay, off northern Spain (Laubier 1974, Salazar-Vallejo *et al.* 2007, Budaeva *et al.* 2014)
**Habitat:** Water column, 4,455 m

***Flabelligella* Hartman, 1965** (Fig. 7.3.1.7.5)
**Type species:** *Flabelligella papillata* Hartman, 1965
Four species
**Diagnosis** (Gillet 2001)**:** Benthic Acrocirridae. Body cylindrical, with 20–30 segments. Prostomium rounded or heart shaped. Cephalic hood absent; head retractile into trunk anterior segments. Palps and branchiae absent. Nephridiopore papillae on segment enlarged segment 1. Body surface densely covered with epidermal papillae, often adhering detritus or sand grains. Anterior segments uniramous, biramous subsequently. Notochaetae capillary cross-barred, neurochaetae compound.
**Remarks:** Species of *Flabelligella* are morphologically similar to those in *Flabelligena*, differing only in the absence of main branchiae and palps in *Flabelligella*, as well as in the morphology of the notochaetae, which is spinigerous in *Flabelligella* and cross-barred in *Flabelligena*. Palps and branchiae are easily lost in Acrocirridae, and most species of *Flabelligella* have been described from very few specimens, raising doubts on the validity of the character. Furthermore, the structure of the notochaetae demands scanning electron microscopy analyses that have not yet been performed in many of the species of these groups (Osborn and Rouse 2011). This all stresses the urgent need for a systematic review on both genera (Aguirrezabalaga and Ceberio 2006).
**Distribution and habitat:** *Flabelligella* consists of four described species, mostly dredged from great depths. Consequently, most of them are only known from the type locality and very few individuals.

***Flabelligella macrochaeta* (Fauchald, 1972)**
**Type locality:** Off Islas Tres Marías, San Blas, Nayarit (Mexico) (Fauchald 1972, Light 1978)
**Habitat:** Substrate unknown, 1,536 m depth

***Flabelligella mexicana* Fauchald, 1972**
**Type locality:** Isla Cedro, Baja California (Mexico)
**Habitat:** Green mud, 1,723–1,750 m depth

***Flabelligella minuta* Hartman, 1965**
**Type locality:** upper end of canyon just west of Atlantis Canyon, off New England (USA) (Hartman 1965)
**Habitat**: Substrate unknown, 400 m

***Flabelligella papillata* Hartman, 1965**
**Type locality:** off Bermuda (Bermuda) (Hartman 1965)
**Additional localities:** Atlantic Ocean (Hartman 1965, Detinova 1985, Budaeva *et al.* 2014) and Antarctic Ocean (Clarke and Johnston 2003)
**Habitat:** Substrate unknown, 770–2,000 m

***Flabelligena* Gillet, 2001** (Fig. 7.3.1.7.6)
Type species: *Flabelligena cirrata* (Hartman and Fauchald, 1971)
Six species
**Diagnosis:** Benthic Acrocirridae. Body cylindrical body with 15–30 segments. Prostomium rounded or heart

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shaped. Cephalic hood absent; head retractile into the anterior segments. Palps short, globular, inserted frontally on the peristomium. One to three pairs of main branchiae. Nephridiopore papillae on enlarged segment 1. Body surface covered with epidermal papillae, often adhering detritus or sand grains. A pair of large, cylindrical-conical ventral papillae on segments 5–6 or 6–7 in three species. Parapodia reduced; uniramous on chaetigerous 1–3, biramous subsequently. Notochaetae as spinous or serrated capillaries; neurochaetae compound.

**Remarks:** See *Flabelligella*.

**Distribution and habitat:** *Flabelligena* consists of six described species, mostly dredged from moderate or great depths. Many taxa in the genus are only known from the type locality and very few individuals

***Flabelligena amoureuxi* Gillet, 2001**

**Type locality:** Crozet Islands, South West Indian Ocean (French Southern and Antarctic Lands) (Gillet 2001).

**Habitat**: Clay or clay-sand, 245–980 m depth

***Flabelligena biscayensis* (Kolmer, 1985)**

**Type locality:** Bay of Biscay, off Bretagne (France) (Kolmer 1985)

**Habitat:** Substrate unknown, 2,120 m depth

***Flabelligena cirrata* (Hartman & Fauchald, 1971)**

**Type locality:** Off New England (USA) (Hartman and Fauchald 1971)

**Additional localities:** Eastern Atlantic (Kolmer 1985)

**Habitat:** Substrate unknown, 530–4,144 m depth

***Flabelligena erratica* (Orensanz, 1974)**

**Type locality:** Slope off Argentina (Argentina) (Orensanz 1974)

**Habitat:** *Macrocystis* holdfast drifting on the bottom, 288 m

***Flabelligena gascognensis* Aguirrezabalaga & Ceberio, 2006**

**Type locality:** Capbreton canyon, Bay of Biscay (France) (Aguirrezabalaga and Ceberio 2006)

**Habitat:** Soft bottom, 545–1,113 m

***Flabelligena mediterranea* (Kolmer, 1985)**

**Type locality:** Off Crete (Greece) (Faulwetter *et al.* 2017, Kolmer 1985)

**Habitat:** Substratum unknown, 4,690 m depth.

***Flabelliseta* Hartman, 1978**

**Type species:** *Flabelliseta incrusta* Hartman, 1978

Monotypic

**Diagnosis:** Benthic Acrocirridae with rounded body. Prostomium small and triangular. Cephalic hood absent, head nonretractile. Palps present, but morphology unknown. Two pairs of main branchiae on segments 1–2. Nephridiopore as papillae not observed. Body covered with few reduced papillae; larger clavate papillae associated with the parapodium. Body covered with a thick tunic adhering foreign particles. Parapodia uniramous. Neurochaetae as compound hooks. First parapodia without chaetae.

**Distribution and habitat:** This monotypic genus was described from two individuals collected at great depth.

***Flabelliseta incrusta* Hartman, 1978**

**Type locality**: Weddell Sea (Antarctica) (Hartman 1978)

**Habitat**: Substrate unknown, 2,936 m depth

***Helmetophorus* Hartman, 1978** (Fig. 7.3.1.7.7)

**Type species**: *Helmetophorus rankini* Hartman, 1978

Monotypic

**Diagnosis:** Bathypelagic Acrocirridae. Body cylindrical, tapering posteriorly, with maximum 21 segments. Prostomium small and triangular. Palps unknown; however, palp scars always present. Nuchal organs convoluted. Cephalic hood dorsally elongate, truncate ventrally. Three pairs of cirriform branchiae on segment 1–2. Head branchiae present. Body surface with a few epidermal papillae; interramal papillae long, and clavate. Parapodia biramous. Noto- and neurochaeta simple, straight, and spinous.

**Distribution and habitat:** This monotypic genus is exclusively known from Antarctic Ocean at great depths.

***Helmetophorus rankini* Hartman, 1978**

**Type locality:** Coast Land, Weddell Sea, Antarctic Ocean.

**Habitat:** water column, 3,100 m depth.

***Macrochaeta* Grube, 1850** (Fig. 7.3.1.7.4)

Synonym: *Ledon* (Webster and Benedict 1887)

**Diagnosis:** Benthic Acrocirridae. Body cylindrical with less than 50 segments. Prostomium rounded or heart shaped. Cephalic hood absent, head nonretractile. Nuchal organs ciliated dorso-lateral grooves. Peristomial palps short, with bases separated by at least the width of the palps. Four to six pairs of branchiae. Nephridiopore papillae on segment 3 ventral to the branchiae, sometimes inconspicuous. Trunk divided into thoracic and abdominal regions based on the chaetal arrangement; thoracic region with a variable number of segments. Epidermis with a variable coverage of papillae, interramal papillae present. Parapodia with conspicuous lobes in few species. Parapodia 1–2 uniramous; biramous subsequently. Notochaetae spinous capillary; neurochaetae as compound, pseudocompound or simple hooks.

**Remarks:** See *Acrocirrus*.

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**Type species:** *Macrochaeta clavicornis* (M. Sars, 1835)
12 described species
**Distribution and habitat:** *Macrochaeta* consists of 12 described species, mostly described from marine sediments between 0–300 m depth.

***Macrochaeta australiensis* Kudenov, 1976**
**Type locality:** Point Gellibrand, Port Phillip Bay, Victoria (Australia) (Kudenov 1976)
**Habitat:** Intertidal pool, silt under rocks

***Macrochaeta bansei* Hartmann-Schröder, 1974**
**Type locality:** Orkneys Island (United Kingdom) (Hartmann-Schröder 1974)
**Additional records:** Northeastern Atlantic (Hartmann-Schröder 1996)

***Macrochaeta clavicornis* (M. Sars, 1835)**
**Type locality**: Norway (Sars 1835).
**Additional localities:** Atlantic Ocean (Grube 1850, Southern 1914, McIntosh 1923, Fauvel 1927, Southward 1957, Eliason 1962, Cabioch *et al*. 1968, Banse 1969, Hartmann-Schröder 1996, Kirkegaard 1996, Fauchald *et al*. 2009) and Mediterranean Sea (Bellan 1963).
**Habitat**: Coarse sediments, in shallow waters

***Macrochaeta helgolandica* Friedrich, 1937**
**Type locality:** Helgoland (Germany) (Friedrich 1937)
**Additional localities:** Northeastern Atlantic (Eliason 1962, Banse 1969, Hartmann-Schröder 1996, Muller 2004)
**Habitat:** Coarse sediments, in shallow waters

***Macrochaeta leidyi* (Verrill, 1882)**
**Type locality:** Woods Hole, New England (USA) (Verrill 1882)
**Additional records:** Northwestern Atlantic (Hartman 1942, 1944, 1959, Trott 2004)
**Habitat:** Coarse sand in shallow waters

***Macrochaeta multipapillata* Westheide, 1981**
**Type locality:** Academy Bay, Santa Cruz Island, Galapagos (Ecuador) (Westheide 1981)
**Additional records:** Pacific Ocean (Westheide 1981)
**Habitat:** coarse sand in shallow waters.

***Macrochaeta natalensis* Hartmann-Schröder, 1996**
**Type locality:** Unkomaas, Natal (South Africa) (Hartmann-Schröder 1974)
**Habitat**: Fine sand, 20 m depth

***Macrochaeta papillosa* Ehlers, 1913**
**Type locality**: Posadowsky Bay, Kaiser Wilhelm II Land (Antarctica) (Ehlers 1913)
**Additional records:** Antarctic Ocean (Fauvel 1936, Banse 1969, Clarke and Johnston 2003).
**Habitat:** Substrate not recorded, 385 m

***Macrochaeta pege* Banse, 1969**
**Type locality:** San Juan Island, Puget Sound, Washington (USA) (Banse 1969)
**Habitat:** Coarse sand, 60–100 m depth

***Macrochaeta polyonyx* Eliason, 1962**
**Type locality**: Skagerrak (Sweden) (Eliason 1962)
**Additional localities:** Northeastern Atlantic (Banse 1969, Hartmann-Schröder 1996)
**Habitat:** Grey mud, 300 m depth

***Macrochaeta sexoculata* (Webster & Benedict, 1887)**
**Type locality**: Eastport, Maine (USA) (Webster and Benedict 1887)
**Additional records:** Northwestern Atlantic (Banse 1969, Trott 2004)

***Macrochaeta westheidei* Santos & Silva, 1993**
**Type locality**: Praia Vermelha, Rio de Janeiro (Brazil) (Santos and Silva 1993).
**Habitat:** Coarse sand, 2–4 m depth

Undescribed species have been recorded from submarine and anchialine caves in the Canary Islands (Spain) (Núñez *et al*. 1997, Martínez *et al*. 2009, Riera *et al*. 2017) and Quintana Roo (Mexico) (Gonzalez *et al*. 2012, Rubio *et al*. 2016).

***Swima* Osborn, Haddock, Pleijel, Madin & Rouse, 2009**
**Diagnosis:** Bathypelagic Acrocirridae. Body cylindrical, tapering posteriorly. Prostomium reduced to the tissue surrounding the nuchal organs. Eyes absent. Cephalic hood absent, head not retractable. Palps comparatively long and filiform. Nuchal organs varying from simple oblique, slightly raised ridges to spiral and branched structures free-standing above body wall. Four pairs of main branchiae modified as ellipsoid bioluminescent structures or elongate with tapered distal tips. Body surface covered with a thick or thin gelatinous sheath penetrated by clavate epidermal papillae. Parapodial lobes well developed, with one or more lollipop-shaped interramal papillae both projecting beyond gelatinous sheath. Parapodial biramous, noto- and neurochaetae with numerous simple, spinose chaetae.
**Type species**: *Swima bombiviridis* Osborn, Haddock, Pleijel, Madin & Rouse, 2009
Three described species
**Distribution and habitat:** *Swima* consists of three described species, all pelagic and occurring at great depths.

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***Swima bombiviridis* Osborn, Haddock, Pleijel, Madin & Rouse, 2009**
**Type locality**: Off the central coast of California (Osborn *et al*. 2009)
**Habitat:** Water column, 3,054 m depth

***Swima fulgida* Osborn, Haddock & Rouse, 2011**
**Type locality**: Off central coast of California (Osborn *et al*. 2011a)
**Additional records:** Pacific Ocean (Osborn *et al*. 2009, Osborn and Rouse 2011)
**Habitat:** Water column, 3,267–3,625 m depth

***Swima tawitawiensis* Osborn, Haddock & Rouse, 2011**
**Type locality:** Off Tawi-Tawi, Celebes Sea (Philippines) (Osborn *et al*. 2011a)
**Additional records:** Pacific Ocean (Osborn *et al*. 2009, Osborn and Rouse 2011)
**Habitat:** Water column, 2,836 m depth

***Teuthidodrilus* Osborn, Maddin & Rouse, 2011**
**Diagnosis:** Bathypelagic Acrocirridae. tapering posteriorly, with 25–32 segments. Prostomium reduced to the tissue surrounding the nuchal organs. Eyes absent. Cephalic hood absent, head not retractable. Grooved palps longer than body. Branchial membrane dorsal, with four pairs of elongate, tapered branchiae equal in length to the body. Nuchal organs as ciliated ridge continuous on six pairs of free-standing, oppositely branched structures. Achaetous anterior segments absent. Body covered with a thin gelatinous sheath and few small, body surface bearing few clavate papillae, reduced to a ventrolateral row on each segment and a longitudinal row between noto- and neuropodial lobes. Gonopores as broad papillae ventral to neuropodia on chaetigers 2–3. Parapodia well developed; prominent notopodial lobes with more than 50 simple, flattened, concavo-convex chaetae that taper abruptly at the tip forming a fine point. Neuropodia with two to four simple, flattened chaetae. All chaetae spinose, tiny spines more obvious at distal tips.
**Type species**: *Teuthidodrilus samae* Osborn, Madin & Rouse, 2011
Monotypic.
**Distribution and habitat:** *Teuthidodrilus* is a monotypic pelagic genus, known from the Pacific Ocean at great depths.

***Teuthidodrilus samae* Osborn, Madin & Rouse, 2011**
**Type locality**: Celebes sea (Philippines) (Osborn *et al*. 2011b)
**Additional records:** Pacific Ocean (Osborn *et al*. 2011a, Osborn and Rouse 2011)
**Habitat**: water column, 2,028–2,830 m depth

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**References**

Aguirrezabalaga, F. & Ceberio, A. (2006): *Flabelligena gascognensis* sp. nov. (Polychaeta: Acrocirridae), a new species from the Capbreton Canyon (Bay of Biscay, NE Atlantic) *Scientia Marina* 70: 141–147.
Annenkova, N. (1938): Polychaeta of the north Japan Sea and their horizontal and vertical distribution. USRR Hydrological Expedition in 1934 to the Japan Sea. *Akademiia Nauk (Leningrad)* 81–230. http://marinespecies.org/aphia.php/aphia.php?p=sourcedetails&id=48950.
Annenkova, N.v. (1934): Kurze Ubersicht der Polychaeten der Litoralzone der Bering-Insel (Kommandor-Inseln) nebst Beschreibung neuer Arten. *Zoologischer Anzeiger* 106: 322–331.
Averincev, V.G. (1980a): *Chauvinelia arctica*, sp. n. (Acrocirridae, Polychaeta) from the Canadian plain. *Issledovaniye Fauni Moreyi* 25: 57–62.
Averincev, V.G. (1980b): The role of drifting islands of seaweeds in the distribution of bottom polychetes. *Biologiya Morya* 1: 80–83.
Banse, K. (1969): Acrocirridae n. fam. (Polychaeta Sedentaria). *Journal of the Fisheries Board of Canada* 26(10): 2595–2620.
Banse, K. (1979): *Acrocirrus columbianus* and *A. occipitalis*, two new polychaetes (Acrocirridae) from the northeast Pacific Ocean. *Proceedings of the Biological Society of Washington* 91: 923–928.
Bellan, G. (1963): Nouvelle contribution a l'étude de la microfaune annélidienne de la region de Marseille. *Recueil des Travaux de la Station Marine d'Endoume* 29: 43–57.
Blake, J.A. (2000): 2. Family Acrocirridae Banse, 1969. In: Blake, J.A., Hilbig, B. & Scott, P.H. (eds.) *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel. Volume 7 – The Annelida Part 4. Polychaeta: Flabelligeridae to Sternaspidae.* Santa Barbara Museum of Natural History, Santa Barbara: 25–29.
Budaeva, N., Savilova, T., Zhirkov, I. & Paterson, G.L. (2014): Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Polychaeta. *Invertebrate Zoology* 11: 217–230.
Cabioch, L., L'Hardy, J.P. & Rullier, F. (1968): *Inventaire de la faune marine de Roscoff. Annélides*. Station Biologique de Roscoff, N.S. 17: 1–95.
Clarke, A. & Johnston, N.M. (2003): Antarctic marine benthic diversity. *Oceanography and Marine Biology* 41: 47–114.
Detinova, N.N. (1985): Polychaetous annelids of Rejkjanes Ridge (North Atlantic). *Trudy Instituta Okeanologii, Akademiya Nauk SSSR* 120: 96–136.
Ehlers, E. (1913): Die Polychaeten-Sammlungen der deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition* 13: 397–598.
Eliason, A. (1962): Die Polychaeten der Skagerak-Expedition 1933. *Zoologiska Bidrag från Uppsala* 33: 207–293.

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

Fauchald, K., Granados-Barba, A. & Solís-Weiss, V. (2009): Polychaeta (Annelida) of the Gulf of Mexico. *Gulf of Mexico Origin, Waters, and Biota* 1: 751–788.

Faulwetter, S., Simboura, N., Katsiaras, N., Chatzigeorgiou, G. & Arvanitidis, C. (2017): Polychaetes of Greece: an updated and annotated checklist. *Biodiversity Data Journal* 5: e20997.

Fauvel, P. (1927): Polychètes sédentaires. *Faune de France* 16: 1–494.

Fauvel, P. (1936): *Expedition Antartique Belgue. Resultats du voyage de la Belgica en 1897–1899 sous le commandement de A. de Gerlache de Gomery. Rapports scientifiques. Zoologie, Polychetes. J.* E. Buschman, Anvers.

Friedrich, H. (1937): Polychaetenstudien. I–III. *Kieler Meeresforschungen* 1: 343–351.

Gillet, P. (2001): *Flabelligena amoureuxi,* new genus, new species (Polychaeta: Acrocirridae) from Crozet Islands (Indian Ocean). *Bulletin of Marine Science* 68: 125–131.

Glasby, C.J. & Fauchald, K. (1991): Redescription of *Helmetophorus rankini* Hartman, 1978 (Polychaeta: Helmetophoridae) and its transfer to the Flabelligeridae. *Proceedings of the Biological Society of Washington* 104: 684–687.

Glasby, C.J. & Fauchald, K. (2001): An interactive key to the polychaetes families of the world. CSIRO Publishing. Melbourne [CD-ROM].

Gonzalez, B.C., Borda, E., Carvalho, R. & Schulze, A. (2012): Polychaetes from the Mayan underworld: phylogeny, evolution, and cryptic diversity. *Natura Croatica* 21: 51–53.

Gonzalez, B.C., Worsaae, K., Fontaneto, D. & Martínez, A. (2017): Troglomorphism in Annelida: anophthalmia and elongation of body appendages in cave scale worms (Aphroditiformia, Annelida). *Zoologica Scripta* 47: 106–121.

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

Grube, A.E. (1861): *Ein Ausflug nach Triest und dem Quarnero. Beiträge zur Kenntniss der Thierwelt dieses Gebietes*. Nicolaische Verlagsbuchhandlung, Berlin.

Grube, A.E. (1873): Die Familie der Cirratuliden. *Jahres-Bericht der Schlesischen Gesellschaft für vaterländische Cultur, Breslau* 50: 59–66.

Hartman, O. (1942): A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin of the Bingham Oceanographic Collection* 8: 1–98.

Hartman, O. (1944): New England Annelida. Part 2. Including the unpublished plates by Verrill with reconstructed captions. *Bulletin of the American Museum of Natural History* 82: 327–344.

Hartman, O. (1948): The polychaetous annelids of Alaska. *Pacific Science* 2: 3–59.

Hartman, O. (1955): Quantitative survey of the benthos of San Pedro Basin, southern California. Part I. Preliminary results. *Allan Hancock Pacific Expedition* 19: 1–185.

Hartman, O. (1959): Catalogue of the polychaetous Annelids of the world. Part II. *Allan Hancock Foundation Publications Occasional Paper* 23: 355–628.

Hartman, O. (1961): Polychaetous annelids from California. *Allan Hancock Pacific Expeditions* 25: 1–226.

Hartman, O. (1963): Submarine canyons of Southern California. Part III. Systematics: polychaetes. *Allan Hancock Pacific Expedition* 27: 1–93.

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

Hartman, O. (1978): Polychaeta from the Weddell Sea Quadrant, Antarctica. *Antarctic Research Series* 26: 125–217.

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

Hartmann-Schröder, G. (1974): Polychaeten von Expeditionen der "Anton Dohrn" in Nordsee und Skagerrak. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 14: 169–274.

Hartmann-Schröder, G. (1996): Annelida, Borstenwürmer, Polychaeta. 2., neubearbeitete Auflage. *Tierwelt Deutschlands* 58: 1–648.

Imajima, M. (1963): Polychaetous annelids collected off the west coast of Kamchatka II. Notes on species found in the collection of 1959. *Publications of the Seto Marine Biological Laboratory* 9: 345–372.

Imajima, M. & Hartman, O. (1964): The polychaetous annelids of Japan. Part 2. *Allan Hancock Foundation Publications. Occasional Paper* 26: 239–452.

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

Jirkov, I.A. (2001): *Polychaeta of the Arctic Ocean*. Yanus-K Press, Moscow, 632 pp.

Kirkegaard, J.B. (1982): New records of abyssal benthic polychaetes from the Polar Sea. *Steenstrupia* 8: 253–260.

Kirkegaard, J.B. (1996): *Havborsteorme. II. Sedentaria*. Vinderup Bogtrykkeri A/S, Vinderup.

Kolmer, D.W. (1985): Acrocirridae (Annélides polychètes) abyssaux: Golfe de Gascogne et Mediterranee. In: Laubier, L. & Monniot, C. (eds.) *Peuplements profonds du golfe de Gascogne*. Ifemer, Brest: 355–364.

Kudenov, J.D. (1975): Sedentary polychaetes from the Gulf of California, Mexico. *Journal of Natural History* 9: 205–231.

Kudenov, J.D. (1976): Polychaeta from southeastern Australia 1. Acrocirridae Banse, 1969, from Victoria and New South Wales. *Records of the Australian Museum* 30: 137–151.

Laubier, L. (1974): *Chauvinelia biscayensis* gen. sp. nov., un Flabelligeridae (annélide polychète sédentaire) aberrant de l'étage abyssal du Golfe de Gascogne. *Bulletin de la Société Zoologique de France* 99: 391–399.

Light, W.J. (1978): Reexamination of the species referred to the genus *Flabelliderma* Hartman (Polychaeta: Flabelligeridae and Acrocirridae). *Proceedings of the Biological Society of Washington* 91: 681–690.

Liu, L. (2008): *Checklist of Marine Biota of China Seas*. Institute of Oceanography, Chinese Academy of Science, China.

Magalhães, W.F. & Bailey-Brock, J.H. (2012): A new species of *Acrocirrus* (Polychaeta: Acrocirridae) from Coconut Island, Oahu, Hawaii. *Journal of the Marine Biological Association of the United Kingdom* 92: 1019–1022.

von Marenzeller, E. (1879): Südjapanische Anneliden. *Denkschriften der Akademie der Wissenschaften* 41: 109–152.

Marion, A.-F. (1874): Sur les Annélides du golfe de Marseille. *Comptes Rendus de l'Academie des Sciences* 79: 398–401.

Marion, A.-F. & Bobretzky, N. (1875): Étude des Annélides du Golfe de Marseille. *Annales des Sciences Naturelles* 2: 1–106.

Martínez, A., Di Domenico, M. & Worsaae, K. (2013): Evolution of cave *Axiokebuita* and *Speleobregma* (Scalibregmatidae, Annelida). *Zoologica Scripta* 42: 623–636.

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Martínez, A., Kvindebjerg, K., Iliffe, T.M. & Worsaae, K. (2016): Evolution of cave suspension feeding in Protodrilidae (Annelida). *Zoologica Scripta* 46: 214–226.

Martínez, A., Palmero, A.M., Brito, M.d.C., Núñez, J. & Worsaae, K. (2009): Anchialine fauna of the Corona lava tube (Lanzarote, Canary Islands): diversity, endemism and distribution. *Marine Biodiversity* 39: 169–187.

McIntosh, W.C. (1923): Notes from the Gatty Marine Laboratory, St. Andrews. No. 45. 1. On certain features in the British species Lepadogaster. 2. On the rarity of abnormality in the incisors of the wild rabbit, and on its coloration. 3. On the fragmentary skull of the Airthrey Whale in the Royal Scottish Museum, and remarks on humpback, blue, and finner whales. 4. On a fragmentary skull of *Balena australis*, Desmoulins, in the British Museum. 5. On *Amphinome rostrata* Pallas in the Atlantic and India. *Annals and Magazine of Natural History* 12: 65–94.

Mesnil, F. (1899): La position systématique des Flabelligériens St. Joseph (Chlorémiens Quatrefages) et des Sternaspiens. *Zoologischer Anzeiger* 22: 81–85.

Moore, J.P. (1923): The polychaetous annelids dredged by the U.S.S. "Albatross" off the coast of Southern California in 1904. IV Spionidae to Sabellariidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 75: 179–259.

Muller, Y. (2004): *Faune et flore du littoral du Nord, du Pas-de-Calais et de la Belgique: inventaire [Coastal Fauna and Flora of the Nord, Pas-de-Calais and Belgium: Inventory]*. Commission Régionale de Biologie Région Nord Pas-de-Calais: France.

Núñez, J., Ocaña, O. & Brito, M.C. (1997): Two new species (Polychaeta: Fauveliopsidae and Nerillidae) and other polychaetes from the marine lagoon cave of Jameos del Agua, Lanzarote (Canary Islands). *Bulletin of Marine Science* 60: 252–260.

Okuda, S. (1934): The polychaete genus, Acrocirrus, from Japanese waters. *Journal of the Faculty of Science, Hokkaido University* 2: 197–209.

Orensanz, J.M. (1974): Los anélidos poliquetos de la provincia biogeográfica Argentina. X. Acrocirridae. *Neotropica* 20: 113–118.

Osborn, K.J., Haddock, S.H. & Rouse, G.W. (2011a): *Swima* (Annelida, Acrocirridae), holopelagic worms from the deep Pacific. *Zoological Journal of the Linnean Society* 163: 663–678.

Osborn, K.J., Haddock, S.H.D., Frederik, P., Madin, L.P. & Rouse, G.W. (2009): Deep-sea, swimming worms with luminescent "bombs." *Science* 325: 964.

Osborn, K.J., Madin, L.P. & Rouse, G. (2011b): The remarkable squidworm is an example of discoveries that await in deep-pelagic habitats. *Biology Letters* 7: 499–453.

Osborn, K.J. & Rouse, G.W. (2011): Phylogenetics of Acrocirridae and Flabelligeridae (Cirratuliformia, Annelida). *Zoologica Scripta* 40: 204–219.

Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D. & Vinther, J. (2016): The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society B* 283: 20161378.

Peres, J.M. (1954): Contribution a l'etude des annélides polychètes de la Mediterranee occidentale. *Travaux de la Station Marine d'Endoume* 13: 83–154.

Riera, R., Monterroso, Ó., Núñez, J. & Martínez, A. (2017): Distribution of meiofaunal abundances in a marine cave complex with secondary openings and freshwater filtrations. *Marine Biodiversity* 48(1): 203–2015.

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

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

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

Rubio, F., Rolán, E., Worsaae, K., Martínez, A. & Gonzalez, B.C. (2016): Description of the first anchialine gastropod from a Yucatán cenote, *Teinostoma brankovitsi* n. sp. (Caenogastropoda: Tornidae), including an emended generic diagnosis. *Journal of Molluscan Studies* 82: 169–177.

Salazar-Vallejo, S.I., Gillet, P. & Carrera-Parra, L.F. (2007): Revision of *Chauvinelia*, redescriptions of *Flabelliseta incrusta*, and *Helmetophorus rankini*, and their recognition as acrocirrids (Polychaeta: Acrocirridae). *Journal of Marine Biology Association U.K.* 87: 465–477.

Salazar-Vallejo, S., Carrera-Parra, L. & Fauchald, K. (2008): Phylogenetic affinities of the Flabelligeridae (Annelida, Polychaeta). *Journal of Zoological Systematics and Evolutionary Research* 46: 203–215.

Santos, P.J.P.d. & Silva, V.M.A.P.d. (1993): *Macrochaeta westheidei* n.sp., first record of Acrocirridae for the Brazilian coast (Annelida, Polychaeta). *Nerítica* 7: 7–12.

Sars, M. (1835): *Beskrivelser og Iagttagelser over nogle moerkelige eller nye i Havet ved den Bergenske Kyst levende Dyr af Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort Oversigt over de hidtil af Forfatteren sammesteds fundne Arter og deres Forekommen.* Thorstein Hallagers Forlag hos Christian Dahl, Bergen, R.S.: xii + 81, 15 plates.

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

Southward, E.C. (1957): The distribution of Polychaeta in offshore deposits in the Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* 36: 49–75.

Struck, T.H., Golombek, A., Weigert, A., Franke, F.A., Westheide, W., Purschke, G., Bleidorn, C. & Halanych, K.M. (2015): The evolution of annelids reveals two adaptive routes to the interstitial realm. *Current Biology* 25: 1993–1999.

Trott, T.J. (2004): Cobscook Bay inventory: A historical checklist of marine invertebrates spanning 162 years. *Northeastern Naturalist* 11: 261–324.

Uschakov, P.V. (1955): *Atlas of the Invertebrates from the Far Eastern Seas of the USSR*. Akademia Nauk, SSSR.

Verrill, A.E. (1882): Notice of recent additions to the marine Invertebrata of the northeastern coast o America, with descriptions of new genera and species and critical remarks on others. Part II. Mollusca, with notes on Annelida, Echinodermata, etc. collected by the United States Fish Commission. *Smithsonian Miscellaneous Collections* 22: 356–405.

Webster, H.E. & Benedict, J.E. (1887): The Annelida Chaetopoda from Eastport, Maine. *Report of the United States Commissioner of Fisheries* 1885: 707–755.

Westheide, W. (1981): Interstitielle Fauna von Galapagos. XXVI. Questidae, Cirratulidae, Acrocirridae, Ctenodrillidae (Polychaeta). *Mikrofauna des Meeresbodens* 82: 1–23.

Worsaae, K., Sterrer, W. & Illife, T.M. (2004): *Longipalpa saltatrix*, a new genus and species of the meiofaunal family Nerillidae (Annelida: Polychaeta) from an anchihaline cave in Bermuda. *Proceedings of Biological Society of Washington* 117: 360–376.

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Dieter Fiege

### 7.3.1.8 Sternaspidae Carus, 1863

#### Introduction

Sternaspidae comprise a relatively small group of polychaetes that are enigmatic in their exterior morphology. They superficially resemble echiurans or sipunculans and have been classified as such by early authors. Characteristic is the short, thick, grub-like body shape, the absence of parapodia, and the presence of conspicuous rows of hooks at the anterior end. The anterior end can be retracted, resulting in an ovoid to spherical body shape. The most striking morphological feature is the presence of a prominent, often distinctly colored ventrocaudal shield framed by fascicles of capillary chaetae.

Thirteen species and two subspecies had been described for the single genus *Sternaspis* Otto, 1821 until 2012. However, the validity of a number of these species has been questioned due to insufficient descriptions and the lack of type specimens. Consequently, some authors considered *Sternaspis scutata* (Renier in Ranzani 1817) the only valid species showing a seemingly cosmopolitan distribution (for authorship of the species, see Muir and Petersen 2013). Sendall and Salazar-Vallejo (2013) published a formal revision of the group, accepting 13 of the described species as valid and adding four new species and two new genera. Since then 26 new species have been added including six from the deep Pacific, three from polar regions, ten from SE Asian waters, as well as one from Chile and six from tropical areas bringing the current total of known species to 43 (Salazar-Vallejo and Buzhinskaja 2013, Salazar-Vallejo 2014a,b; Wu *et al*. 2015, Zhadan *et al*. 2017, Wu & Xu 2017, Díaz-Díaz & Rozbaczylo 2017, Salazar-Vallejo 2017) (Tab. 7.3.1.8.1, Fig. 7.3.1.8.10)

#### Morphology

##### External morphology

**Prostomiun and Peristomium.** Sternaspidae are short, thick, grub-like polychaetes reaching about 30 mm length and 10–15 mm width for 30–34 segments (pro- and peristomium not included) (Petersen 2000a, Rouse 2001) (Figs. 7.3.1.8.1 A, B and 7.3.1.8.3 A). The prostomium is a smooth, small round cupule (Figs. 7.3.1.8.1 A, 7.3.1.8.3 A, B, and 7.3.1.8.4 A), and the peristomium is reduced to a mound around the mouth densely covered by papillae (Figs. 7.3.1.8.1 A, 7.3.1.8.2 A, 7.3.1.8.3 A, B, 7.3.1.8.4 A, and 7.3.1.8.5 A). Pro- and peristomial appendages are absent. Peristomial palp-like appendages were shown uniquely for *Sternaspis spinosa* Sluiter, 1882. Petersen (2000a) suggested these appendages to represent an extruded gut, but this view is contradicted by histological details given by Sluiter (1882). Nuchal organs and eyes are absent.

**Segments.** Segmentation is distinct, with the anterior (segments 1–6), middle (segments 7–14), and posterior (segments 15–20) body regions clearly discernable. Parapodia, aciculae, and dorsal and ventral cirri are absent. A pair of ventral genital papillae protrudes at the border of segments 6 and 7, distinguishing anterior and midbody region. The anterior region up to segment 6, sometimes called introvert, is retractable, leaving the genital papillae extended (Figs. 7.3.1.8.1 A, C and 7.3.1.8.3 A). Segments 1–3 are each equipped with a single row of 10–19 strong spinelike chaetae increasing dorsally in length and thickness (Figs. 7.3.1.8.1 A, B and 7.3.1.8.3 A, B). These chaetae are composed of an inner marrow and an outer sheath (Fig. 7.3.1.8.4 F). Observations by Petersen (2000) indicate that these spines are neurochaetae while notochaetae in these segments are minute and emergent in juvenile specimens only have been confirmed by Zhadan *et al*. (2017). Segments 4–6 are constricted forming a kind of "neck" region in extended specimens; chaetae are absent. The midbody consists of about eight segments gradually increasing in diameter caudally. Segmentation is best visible laterally; smooth, seemingly unsegmented regions are found midventrally and middorsally extending to the ventral shield and segments 14–16, respectively (Figs. 7.3.1.8.1 A–C and 7.3.1.8.3 A). Segments 7–13/14 each have one pair of rudimentary chaetal fascicles of short capillary chaetae, which are hardly penetrating the body wall. The posterior body region from segment 13 or 14 onward is ventrally covered by a bilaterally symmetrical shield with a longitudinal midventral groove, which may be indistinct in some species (Figs. 7.3.1.8.1 A, D, 7.3.1.8.3 A, C, and 7.3.1.8.4 B). This sclerotinized shield is usually wider than long. It is made up of mineralized iron supported by a framework of fibers (Bartolomaeus 1992). The shield is framed by 9–10 lateral chaetal fascicles and 5–9 caudal fascicles with shorter capillaries, suggesting the presence of 14–19 body segments being covered by the shield (Fig. 7.3.1.8.3 E). The noto- or neuropodial origin of the fascicles are unresolved, but Vejdovský (1882) assumes a correlation between the position of lateral and posterior chaetal fascicles and the direction of grooves on the ventrocaudal shield. Chaetal types include relatively strong capillaries covered by a feltlike sheath (Fig. 7.3.1.8.4 D, E, G) in lateral fascicles and posterior rows comprising some very long smooth capillaries in the posteriormost lateral bundle, as well as one pair of peg chaetae (a dense group of short chaetae embedded in a fibrous matrix and covered by a common sheath (Zhadan *et al*. 2017)) situated at the posterolateral corners of the shield, accompanied medially

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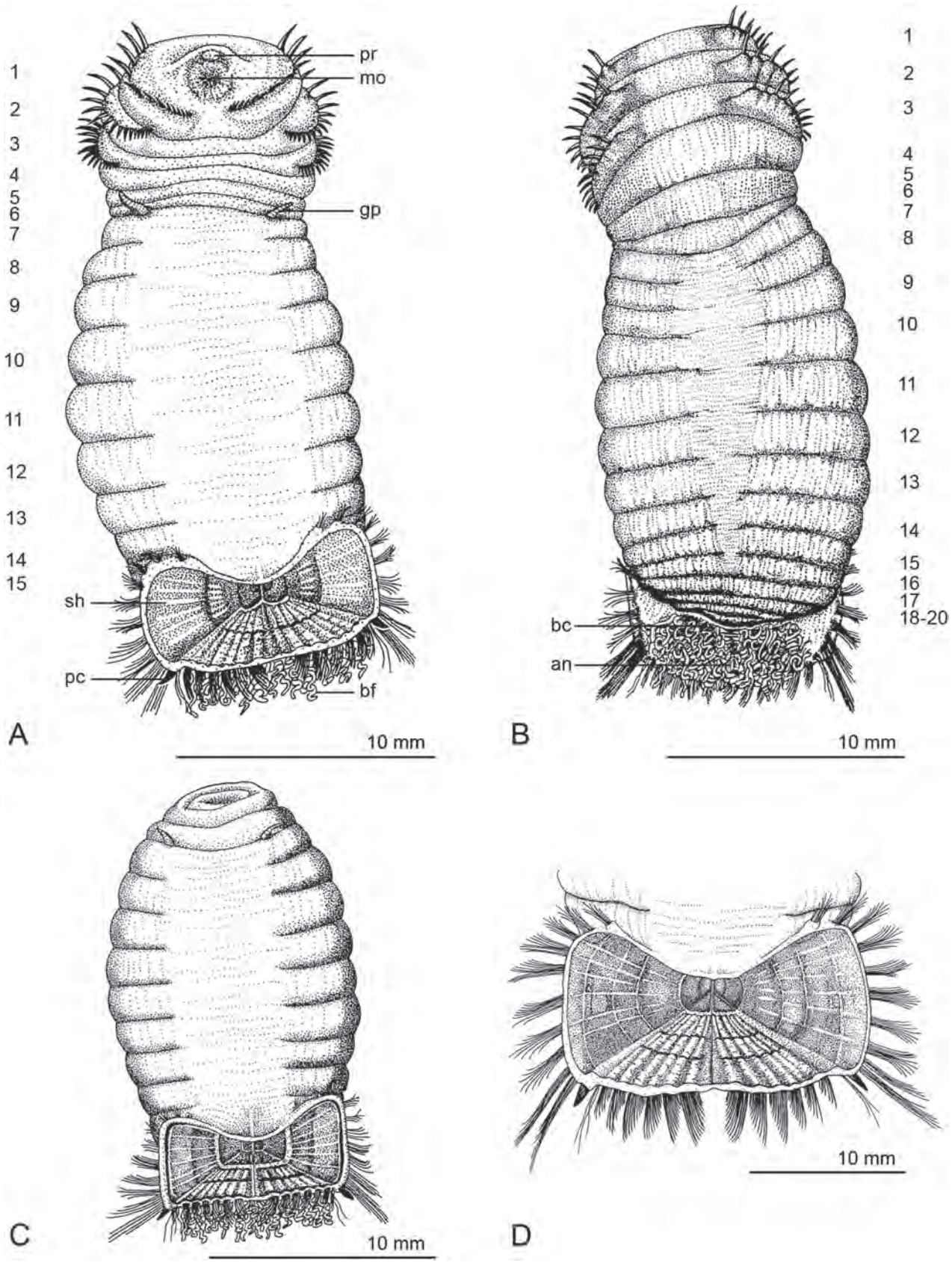


**Fig. 7.3.1.8.1:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423). A, B, Extended specimen: A, ventral view; B, dorsal view. C, Retracted specimen, ventral view. D, ventrocaudal shield. an, anus; bc, branchial cushion; bf, branchial filaments; gp, genital papillae; mo, mouth; pc, peg chaeta; pr, prostomium; sh, ventrocaudal shield. A–D, From B. Bütfering.

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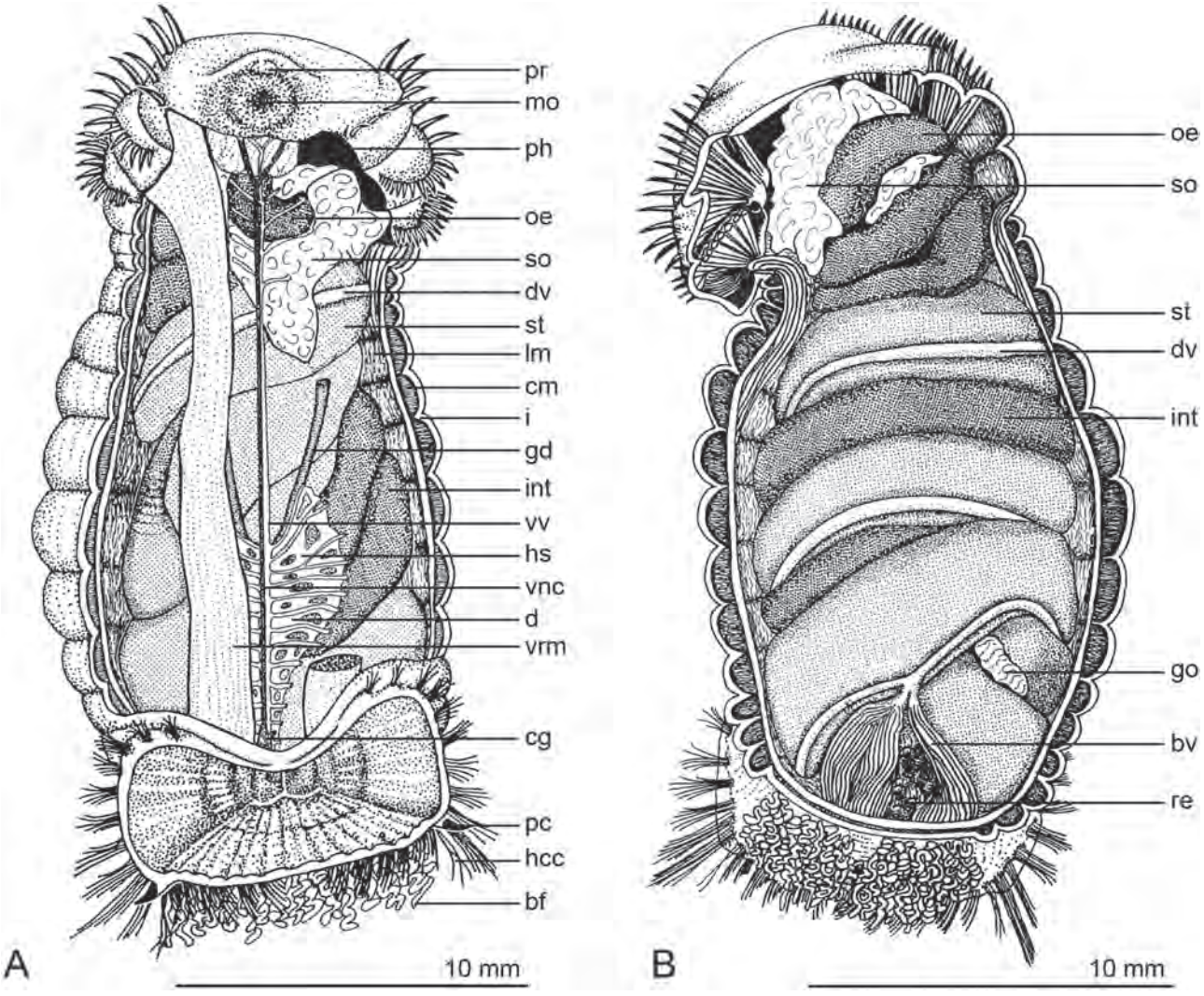


**Fig. 7.3.1.8.2:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423). A, B, Extended specimen, dissected: A, ventral view; B, dorsal view. bf, branchial filaments; bv, branchial vessels; cm, circular muscles; cg, caudal ganglion; d, dissepiment; dv, dorsal vessel; gd, genital duct;, go, gonad; hcc, hair-like capillary chaetae; hs, horizontal septum; i, integument; int, intestine; lm, longitudinal muscles; mo, mouth; oe, esophagus; pc, peg chaeta; ph, pharynx; pr, prostomium; re, rectum; so, segmental organ; st, stomach; vnc, ventral nerve cord; vv, ventral vessel; vrm, ventral retractor muscle. A, B, From B. Bütfering.

by a pair of fascicles of thin capillary hairlike chaetae (Fig. 7.3.1.8.4 H). Chaetae of lateral fascicles are increasing in length caudally. Rallo and Moya (1987) showed bidentate hooks in (?antero-) lateral bundles of *S. scutata* collected from the Bay of Biscay – an observation that has not been confirmed to date. Dorsally, the posteriormost body region is covered by numerous branchial filaments and filiform papillae originating from two oval branchial cushions situated on both sides of the anus. Branchial filaments are threadlike, slightly decreasing in diameter from proximal to distal. A pygidium is not clearly defined. Pygidial cirri are absent (Figs. 7.3.1.8.2 B, 7.3.1.8.3 D, and 7.3.1.8.4 C).

**Color.** Body color in alcohol is light gray to light brown, chaetae yellow to brownish, branchial filaments apricot colored, and ventral shield yellow to brown, dark gray, or even violet. For live specimens, Rietsch (1882) reports body color as whitish to yellow-gray, chaetae yellow-brown, branchiae reddish, and shield reddish-brown to violet.

**Epidermis and cuticle.** The integument consists of an epidermis and cuticle. The cuticle varies between 75 and 150 µm in thickness and is composed of electron-bright fibers partly arranged orthogonally and embedded in an amorphous matrix. The cuticle is formed by a cuboidal monolayer of supporting cells containing a prominent tonofilament system (Bartolomaeus 1992). The body surface, including the ventrocaudal shield, is more or less densely covered with papillae sometimes with adhering sediment

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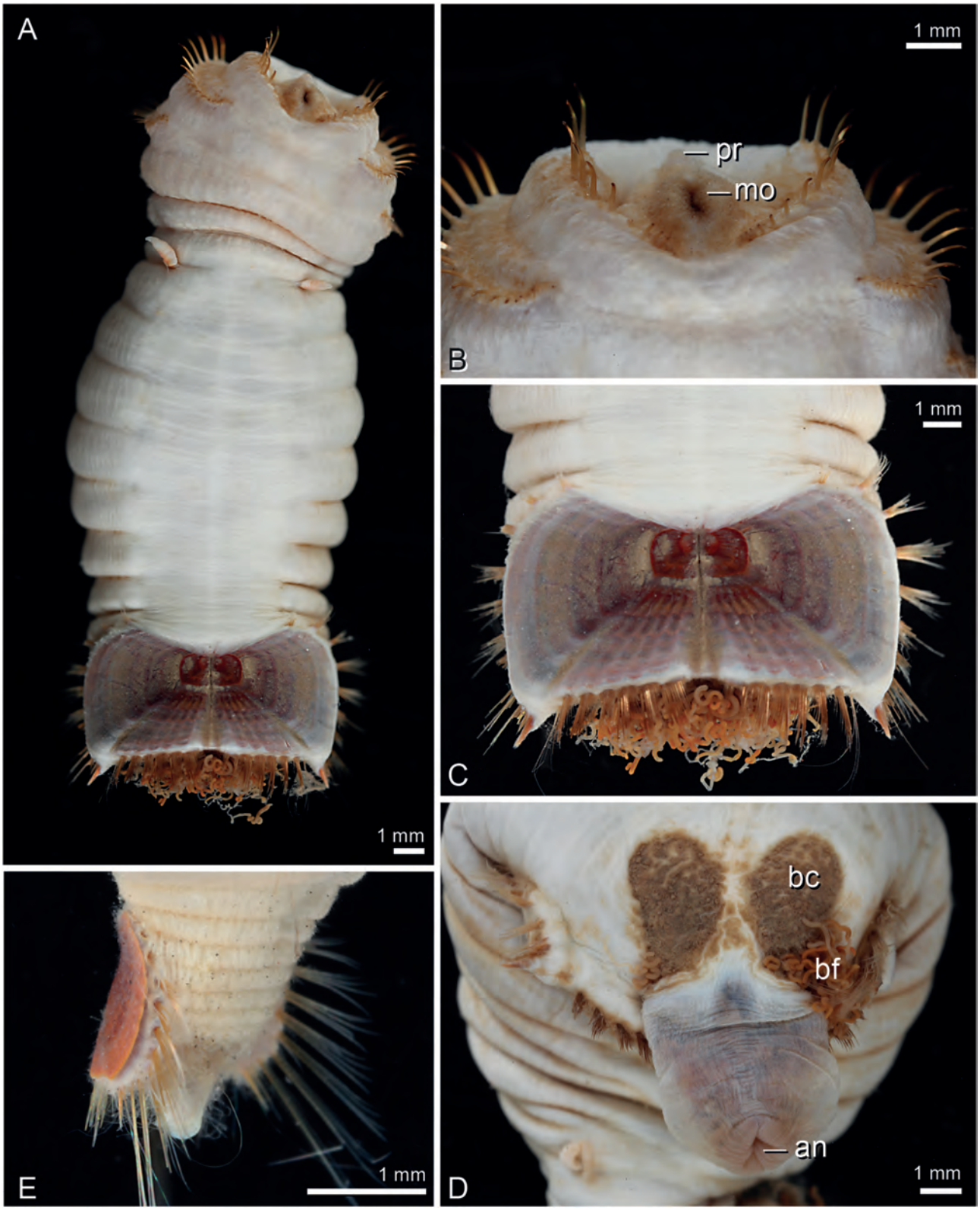


**Fig. 7.3.1.8.3:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423). A, Extended specimen, ventral view. B, Anterior end, ventral view. C, Ventrocaudal shield. D, Posterior region, dorsal view. Most branchial filaments removed, anus everted. E, *Sternaspis* sp. (Mediterranean Sea, SMF 10242), posterior region, lateral view. an, anus; bc, branchial cushion; bf, branchial filaments; mo, mouth; pr, prostomium.

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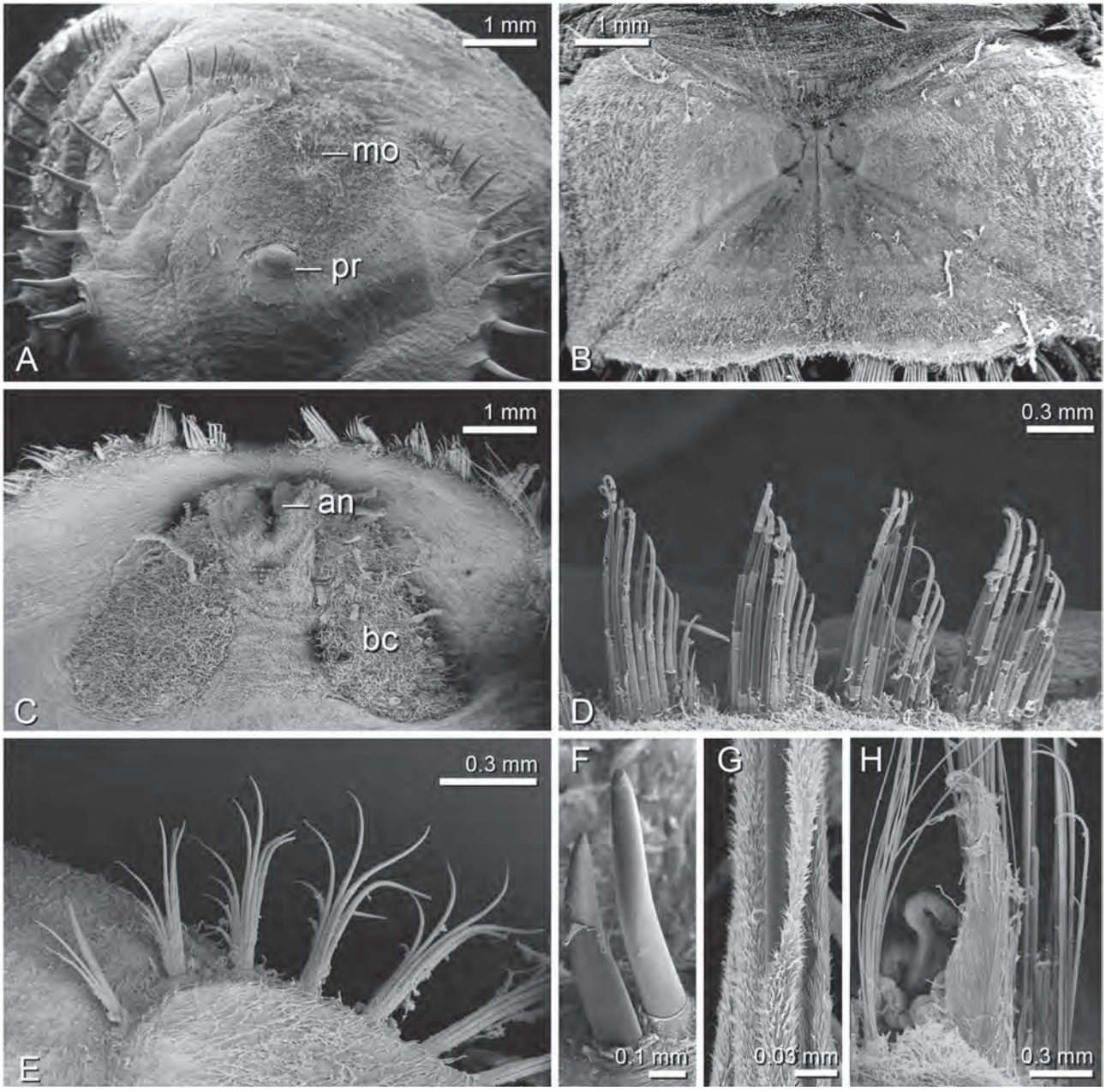


**Fig. 7.3.1.8.4:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423), scanning electron microscopy micrographs. A, Anterior region, frontal view. B, Ventrocaudal shield. C, Posterior region, dorsal view. D, Bundles of chaetae posterior to ventrocaudal shield. E, Bundles of chaetae lateral to ventrocaudal shield. F, Anterior spine-like chaetae. G, Detail of D. H, Peg and capillary hair-like chaetae. an, anus; bc, branchial cushion; mo, mouth; pr, prostomium.

or debris. Vejdovský (1882) distinguishes three types of papillae in the mouth region, and the anterior and posterior body with the first as morphologically most elaborate and those of the posterior body region the simplest. Sendall and Salazar-Vallejo (2013) distinguish five types of papillae (body, mouth, genital, shield, and interbranchial). However, the genital papillae are much bigger and morphologically so different that they should be considered separate structures (Fig. 7.3.1.8.3 A). In scanning electron microscopy (SEM) studies of *S. scutata*, at least two types of papillae, i.e., short, rounded, and elongate, could be distinguished around the mouth (Fig. 7.3.1.8.5 A), whereas those on the body and the ventral shield appear morphologically similar (Fig. 7.3.1.8.5 B).

**Anatomy**

Krohn (1842) was the first to describe the major parts of the nervous system, which led him to correctly define

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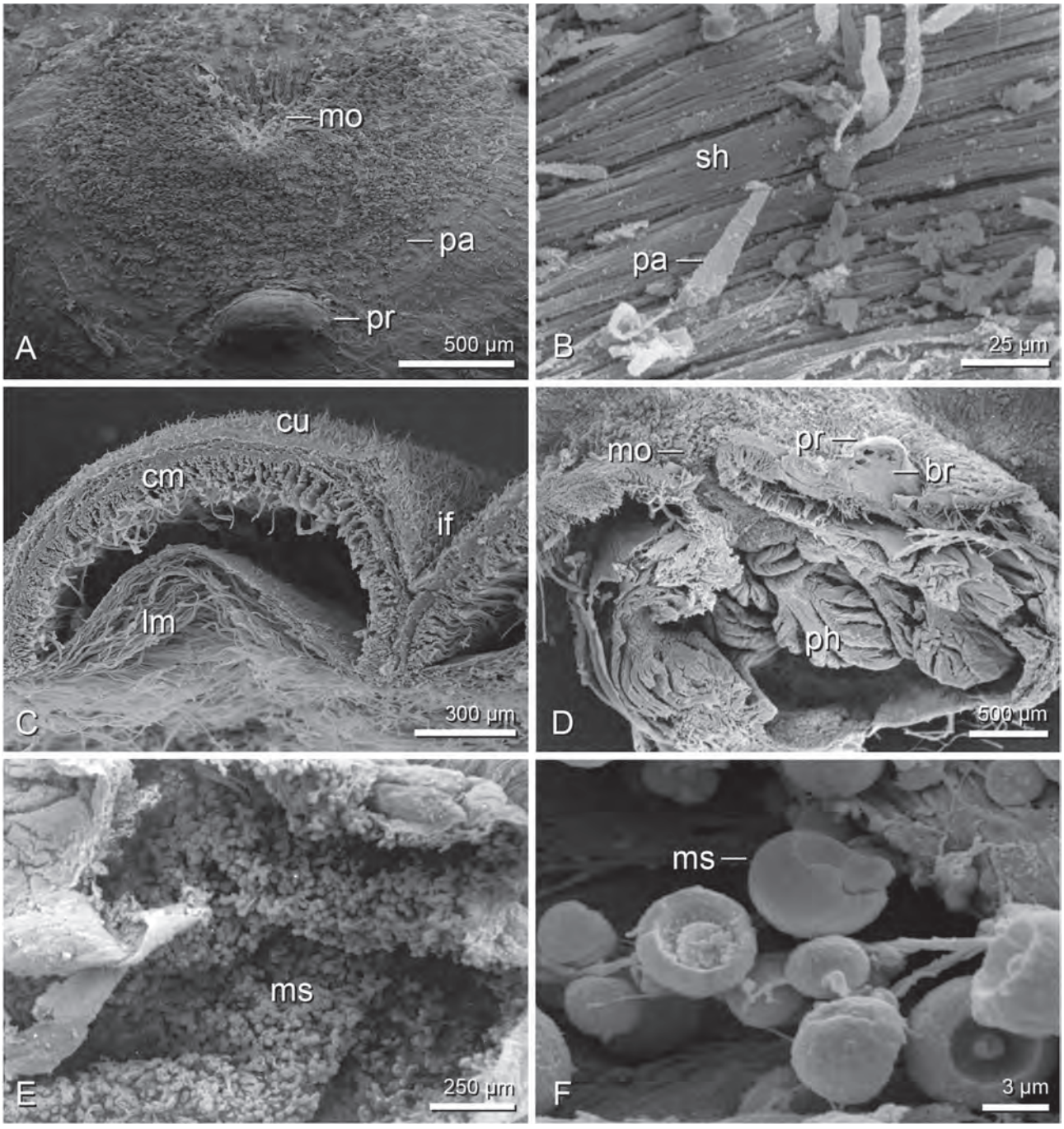


**Fig. 7.3.1.8.5:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423), scanning electron microscopy micrographs. A, Anterior region, frontal view, showing minute papillae around mouth. B, Ventrocaudal shield with elongate papillae. C, Cross-section through epitheliomuscular tube with circular and longitudinal musculature connected to each other at intersegmental fold. D, Sagittal section of anterior region showing mouth, eversible pharynx, and prostomium. E, F, Segmental organs: E, interior mushroom-like structures of segmental organ; F, detail of E. br, brain; cm, circular musculature; cu, cuticula; if, intersegmental fold; lm, longitudinal musculature; mo, mouth; ms, mushroom-like structures; pa, papillae; ph, pharynx; pr, prostomium; sh, ventral shield. B, D, E, From B. Bütfering.

the anterior-posterior polarity of sternaspids. His findings were complemented by Müller (1852) with regard to the circulatory, digestive, and sexual organs. The morphology and anatomy of *S. scutata* was studied in detail almost simultaneously but independently by Vejdovský (1882) based on specimens from the Mediterranean Sea (Trieste, northern Adriatic Sea) and by Rietsch (1882) based on specimens from the Atlantic (Cap Breton, Golfe de Gascogne) and the Mediterranean Sea (Golfe de Marseille).

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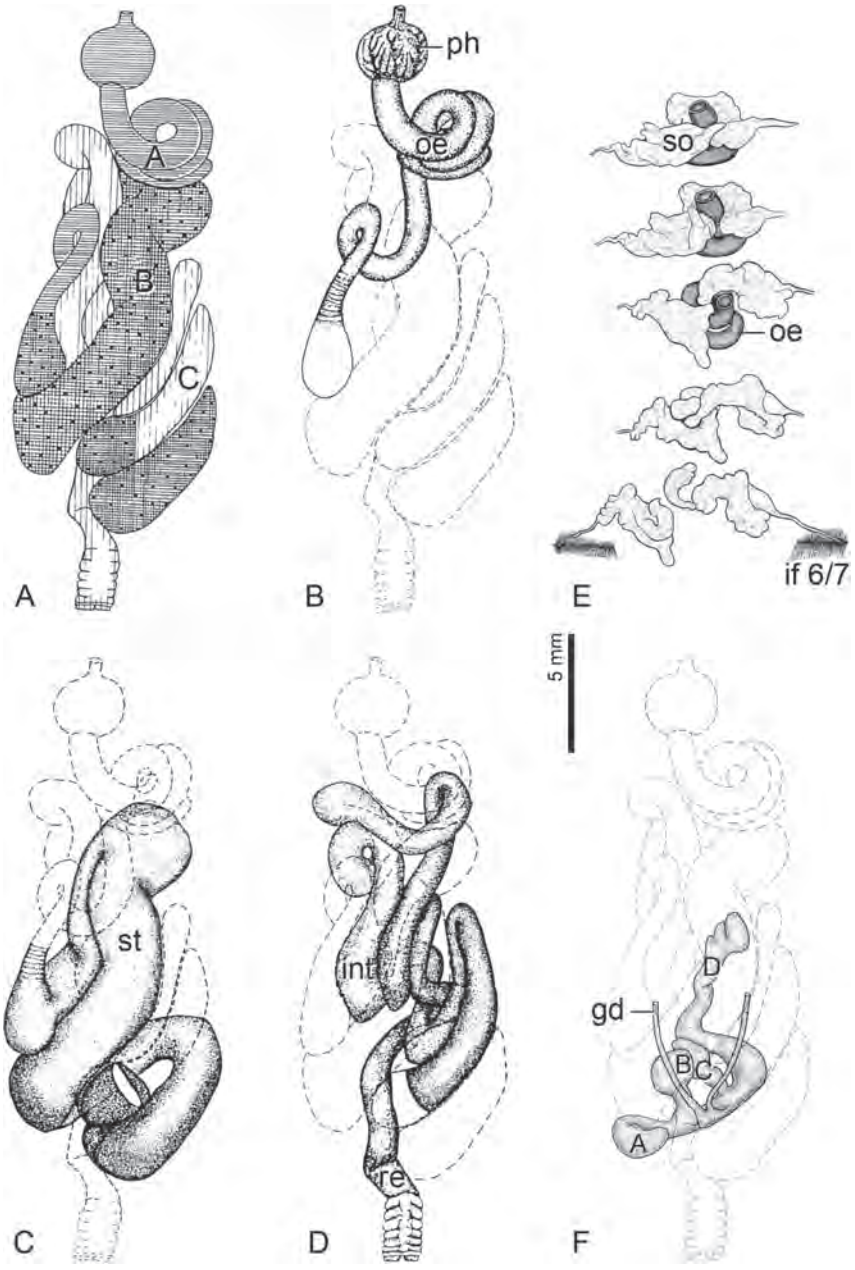


**Fig. 7.3.1.8.6:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423), schematic drawings. A–D, Intestinal system, ventral view: A, overview highlighting different parts (A–C); B, overview highlighting pharynx and esophagus; C, overview highlighting stomach; D, overview highlighting intestine and rectum. E, schematic view of arrangement of segmental organs, ventral view. F, Overview highlighting male gonad with four diverticula (A–D) and paired genital ducts, ventral view. gd, genital duct; if, intersegmental fold; int, intestine; oe, esophagus; ph, pharynx; re, rectum; st, stomach; so, segmental organ. A–F, From B. Bütfering.

**Musculature.** The major parts of the musculature consist of an epitheliomuscular tube composed of longitudinal and circular musculature, the dorsal and ventral retractor muscles, and the chaetal retractor muscles in segments 1–3. Longitudinal and circular musculatures seem to be attached to each other only at the intersegmental folds (Vejdovský 1882, Bütfering 1996) (Fig. 7.3.1.8.5 C). The development of the epitheliomuscular tube varies among the different body regions. Circular musculature covers the inner side of the epidermis completely in the six anteriormost segments, but in the posterior body, it is confined to the sides of the body and discontinued dorsally and ventrally, resulting in a seemingly unsegmented body surface in these areas (Rietsch 1882, Vejdovský 1882, Bütfering 1996) (Figs. 7.3.1.8.1 A–C and 7.3.1.8.3 A). The somatic muscular system in *S. scutata* is lined by a peritoneum composed of peritoneal cells separated from the underlying muscle cells by a perimuscular extracellular matrix (ECM) (Bartolomaeus 1994).

Longitudinal muscle fibers inserting at the intersegmental folds of segments 1/2, 2/3, and 4/5 form a pair of well-developed retractor muscles running ventrally to the caudal shield (Fig. 7.3.1.8.2 A). Dorsally, a thin layer of retractor muscles is formed running to intersegmental folds cranially of the branchial cushions (Vejdovský 1882, Bütfering 1996).

The ventral shield acts as support for the retractor muscles when the anterior segments are retracted and the

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circular musculature of the posterior region, together with coelomic pressure, acts as the respective antagonists for eversion of the anterior region (Goodrich 1898).

**Digestive system.** The body cavity appears to be completely filled with the densely coiled intestinal tract, which can be morphologically subdivided into three parts, an anterior (mouth, pharynx, and esophagus), middle (stomach), and posterior (intestine, rectum, and anus) part (Vejdovský 1882) (Figs. 7.3.1.8.2 A, B and 7.3.1.8.6 A). The eversible pharynx of sternaspids (Fig. 7.3.1.8.5 D) is simple and axial; no gular membrane has been described (Rouse and Fauchald 1997). In the anterior segments, the esophagus runs more or less straight caudally, then turns into several narrow loops. It continues to the right side and discharges into the stomach (Fig. 7.3.1.8.6 B). The stomach forms a wide U-shaped loop running anteriorly, then turning caudally and – after two more loops – continuing into the intestine without any externally visible distinction (Fig. 7.3.1.8.6 C). The dorsal vessel accompanies the stomach for its whole length (Rietsch 1882, Bütfering 1996) (Fig. 7.3.1.8.2 B). Inside the stomach, a well-visible, darkly ciliated groove runs from the stomach entrance all the way to the rectum (Rietsch 1882). The longest section of the intestinal tract consists of the densely coiled intestine that is characterized by several transversal and longitudinal loops running anterior- and posteriorward (Fig. 7.3.1.8.6 D). Observations regarding an eversion of the rectum, such as shown in Fig. 7.3.1.8.3 D, are considered artifacts as they are restricted to dead specimens and have not been confirmed for live ones (Rietsch 1882, Vejdovský 1882).

In contrast to Rietsch (1882), who reported the body cavity to be completely undivided, mesenteries and septal muscle fibers, together with connective tissue accompanying numerous thin branches of the ventral vessel, stabilize the intestinal tract in its position (Vejdovský 1882, Bütfering 1996). A horizontal septum, i.e., a fenestrated double layer of coelomic epithelium, is present in the posterior half of the body cavity, extending from the genital ducts to the rectum, separating the coelom into a dorsal cavity containing intestine and gonads and a ventral one containing the nerve cord and the origins of the chaetae surrounding the ventral shield (Goodrich 1905, Bütfering 1996) (Fig. 7.3.1.8.2 A).

**Excretory organs.** Two voluminous sac-like organs are intertwined with each other and fill the space between two esophageal loops in anterior segments forming the so-called segmental organs (Figs. 7.3.1.8.2 A, B and 7.3.1.8.6 E). Both organs are ventro-laterally continuing into thin ducts running to the intersegmental border between segments 6 and 7. An excretory function was supposed by Rietsch (1882) and Vejdovský (1882) for these organs, but no opening into the body cavity or into the esophagus or any exterior opening could be found by these authors. Likewise, no exterior opening was found in SEM studies of numerous specimens of *S. scutata* by Bütfering (1996). However, openings are reported for *S. spinosa* by Sluiter (1882) to be situated in the segment anterior to the genital papillae, and Goodrich (1898) described a ciliated funnel opening into the coelomic cavity. The interior of the segmental organs is characterized by a central lumen with the walls densely covered by stalked bulbous, mushroom-like structures (Fig. 7.3.1.8.5 E, F). The histology of the segmental organs was described by Goodrich (1898), who assumed their function in the accumulation of excretory products. According to Goodrich (1945), sternaspids show a specialization of mixonephridia into an anterior excretory pair and a posterior reproductive one – a situation that is also known for other polychaetes (e.g., Kremer *et al*. 2011).

**Genital organs and gametes.** Sternaspids are gonochoristic showing no signs of sexual dimorphism. The gonads are situated in the median part of the body, filling the space between loops of the intestinal tract (Figs. 7.3.1.8.2 B and 7.3.1.8.6 F). Paired gonoducts continue into a pair of long exterior genital papillae originating from the intersegmental groove between segments 6 and 7. The gonads in both sexes comprise four diverticula of varying shapes and sizes. Testes and ovaries differ in surface structure and color, and sperm is whitish whereas eggs are reddish (Rietsch 1882, Vejdovský 1882). Sperm cells are arranged in clusters; ripe sperm cells show a conically pointed head and long thin tail (Fig. 7.3.1.8.7 A). Young oocytes are pear shaped and connected to the ovary wall by a short stalk; ripe eggs are spherical but slightly tipped at both ends (Fig. 7.3.1.8.7 B). They are found free in the lumen of the ovary (Vejdovský 1882, Bütfering 1996). Sperm and eggs are presumably discarded via gonoducts and the genital papillae into the surrounding water, but Kowalevsky found eggs in various stages of cleavage in the lower oviduct, suggesting internal fertilization (Kowalevsky 1870 *fide* Vejdovský 1882). Dales (1963) considered the genital papillae to be special copulatory appendages but did not provide any further information supporting this assumption.

**Blood vascular system.** The main components of the circulatory system are the dorsal and ventral blood vessel, circular vessels in the body wall, branchial vessels, and the branchial filaments (Fig. 7.3.1.8.2 A, B). The dorsal blood vessel originates from two major branches formed by big bundles of numerous branchial vessels situated on both sides of the rectum (Rietsch 1882, Vejdovský 1882) (Fig. 7.3.1.8.7 C). It accompanies the intestinal tract anteriorward to the pharynx, where it bifurcates into two branches, which are directed ventrally and rejoin to form the

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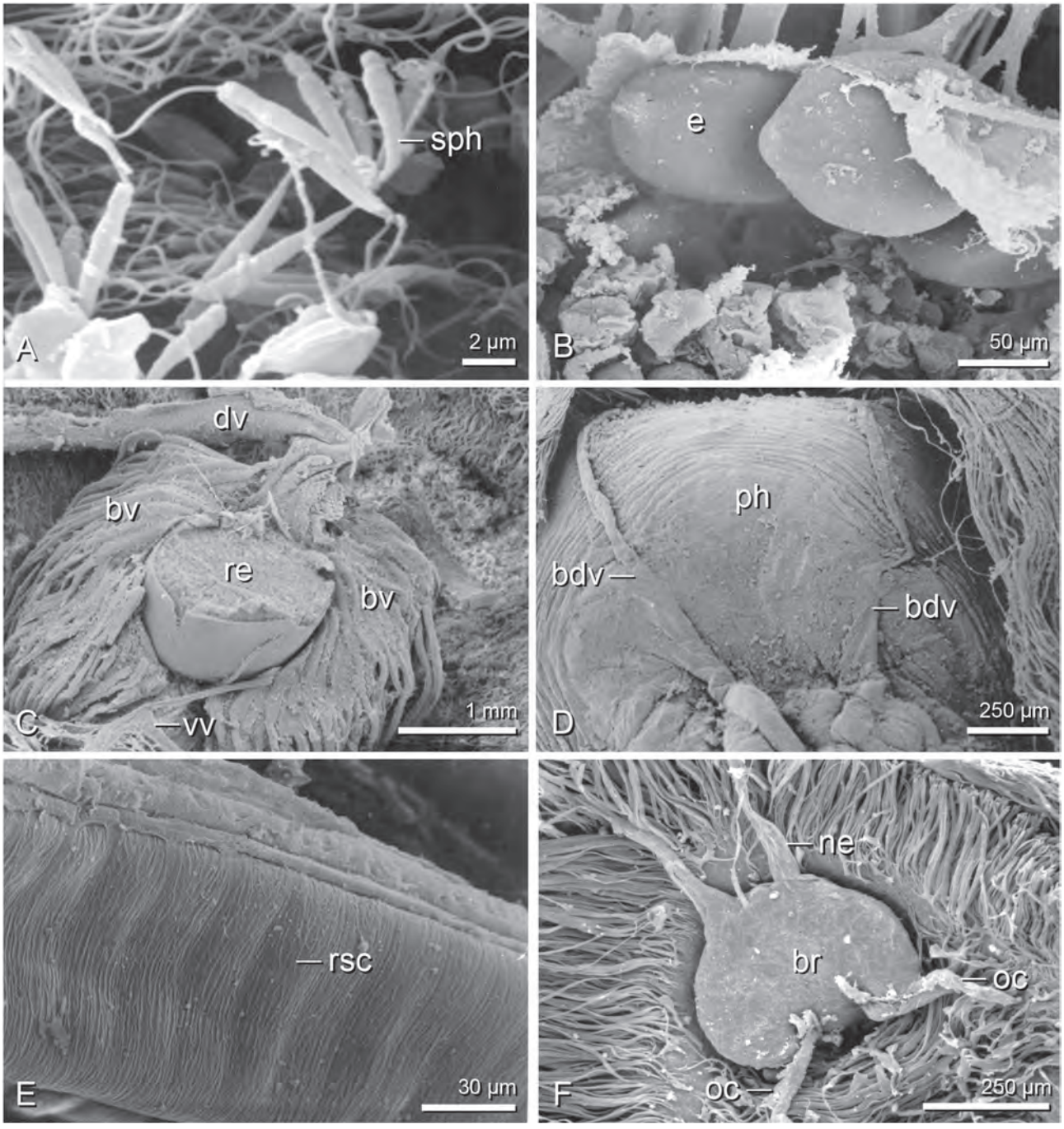


**Fig. 7.3.1.8.7:** *Sternaspis scutata* (Mediterranean Sea, SMF 4423), scanning electron microscopy micrographs. A, Sperm in male gonad. B, Eggs in female gonad. C, Cross-section of rectum with bundles of branchial vessels entering the dorsal vessel. D, Branching of dorsal vessel reaching the pharynx. E, Branchial vessel, detailed view of ring-shaped cells of the second and third region. F, Brain with anterior nerves and esophageal connectives. br, brain; bdv, branch of dorsal vessel; bv, branchial vessel; dv, dorsal vessel; e, egg; ne, nerv; oc, esophageal connective; ph, pharynx; re, rectum; rsc, ring-shaped cell; sph, sperm head; vv, ventral vessel. A–D, F: From B. Bütfering.

▸ **Fig. 7.3.1.8.8:** *Sternaspis scutata* (Phuket, Thailand), transmission electron microscopy micrographs (A–C). A, B, Branchial vessels of region 2: A, myoepithelial cell of the branchial vessel close to the epitheliomuscular tube showing mesh of myofilament bundles with fibers running at 90° to each other parallel and circular to the orientation of the vessel; B, myoepithelial cells of two blood vessels separated by a layer of coelenchym. C, D, Sensory papilla: C, longitudinal section showing nerve fibers entering the pad of electron dense material topped by microvilli (arrows); D, schematic drawing of sensory papilla. bv, branchial vessel; cm, circular muscle; co, coelenchym; cu, cuticula; ecm, extracellular matrix; em, electron dense material; ep, electron dense pad; lm*, cm*, epithelomuscular tube; lm, longitudinal muscle; mi, mitochondria; nf, nerve fiber; n, nucleus; mv, microvilli; tnf, terminal filaments of nerve. A–D, From C. Meyer.

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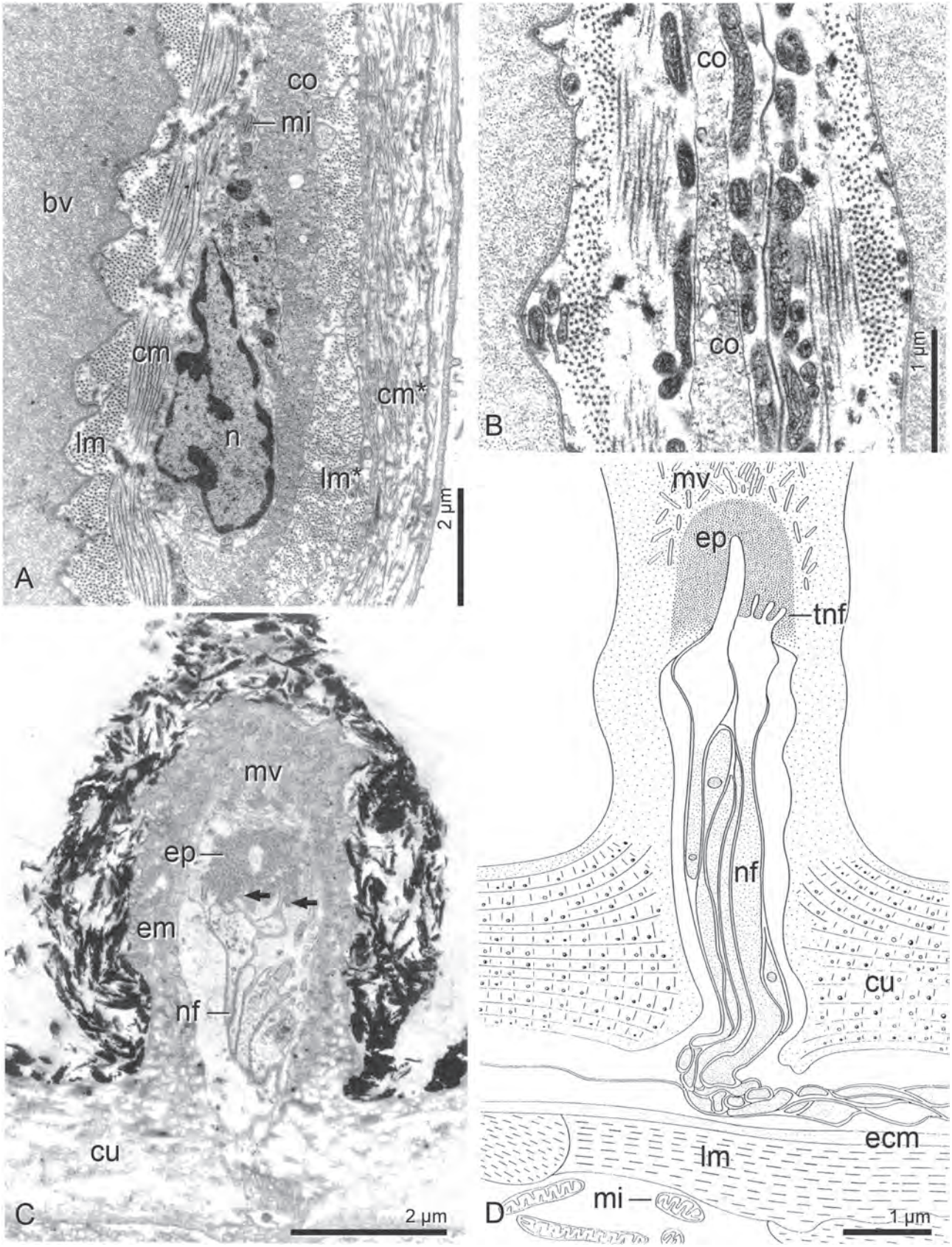


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ventral blood vessel running posteriorly (Fig. 7.3.1.8.7 D). From the ventral vessel, pairs of lateral branches supply the body wall, the segmental organs, gonads, and other organs and support the horizontal septum in the posterior half of the body. The dorsal and ventral blood vessels communicate via smaller vessels in the wall of the intestine and circular vessels of the epitheliomuscular tube (Rietsch 1882, Vejdovský 1882). Vejdovský (1882) proposed a closed circulatory system for *S. scutata*, with the blood entering each branchial filament via a "vein" originating from the ventral vessel and leaving the branchial filament through the respective branchial vessel ("artery") running toward the origin of the dorsal blood vessel.

The structure of the outer branchial filaments and inner branchial vessels was described in detail by Goodrich (1905) partly contradicting earlier descriptions by Rietsch (1882) and Vejdovský (1882, 1883). Goodrich distinguished three different regions along the branchial vessels (starting from the dorsal vessel): (1) region marked by a conspicuous swelling, (2) intermediate region, generally swollen and differing in structure from the other two, and (3) a much longer and narrower region connected to the gill filaments. The contractile walls of the branchial vessels of the second and third region are formed of a regular series of ring-shaped cells (Goodrich 1905, Bütfering 1996) (Fig. 7.3.1.8.7 E), representing a single layer of myoepithelial cells comprising bundles of myofilaments. Transmission electron microscopy (TEM) investigations showed a mesh of myofilament bundles present in cells of region 2 with fibers running at 90° to each other parallel and circular to the orientation of the vessel (Fig. 7.3.1.8.8 A, B). Myoepithelial cells in region 3, i.e., next to the branchial filaments, have less myofilaments than do cells in region 2 (Meyer 1996). Myoepithelial cells are also enveloping the dorsal and ventral vessel, whereas smaller lateral vessels and capillaries are enveloped by peritoneal cells only (Meyer 1996). The branchial vessels are also characterized by a peculiar intravasal rod of tissue ("axis"), which is strongest in the intermediate region (region 2) and only a thin thread in region 1 close to the dorsal vessel. Here, the end of the axis forms a plug acting as a valve. The intravasal axis is supposed to provide stability when the blood is propelled forward by waves of contractions of the myoepithelial cells (Goodrich 1905). Meyer (1996) described the ultrastructure of three different types of cells forming intravasal cell complexes in the various regions of the branchial vessels (cell type 1 and 2) and also in other blood vessels, e.g., along the intestine and the ventral nerve cord (type 2 and 3). The intravasal position of these cell complexes is similar to the heart bodies described for other polychaetes, but the number of cells in each complex is very low and their structure different. From their positioning, these intravasal cell complexes seem to represent the "intravasal rod" described by Goodrich (1905) and earlier authors. However, Meyer (1996) assumes a hematopoietic function and suggests cell types 1–3 to represent different developmental stages.

**Branchiae.** The ultrastructure of the branchial filaments consists of an outer cuticle and a monolayer of epidermal cells resting on subepidermal ECM enveloping two parallel tubes formed by longitudinally oriented muscle cells with a central lumen each of coelomic origin (Bartolomaeus 1992), thus confirming earlier observations by Goodrich (1905). Bartolomaeus (1992) suggested that the rhythmical contraction of branchiae observed in living specimens is the result of alternating contractions of longitudinal muscle fibers in each half of the filament, thus pumping blood from the outer branchial filaments into the inner branchial vessels.

**Nervous system.** The nervous system of sternaspids has been studied by Vejdovský (1882), Rietsch (1882), and Dahl (1955). In *S. scutata*, the major parts comprise the supraesophageal ganglion (brain) situated in the cone-shaped prostomium, the esophageal connectives, the ventral nerve cord, and the peripheral nerves (Fig. 7.3.1.8.5 D and 7.3.1.8.7 F). The esophageal connectives fuse to a ventral nerve cord in the area where the pharynx continues into the esophagus. The ventral cord is embedded between the ventral retractor muscles forming a bilaterally symmetrical strand surrounded by a common sheath (Rietsch 1882, Vejdovský 1882, Dahl 1955). No ganglionic swellings are visible along the ventral cord. The number of nerve pairs originating from the chord is higher and not correlated to the number of segments. The diameter of the ventral chord increases posteriorly to segment 14, forming a terminal enlargement (Dahl 1955: "terminal ganglion") attached to the ventrocaudal shield. Based on the number

▸ **Fig. 7.3.1.8.9:** *Sternaspis scutata* (Phuket, Thailand). Transmission electron microscopy micrographs (A, C). A, Bundle of elongated sensory cells in the prostomium (arrows) embedded among epidermal cells. B, Schematic drawing of bundle of elongated sensory cells (1–3). C, Photoreceptive sensory cell with photoreceptive complex situated in extracellular space. Subcuticular space filled with particles and penetrated by ciliated tips of elongated sensory cells (see A, B). D, Schematic reconstruction of multicellular photoreceptive complex (posterior and lateral cells omitted for better orientation). ci, cilia; cu, cuticula; ec, epidermal cells; es, extracellular space; mi, mitochondria; n, nucleus; phc, photoreceptive complex; ss, subcuticular space A–D, From C. Meyer.

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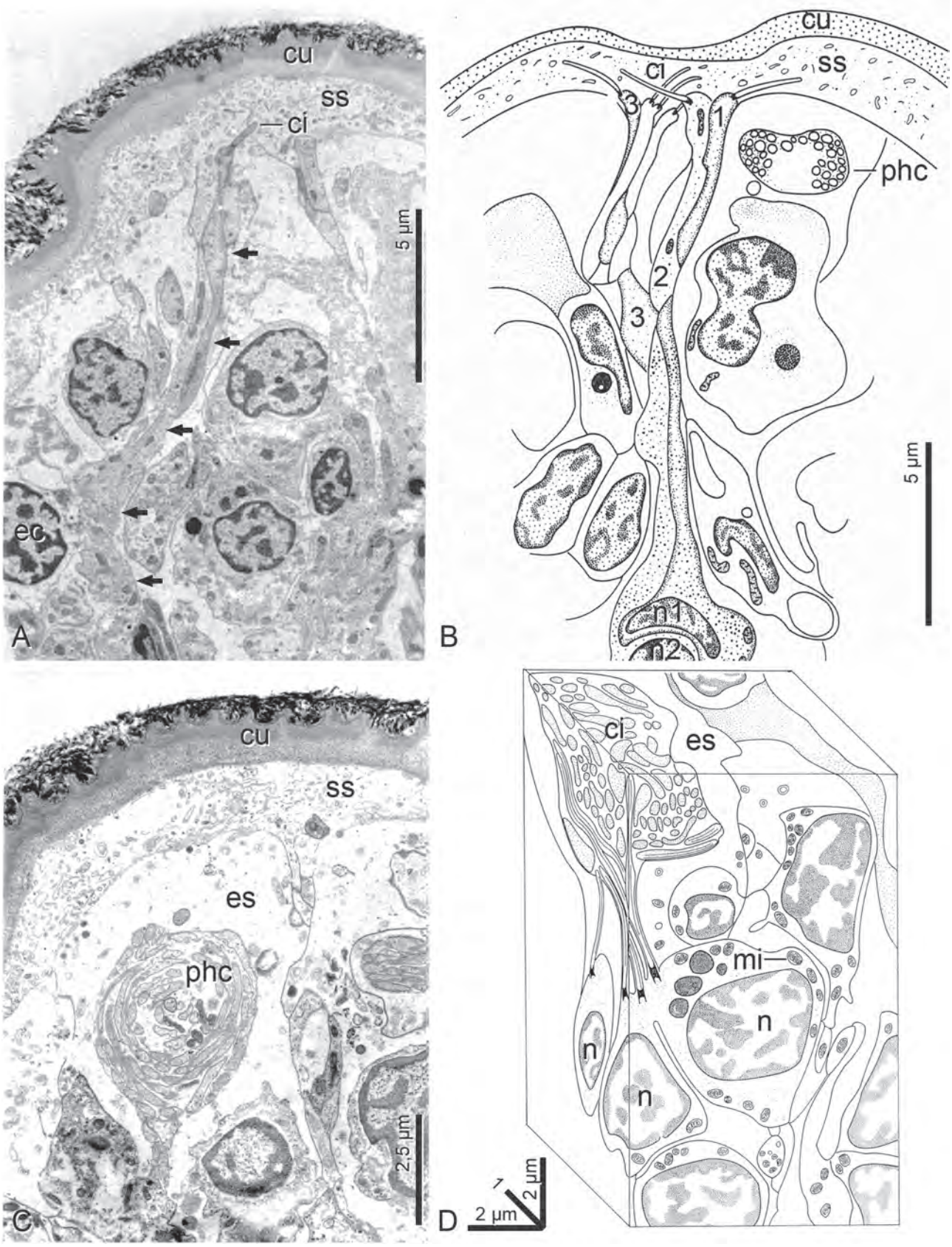


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of constrictions, Rietsch (1882) and Dahl (1955) assumed many segmental ganglia in this area, i.e., 25 and >60, respectively, suggesting the presence of more segments fused than apparent externally. However, the number of constrictions does not correspond to segmentation of muscles or chaetal fascicles framing the ventral shield (Dahl 1955). Neither bilateral symmetry nor ganglia are discernible in the ventral cord of *S. spinosa* Sluiter, 1882.

**Sensory organs.** Sensory organs such as nuchal organs and eyes are generally absent in sternaspids but have been assumed by Petersen (2000a) as present in *Sternaspis fossor* Stimpson, 1854 from Passamaquoddy Bay (Bay of Fundy, Canada) and some (partly juvenile) specimens of *S.* cf. *fossor* from California, respectively. Dahl (1955) described a group of possible sensory cells situated on each side near the lateral margin of the brain. From these groups, the numerous cuticular papillae of the lip area situated anterior to the brain are innervated by the so-called "upper lip nerve." Rouse and Fauchald (1997) assumed this nerve (or rather the groups of sensory cells described by Dahl?) to represent a possible remnant of a nuchal organ.

Rietsch's (1882) assumption that the epidermal papillae are innervated sensory organs was confirmed by Dahl (1955). Bartolomaeus (1992) did not mention gland or sensory cells, but Meyer (1996) confirmed the sensory nature of (some) papillae for juvenile *S. scutata* from Thailand using TEM. Up to six neurites originating from epidermal nerves enter the papilla either forming cylindrical appendages ending in an electron dense pad or forming microvilli-like tips penetrating the electron dense pad and reaching the tip of the papilla (Meyer 1996) (Fig. 7.3.1.8.8 C, D). In the prostomial cupule of *S. scutata*, about 40 elongated sensory cells are situated centrally and laterally to the prostomial tip and oriented parallel to the body axes. These cells are presumed to be mechano- or chemoreceptors (Meyer 1996) (Fig. 7.3.1.8.9 A, B). Another type of sensory cell bearing two elongated cilia each forms at least four groups consisting of one to four cells each, which are situated on both sides of the prostomial cupule close to the subcuticular space. These cell complexes are presumed to be ciliary photoreceptors (Meyer 1996) (Fig. 7.3.1.8.9 C, D).

## Biology and ecology

Most sternaspid species have been recorded from low intertidal to shelf depths, but *Sternaspis maior* Chamberlin, 1919, *Sternaspis princeps* Selenka, 1885, *Sternaspis rietschi* Caullery, 1944, and *Caulleryaspis gudmundssoni* Sendall and Salazar-Vallejo, 2013 and six additional species described by Salazar-Vallejo and Buzhinskaja (2013) have been recorded from deep water down to more than 4,000 m. Sternaspids have a burrowing mode of life. According to Rietsch (1882), the occurrence of *S. scutata* is restricted to muddy bottoms, but sternaspids have been recorded from a variety of sediments (Sendall and Salazar-Vallejo 2013). Specimens are reported to lie in the sediment mostly with their dorsal side up and the branchial filaments extending into the water column or spreading over the sediment surface and the anterior part of the body retracted (Rietsch 1882). But according to observations reported by Jumars, *S. scutata* stayed burrowed completely in the sediment for prolonged periods of time (Jumars *et al.* 2015). In live specimens, the branchial filaments are slowly coiled and uncoiled by alternating contractions of muscles, thus maintaining the flow of the blood (Bartolomaeus 1992). Besides spending long periods in the same position, sternaspids are able to quickly move through the sediment by extending and retracting their anterior end using the spinelike chaetae as backing (Rietsch 1882, Dales 1962). Fauchald and Jumars (1979) and Jumars *et al.* (2015) classified sternaspids as microphagous subsurface deposit feeders. For feeding, their eversible saclike pharynx is extruded and particles ingested by the movement of cilia (Rietsch 1882). The preferred particle size was found to be between 0.5 and 15 µm (Self and Jumars 1988).

Sternaspids can be locally abundant and have been reported to dominate benthic communities in Korea, China, Brazil, Chile, and some Arctic regions. Occasionally, they reach very high densities, e.g., up to 1,335 spms/$m^2$ on the southwest coast of India (see Sendall and Salazar-Vallejo 2013 for details). Apicomplexan parasites have been observed in the coelomic cavity of *S. scutata* by Rietsch (1882) and Meyer (1996).

Sternaspids are gonochoristic. Gonads are situated behind segment 6 and a pair of ducts leads to genital papillae at the border of segments 6 and 7. Eggs of *S. scutata* are 150 µm in diameter, and sperm is ca. 15 µm long with cylindrical heads (Rietsch 1882). The ultrastructure of the cortical envelopes, the germinal vesicle, and the cortex and also the polar plasm of ripe ovarian eggs of *Sternaspis* have been studied by Villa Notarbartolo (1970) and by Villa (1976), respectively. Early development and larval stages have been described by Kowalevsky (1870), Rietsch (1882), Vejdovský (1882), and Child (1900). The cleavage is holoblastic, unequal. Fertilization is external and larvae are lecitotrophic with short planktonic life lasting less than 2 days (Rietsch 1882). Vejdovský (1882) reports hatching of small free-swimming larvae (0.4 mm long) about 16 hours after fertilization. Larvae are completely covered by short cilia, with an apical tuft of much

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**Tab. 7.3.1.8.1:** List of Sternaspidae species known to date.

| | |
|---|---|
| 1. | *Caulleryaspis fauchaldi* Salazar-Vallejo & Buzhinskaja, 2013 |
| 2. | *Caulleryaspis gudmundssoni* Sendall & Salazar-Vallejo, 2013 |
| 3. | *Caulleryaspis laevis* (Caullery, 1944) |
| 4. | *Caulleryaspis nuda* Salazar-Vallejo & Buzhinskaja, 2013 |
| 5. | *Caulleryaspis villamari* Salazar-Vallejo, 2017 |
| 6. | *Petersenaspis capillata* (Nonato, 1966) |
| 7. | *Petersenaspis deani* Salazar-Vallejo, 2017 |
| 8. | *Petersenaspis harrisae* Salazar-Vallejo, 2017 |
| 9. | *Petersenaspis palpallatoci* Sendall & Salazar-Vallejo, 2013 |
| 10. | *Petersenaspis salazari* Wu & Xu, 2017 |
| 11. | *Sternaspis affinis* Stimpson, 1864 |
| 12. | *Sternaspis africana* Augener, 1918 |
| 13. | *Sternaspis andamanensis* Sendall & Salazar-Vallejo, 2013 |
| 14. | *Sternaspis annenkovae* Salazar-Vallejo & Buzhinskaja, 2013 |
| 15. | *Sternaspis britayevi* Zhadan, Tzetlin & Salazar-Vallejo, 2017 |
| 16. | *Sternaspis buzhinskajae* Salazar-Vallejo, 2014 |
| 17. | *Sternaspis chilensis* Díaz-Díaz & Rozbaczylo, 2017 |
| 18. | *Sternaspis chinensis* Wu, Salazar-Vallejo & Xu, 2015 |
| 19. | *Sternaspis costata* Marenzeller, 1879 |
| 20. | *Sternaspis fossor* Stimpson, 1854 |
| 21. | *Sternaspis islandica* Malmgren, 1867 |
| 22. | *Sternaspis lindae* Salazar-Vallejo, 2017 |
| 23. | *Sternaspis liui* Wu, Salazar-Vallejo & Xu, 2015 |
| 24. | *Sternaspis londognoi* Salazar-Vallejo, 2017 |
| 25. | *Sternaspis maior* Chamberlin, 1919 |
| 26. | *Sternaspis maureri* Salazar-Vallejo & Buzhinskaja, 2013 |
| 27. | *Sternaspis monroi* Salazar-Vallejo, 2014 |
| 28. | *Sternaspis nana* Zhadan, Tzetlin & Salazar-Vallejo, 2017 |
| 29. | *Sternaspis papillosa* Zhadan, Tzetlin & Salazar-Vallejo, 2017 |
| 30. | *Sternaspis piotrowskiae* Salazar-Vallejo, 2014 |
| 31. | *Sternaspis princeps* Selenka, 1885 |
| 32. | *Sternaspis radiata* Wu & Xu, 2017 |
| 33. | *Sternaspis rietschi* Caullery, 1944 |
| 34. | *Sternaspis scutata* (Renier in Ranzani, 1817) |
| 35. | *Sternaspis sendalli* Salazar-Vallejo, 2014 |
| 36. | *Sternaspis sherlockae* Salazar-Vallejo, 2017 |
| 37. | *Sternaspis spinosa* Sluiter, 1882 |
| 38. | *Sternaspis sunae* Wu & Xu, 2017 |
| 39. | *Sternaspis thalassemoides* Otto, 1821 |
| 40. | *Sternaspis thorsoni* Sendall & Salazar-Vallejo, 2013 |
| 41. | *Sternaspis uschakovi* Salazar-Vallejo & Buzhinskaja, 2013 |
| 42. | *Sternaspis williamsae* Salazar-Vallejo & Buzhinskaja, 2013 |
| 43. | *Sternaspis wui* Wu & Xu, 2017 |

longer cilia. Eyes are absent and no anterior or posterior opening was observed. Thus, Vejdovský (1882) compared the habitus of the larvae to the planula of hydrozoans. The reproductive period for *S. scutata* is end of February to end of March. During summer months, gonads degenerate and artificial fertilization proved unsuccessful (Rietsch 1882). However, year-round recruitment with a peak in summer has been reported by Lim and Hong (1996) for shallow water habitats in South Korea. Ovigerous females of *Sternaspis costata* Marenzeller, 1879 were found throughout most of the year, except in October and March, in Ariake Bay, Japan, with the highest percentage of ovigerous females observed in September (Yoshino *et al*. 2016).

## Phylogeny and taxonomy

Sternaspids have probably been mentioned for the first time as early as 1760 (Petersen 2000a), but the first valid description of a taxon is that of *Sternaspis scutatus* (Renier in Ranzani 1817 as *Thalassema*). Otto (1821) erected the genus *Sternaspis* based on Ranzani's *Thalassema scutatus*, renaming it *Sternaspis thalassemoides*. Between 1821 and 1966, 13 species and two subspecies have been described. However, the validity of a number of these species has been questioned due to insufficient descriptions and the lack of type specimens. For example, Hartman (1959) accepted only five species as valid in her catalogue of Polychaeta. Some authors (e.g., Fauvel 1927, Pettibone 1954, Uschakov 1955, Day 1967) even considered *S. scutata* the only valid species with seemingly cosmopolitan distribution. Petersen (2000a) reviewed the group and suggested that species could be separated into two groups, the *S. scutata* group, with minute papillae evenly distributed over most of the surface, and the *S. fossor* group, with more or less conspicuous clusters of papillae resembling rows of pompoms. Sendall and Salazar-Vallejo (2013) split the genus *Sternaspis* into three separate genera, *Sternaspis* Otto, 1821, *Caulleryaspis* Sendall & Salazar-Vallejo, 2013, and *Petersenaspis* Sendall & Salazar-Vallejo, 2013, based on characters of the ventral shield, the hooks of the anterior segments, and the number of abdominal segments (see generic diagnoses further in the chapter). Since then 26 new species have been added bringing the current total of known species to 43 (Tab. 7.3.1.8.1, Fig. 7.3.1.8.10).

The systematic position of sternaspids received much discussion. They were put among the Echiura, Sipuncula, or even Echinodermata (namely, holothurians) by early authors (e.g., Ranzani 1817, de Blainville 1828, Selenka 1885). Quatrefages (1866) put them among the Gephyrea armata, although it had already been shown by Krohn (1842) and Müller (1852) that they belonged to the annelids. While Kowalevsky (1870) and Vejdovský (1882) considered sternaspids an intermediate between Polychaeta and Gephyrea, Rietsch (1882) considered them a separate, specialized group of polychaetes. More recently, using molecular data, it became clear that echiurans and sipunculans belong to the annelids or even to polychaetes, thus adding a new perspective on the relationship of sternaspids to echiurans and sipunculans (McHugh 1997, Hessling 2002, Struck *et al*. 2007, 2011, Dordel *et al*. 2010).

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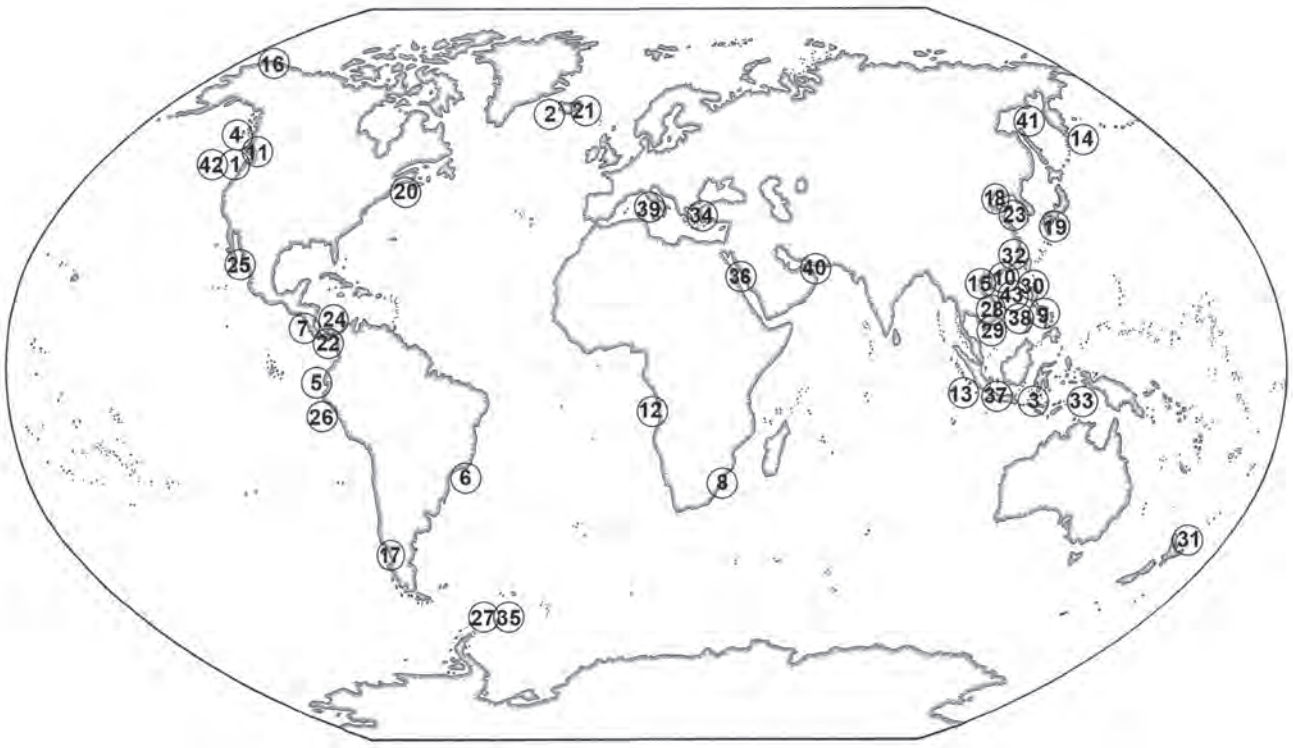


**Fig. 7.3.1.8.10:** Type localities of known species of Sternaspidae.

Among the polychaetes, sternaspids were put close to the Flabelligeridae by Malmgren (1867), a view that was later supported by Dahl (1955). The phylogenetic position of sternaspids among polychaetes has only received little specific attention in cladistic analyses. Rouse and Fauchald (1997) considered them most closely related to Flabelligeridae and Fauveliopsidae, forming part of a larger clade including Poeobiidae, Acrocirridae, and Cirratulidae, which was later termed Cirratuliformia by Rouse and Pleijel (2006). Subsequent analyses based on extensive molecular data sets (Rousset *et al.* 2007, Struck *et al.* 2007) placed *Sternaspis* as a sister group to *Fauveliopsis* (McIntosh 1922) among the Canalipalpata. A total-evidence analysis considering a combination of morphology and six genes found *Sternaspis* (and Fauveliopsidae) next to Cirratuliformia and/or the so-called "Sabelloid-spionoid clade" including Sabellidae, Serpulidae, Sabellariidae, and Spionida sensu strictu, i.e., Spionidae + *Trochochaeta* + *Poecilochaetus* (Zrzavy *et al.* 2009). The monophyly of Cirratuliformia was not supported, thus confirming the morphological results of Rouse and Pleijel (2003), who for their analysis had putatively assumed a homology between cuticular ventral shields of *Sternaspis* and *Fauveliopsis* (Rousset *et al.* 2007). The latter had been described by Petersen (2000b) as present in middle and/or posterior segments of some species of *Fauveliopsis*. A phylogenetic study on the Cirratuliformia comprising Acrocirridae, Cirratulidae, Ctenodrilidae, Fauveliopsidae, Flabelligeridae, Flotidae, Poeobiidae, and Sternaspidae placed *Sternaspis* within the Cirratulidae, but this was considered problematic due to limited information on critical features and only a single taxon included in the study (Salazar-Vallejo *et al.* 2008). In the metatree produced by Struck (2018), *Sternaspis* is placed with the Cirratuliformia, here renamed as Cirratulida.

According to Petersen (2000a) and Sendall and Salazar-Vallejo (2013), important characters for the distinction of *Sternaspis* species are as follows: (1) the ventrocaudal shield, i.e., its shape (especially margins), color, sculpture (ribs, concentric rings, subdivisions into parts, and relative proportions of these), halves closely apposed or separated, presence/absence of sediment adhering to shield, and (2) the anterior spinelike chaetae, i.e., shape, color, number, relative size, relative length of rows, and degree of spacing among spines. Additional useful characters appear to be the cuticular papillae (shape, length, patterns of distribution), the number of chaetigerous segments between genital papillae and the caudal shield, the number of chaetal bundles lateral to the caudal shield, and perhaps the shape of branchial cushions. However, intraspecific and ontogenetic variability needs to be taken into account, especially with respect to the caudal shield; e.g., Lim and Hong (1996), studying distribution and growth patterns of *S. scutata* in Chinhae

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Bay, South Korea, found the width of the ventral shield correlated to body weight. The length of posterior chaetae relative to the size of the caudal shield may be of taxonomic value. The so-called peg chaetae, however, appear to be only of limited taxonomic value because they are sometimes missing or present only on one side.

### Sternaspidae Carus, 1863

#### *Sternaspis* Otto, 1821

**Type species:** *Sternaspis thalassemoides* Otto, 1821 (Fig. 7.3.1.8.10)

**Synonyms:** *Echinorhynchus* Renier, 1804; *Thalassema* Ranzani, 1817

**Diagnosis** (acc. Sendall and Salazar-Vallejo 2013): Sternaspids with introvert hooks falcate, tapered. Preshield region with seven segments. Ventrocaudal shield stiff, usually with radial ribs and concentric lines. Branchial filaments arranged in discrete branchial plates.

#### *Caulleryaspis* Sendall & Salazar-Vallejo, 2013

**Type species:** *Sternaspis gudmundssoni* Sendall & Salazar-Vallejo, 2013 (Fig. 7.3.1.8.10)

**Diagnosis** (acc. Sendall and Salazar-Vallejo 2013): Sternaspids with introvert hooks tapered. Preshield region with seven segments. Ventrocaudal shield flexible with abundant sediment particles adhered.

#### *Petersenaspis* Sendall & Salazar-Vallejo, 2013

**Type species:** *Sternaspis capillata* Nonato, 1966 (Fig. 7.3.1.8.10)

**Diagnosis** (acc. Sendall and Salazar-Vallejo 2013): Sternaspids with introvert hooks subdistally expanded. Preshield region with eight segments. Ventrocaudal shield stiff with feebly developed ribs and no concentric lines.

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### References

Augener, H. (1918): Polychaeta. In: Michaelsen, W. (ed.) *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. Band II. L. Friedrichsen & Co., Hamburg: 69–625.

Bartolomaeus, T. (1992): On the ultrastructure of the cuticle, the epidermis and the gills of *Sternaspis scutata* (Annelida). *Microfauna Marina* 7: 237–252.

Bartolomaeus, T. (1994): On the ultrastructure of the coelomic lining in the Annelida, Sipuncula and Echiura. *Microfauna Marina* 9: 171–220.

de Blainville, H.M.D. (1828): Dictionnaire des sciences naturelles. *Vers* 57: 365–628.

Bütfering, B. (1996): *Untersuchungen zum Bau von* Sternaspis scutata *(Ranzani, 1817) (Polychaeta, Sternaspidae)*. *Schriftliche Hausarbeit im Rahmen des Ersten Staatsexamens*. Westfälische Wilhelms-Universität Münster, FB Biologie, Münster: 117.

Carus, J.V. (1863): Vermes. In: Kükenthal, W. (ed.) *Handbuch der Zoologie*. Vol. 2. Wilhelm Engelmann, Leipzig: 422–454.

Caullery, M. (1944): Polychètes sédentaires de l'expédition du Siboga. Ariciidae, Spionidae, Chaetopteridae, Chlorhaemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. *Siboga-Expeditie* 24(2): 1–204.

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

Child, C.M. (1900): The early development of *Arenicola* and *Sternaspis*. *Archiv für Entwickelungsmechanik der Organismen* 9: 587–723.

Dahl, E. (1955): On the morphology and affinities of the annelid genus *Sternaspis*. *Lunds Universitets Årsskrift, N.F. Avd*. 2(51): 1–22.

Dales, R.P. (1962): The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proceedings of the Zoological Society, London* 139: 389–428.

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

Day, J.H. (1967): *A Monograph on the Polychaeta of Southern Africa. Part 2. Sedentaria*. The British Museum (Natural History), London: 419.

Díaz-Díaz, O. & Rozbaczylo, N. (2017): *Sternaspis chilensis* n. sp., a new species from austral Chilean channels and fjords (Annelida, Sternaspidae). *Zootaxa* 4254(2): 269–276.

Dordel, J., Fisse, F., Purschke, G. & Struck, T.H. (2010): Phylogenetic position of Sipuncula derived from multi-gene and phylogenomic data and its implication for the evolution of segmentation. *Journal of Zoological Systematics and Evolutionary Research* 48: 197–207.

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

Fauvel, P. (1927): Polychètes Sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. *Faune de France* 16: 494.

Goodrich, E.S. (1898): Notes on the anatomy of *Sternaspis*. *Quarterly Journal of Microscopical Science* 40: 233–245.

Goodrich, E.S. (1905): On the branchial vessels of *Sternaspis*. *Quarterly Journal of Microscopical Science* 48: 1–10.

Goodrich, E.S. (1945): The study of nephridia and genital ducts since 1895. *The Quarterly Journal of Microscopical Science* 86: 113–301.

Hartman, O. (1959): Catalogue of the polychaetous annelids of the world. Part II. *Allan Hancock Foundation Publications Occasional Papers* 23: 355–628.

Hessling, R. (2002): Metameric organization of the nervous system in developmental stages of *Urechis caupo* (Echiura) and its phylogenetic implications. *Zoomorphology* 121: 221–234.

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

Kowalevsky, A. (1870): On egg development of *Sternaspis thalassemoides* Otto. *Zapisky Kievskago Obestva Estestvoispytatelej* 1: 287–290 [in Russian].

Kremer, P., Fiege, D. & Wehe, T. (2011): Morphology and ultrastructure of the nephridial system of *Hypania invalida* (Grube, 1860) (Annelida, Polychaeta, Ampharetidae). *Journal of Morphology* 272: 1–11.

Krohn, A. (1842): Ueber den *Sternaspis thalassemoides*. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 1842: 426–432.

Lim, H.-S. & Hong, J.-S. (1996): Distribution and growth pattern of *Sternaspis scutata* (Polychaeta: Sternaspidae) in Chinhae Bay, Korea. *Journal of the Korean Fisheries Society* 29: 537–545.

Malmgren, A.J. (1867): Annulata polychaeta Spetsbergiae, Grönlandiae, Islandiae et Scandinaviae hactenus cognita. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 4: 127–235.

von Marenzeller, E. (1879): Südjapanische Anneliden I. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe* 41: 109–154.

McHugh, D. (1997): Molecular evidence that echiurans and pogonophorans are derived annelids. *Proceedings of the National Academy of Sciences of the United States of America* 94: 8006–8009.

McIntosh, W.C. (1922): I. Notes from the Gatty Marine Laboratory, St. Andrews. No. 44. 1. On a new and rare Polychaeta, Gephyrea, etc., from various regions. *The Annals and Magazine of Natural History* 9(49): 1–12.

Meyer, C. (1996): *Ultrastrukturuntersuchungen an einer Sternaspidenart (Polychaeta, Sternaspidae)*. Diplomarbeit Universität Osnabrück, FB Biologie/Chemie, Osnabrück: 102.

Müller, M. (1852): *Observationes anatomicae de vermibus quibusdam maritimis. Sternaspis thalassemoides (Otto)*. Dissertatio inauguralis Universitate Friderica Guilelma, Berolini, Typis Gustavi Schade: 30.

Muir, A.I. & Petersen, M.E. (2013): Authorship of some polychaete (Annelida) names derived from the works of Renier and Savigny. *Zootaxa* 3717(3): 383–388.

Nonato, E. (1966): *Sternaspis capillata* sp. n. (Annelida, Polychaeta). *Boletim do Instituto Oceanográfico da Universidade de Sao Paulo* 15: 79–83.

Otto, A.G. (1821): Animalium maritimorum, nondum editorum, genera duo. I. *Sternaspis thalassemoides*. *Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Academie der Naturforscher* 2: 619–627.

Petersen, M.E.P. (2000a): 11. Family Sternaspidae Carus, 1863. In: Blake, J.A., Hilbig, B. & Scott, P.V. (eds.). *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 7 – The Annelida Part 4. Polychaeta: Flabelligeridae to Sternaspidae*. Santa Barbara Museum of Natural History, Santa Barbara.

Petersen, M.E. (2000b): A new genus of Fauveliopsidae (Annelida: Polychaeta), with a review of its species and redescription of some described taxa. *Bulletin of Marine Science* 67: 491–515.

Pettibone, M.H. (1954): Marine polychaete worms from Point Barrow, Alaska, with additional records from the North Atlantic and North Pacific. *Proceedings of the United States National Museum* 103: 203–356.

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

Rallo, A. & Moya, J. (1987): Contribucion al conocimiento de la anatomia externa de *Sternaspis scutata* (Renier, 1807) (Annelida: Polychaeta). *Estudiada por microscopia electronica de barrido. Actas VIII Bienal de la Real Sociedad Espaniola de Historia Natural, Pamplona, 21–24 Sept*. 1987: 45–50.

Ranzani, C. (1817): Descrizione di una nova specie del genere Thalassema. *Opusculi Scientifici* I: 112–116.

Renier, S.A. (1804): Prospetto della classe dei Vermi. *Nominati e Ordinati secondo il Sistema de Bosc* 15–26.

Rietsch, M. (1882): Étude sur le *Sternaspis scutata*. *Annales des Sciences Naturelle. Sixième Série. Zoologie* 13: 1–84.

Rouse, G.W. (2001): *Sternaspis* Otto, 1821. In: Rouse, G.W. & Pleijel, F. (eds.) *Polychaetes*. Oxford University Press, Oxford: 229–231.

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

Rouse, G.W. & Pleijel, F. (2003): Problems in polychaete systematics. *Hydrobiologia* 496: 175–189.

Rouse, G.W. & Pleijel, F. (2006): Annelid phylogeny and systematics. In: Rouse, G.W. & Pleijel, F. (eds.) *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield: 3–21.

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

Salazar-Vallejo, S.I. (2014a): *Sternaspis piotrowskiae* sp. nov. (Polychaeta: Sternaspidae) from the Philippine Islands. In: Williams, G.C. & Gosliner, T.M. (eds.) *The Coral Triangle: The Hearst Philippine Biodiversity Expedition*. California Academy of Sciences, San Francisco: 165–169.

Salazar-Vallejo, S.I. (2014b): Three new polar species of *Sternaspis* Otto, 1821 (Polychaeta: Sternaspidae). *Zootaxa* 3861: 333–344.

Salazar-Vallejo, S.I. & Buzhinskaja, G.N. (2013): Six new deep-water sternaspid species (Annelida, Sternaspidae) from the Pacific Ocean. *ZooKeys* 348: 1–27.

Salazar-Vallejo, S.I., Carrera-Parra, L.F. & Fauchald, K. (2008): Phylogenetic affinities of the Flabelligeridae (Annelida, Polychaeta). *Journal of Zoological Systematics and Evolutionary Research* 46(3): 203–215.

Salazar-Vallejo, S.I. (2017): Six new tropical sternaspid species (Annelida, Sternaspidae) with keys to identify genera and species. *Zoological Studies* 56(32): 1–16.

Selenka, E. (1885): Reports of the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. *Zoology* 13, Part 36: 1–24.

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

Sendall, K. & Salazar-Vallejo, S.I. (2013): Revision of *Sternaspis* Otto, 1821 (Polychaeta, Sternaspidae). *ZooKeys* 286: 1–74.

EBSCOhost - printed on 2/13/2023 2:07 PM via . All use subject to https://www.ebsco.com/terms-of-use

Sluiter, C.P. (1882): Über einen indischen *Sternaspis* und seine Verwandschaft zu den Echiuren. *Naturkundig Tijdschrift voor Nederlandsch Indie* 41: 235–287.
Stimpson, W. (1854): Synopsis of the marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge* 6: 28–37.
Stimpson, W. (1864): Descriptions of new species of marine Invertebrata from Puget Sound, collected by the Naturalists of the North-west Boundary Commission, A.H. Campbell, Esq., Commissioner. *Proceedings of the Academy of Natural Sciences Philadelphia* 16: 153–161.
Struck, T.H. (2018): Phylogeny. In: Purschke, G., Böggemann, M. & Westheide, W. (eds.). *Handbook of Zoology. Annelida Vol. 1, Part 1, Chapter 2*, De Gruyter, Berlin: 37–68.
Struck, T.H., Paul, C., Hill, N., *et al.* (2011): Phylogenomic analyses unravel annelid evolution. *Nature* 471: 95–98.
Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007): Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7: 57. DOI: 10.1186/1471-2148-7-57.
Uschakov, P.V. (1955): Polychaeta of the far eastern seas of the U.S.S.R. *Academy of Sciences of the U.S.S.R., Moskau* No. 56: 445 [in Russian].
Vejdovský, F. (1882): Untersuchungen über die Anatomie, Physiologie und Entwicklung von *Sternaspis*. Denkschriften der Kaiserlichen Akademie der Wissenschaften. *Mathematisch-naturwissenschaftliche Classe* 43: 33–90.
Vejdovský, F. (1883): Bemerkungen zur neueren und älteren Literatur über *Sternaspis scutata*. *Sitzungsberichte der königlich böhmischen Gesellschaft der Wissenschaften in Prag. Jahrgang* 1882: 438–450.
Villa, L. (1976). An ultrastructural investigation of the polar plasm of the egg of *Sternaspis* (Annelida, Polychaeta). *Acta embryologiae experimentalis* 2: 153–165.
Villa Notarbartolo, L. (1970). Morfologia ultrastrutturale degli involucri corticali del nucleo dell'uovo ovarico maturo di *Sternaspis*. *Acta embryologiae experimentalis* 1: 133–150.
Wu, X., Salazar-Vallejo, S.I. & Xu, K. (2015): Two new species of *Sternaspis* Otto, 1821 (Polychaeta: Sternaspidae) from China seas. *Zootaxa* 4052(3): 373–382.
Wu, X. & Xu, K. (2017): Diversity of Sternaspidae (Annelida: Terebellida) in the South China Sea, with descriptions of four new species. *Zootaxa* 4244(3): 403–415.
Yoshino, K., Nagayoshi, M., Sato, M., Katano, T., Ito, Y., Fujii, N., Hamada, T. & Hayami, Y. (2016): Life history of *Sternaspis costata* (Sternaspidae: Polychaeta) in Ariake Bay, Japan. *Journal of the Marine Biological Association of the United Kingdom* 96(3): 647–655. doi http://dx.doi.org/10.1017/S0025315415000880
Zhadan, A.E., Tzetlin, B.A., Salazar-Vallejo, S.I. (2017): Sternaspidae (Annelida, Sedentaria) from Vietnam with description of three new species and clarification of some morphological features. *Zootaxa* 4226(1): 75–92.
Zrzavy, J., Riha, P., Pialek, L. & Janouskovec, J. (2009): Phylogeny of Annelida (Lophotrochozoa): total-evidence analysis of morphology and six genes. *BMC Evolutionary Biology* 9: 189. DOI: 10.1186/1471-2148-9-189.

James A. Blake and Nancy J. Maciolek

## 7.3.1.9 Longosomatidae Hartman, 1944

### Introduction

The Longosomatidae contains a single genus, *Heterospio*. Species of *Heterospio* are poorly known. They have been considered as either spioniform (Blake and Arnofsky 1999) or cirratuliform (Wilson 2000) polychaetes. There are now good reasons to consider them closely related to cirratuliform polychaetes.

The bodies of *Heterospio* species are elongate and narrow and have a head that consists of a prostomium and peristomium (Figs. 7.3.1.9.1 B and 7.3.1.9.2 A, B, F). A pair of grooved palps are present, as well as nuchal organs. The first six to eight short biramous segments comprise an anterior thoracic region with long, filamentous branchiae (Fig. 7.3.1.9.2 A) that is followed by a middle abdominal region consisting of 7–16 unusually elongated segments. In some species, the noto- and neurochaetae encircle and form nearly complete rings around each elongated abdominal segment (Fig. 7.3.1.9.1 A). Chaetal fascicles arise from the anterior margin of each anterior and middle body segment. The body terminates in a bulbous posterior section having two to five crowded segments (Fig. 7.3.1.9.2 G), usually with pairs of hooked spines; there are no separate pygidial appendages on the enlarged posterior segments. Segmental chaetae include a variety of capillaries and acicular spines, often with aristate tips.

*Heterospio* has been collected globally from shallow to abyssal depths in soft sediments, but currently, only eight species are recognized (Read and Fauchald 2018). However, the type species, *Heterospio longissima* Ehlers, 1874, has been widely reported, and it is certain that these reports include additional species (see "Taxonomic History" section). In our own benthic programs, specimens of at least seven separate species have been collected from off the U.S. Atlantic coast and the Gulf of Mexico in shelf and slope depths and from SE Asia in deep water off Brunei. Several of these species are new to science.

The literature on *Heterospio* is sparse. The genus *Heterospio* and the first species, *H. longissima*, from the NE Atlantic Ocean, were briefly described by Ehlers (1874) and more fully described and illustrated by Ehlers (1875). It took another 70 years before Hartman (1944) described a second species, *Heterospio catalinensis* (as *Longosoma*), from southern California. Additional species descriptions and reviews include Hartman (1965), Wu and Chen (1966), Laubier *et al.* (1973), Uebelacker (1984), Borowski (1995), Bochert and Zettler (2009), and Parapar *et al.* (2014, 2016).

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Wilson (2000) and Rouse and Pleijel (2001) published brief summaries of *Heterospio*.

In the present review, the adult morphology is presented, together with some unpublished observations on one of our new species, including juveniles. In addition, we have discovered several unpublished illustrations of North Atlantic species from the research files of the late Dr. Mary E. Petersen and include a few of these where relevant. Most information on the biology of *Heterospio* species is speculative. To date, no living specimens have ever been studied and little is known regarding their biology and mode of life.

**Zoobank Registration Number:** urn:lsid:zoobank.org:pub:D8F8CBD5-EC35-46D5-8600-034E743FA44E

## Morphology

### External morphology

**Body shape and color.** The bodies of *Heterospio* species are long, thin, and fragile (Figs. 7.3.1.9.1 A, 7.3.1.9.2 A, and 7.3.1.9.3 A), becoming enlarged only in an expanded posterior end (Figs. 7.3.1.9.2 G and 7.3.1.9.3 F); the latter is rarely attached due to fragmentation during collection. The prechaetigerous region or head is followed by a short dorsoventrally flattened thoracic region formed of six to eight crowded segments with distinct noto- and neuropodia-bearing prominent fascicles of chaetae (Figs. 7.3.1.9.1 A, B, 7.3.1.9.2 A, and 7.3.1.9.3 C). The following segments

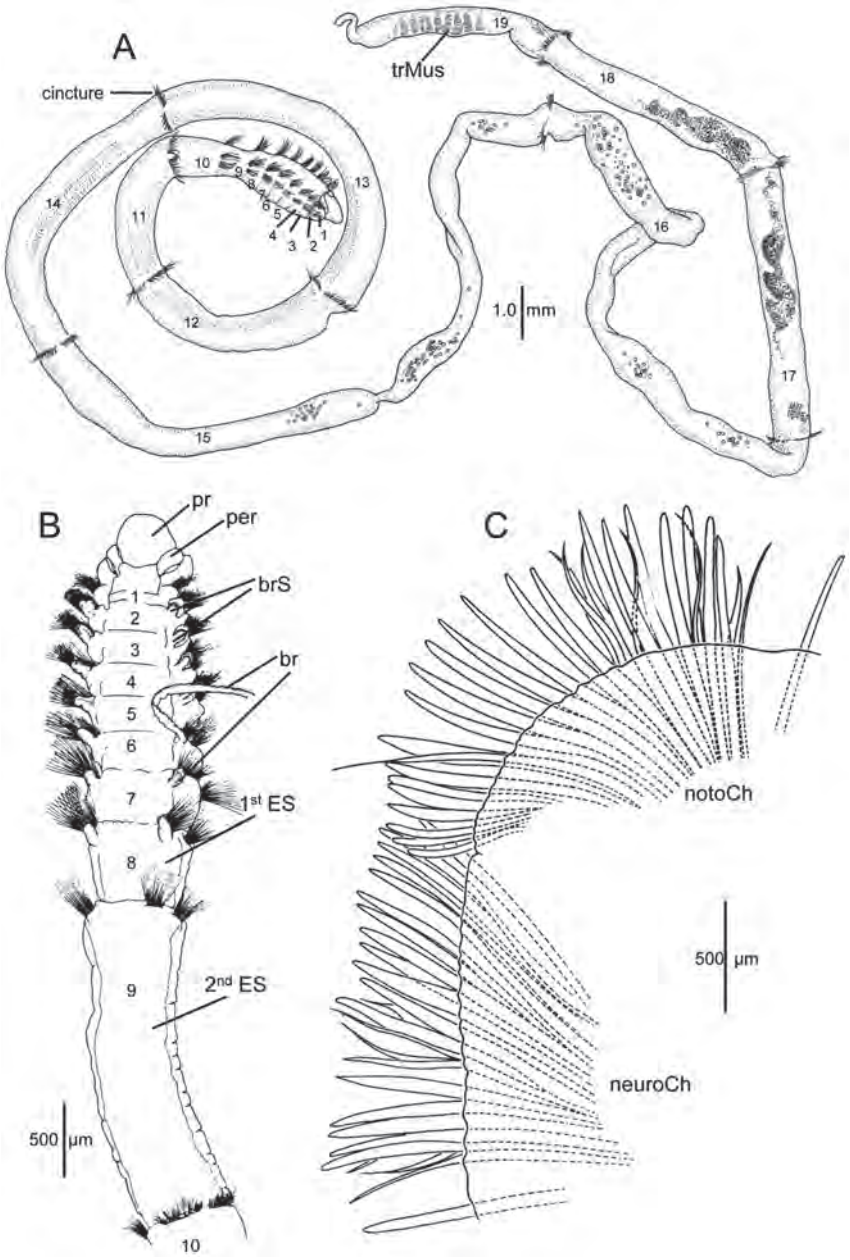


**Fig. 7.3.1.9.1:** *Heterospio* morphology. A, *Heterospio longissima sensu* Hartman (1965), incomplete specimen with 19 chaetigerous segments. B–C, *Heterospio mediterranea*: B, anterior end dorsal view; C, parapodium from elongated segment with cincture of spines and capillaries. br, branchia; brS, branchial scar; ES, elongated segment; neuroCh, neurochaetae; notoCh, notochaetae; per, peristomium; pr, prostomium; trMus, transverse muscle bands. A, Original by the late Dr. Mary E. Petersen, of specimen originally identified as *H. longissima* by Kirkegaard (1980) from NE Atlantic (*Shackleton* Sta. 1903/4) in 4,165 m; B–C, after Laubier *et al*. (1973).

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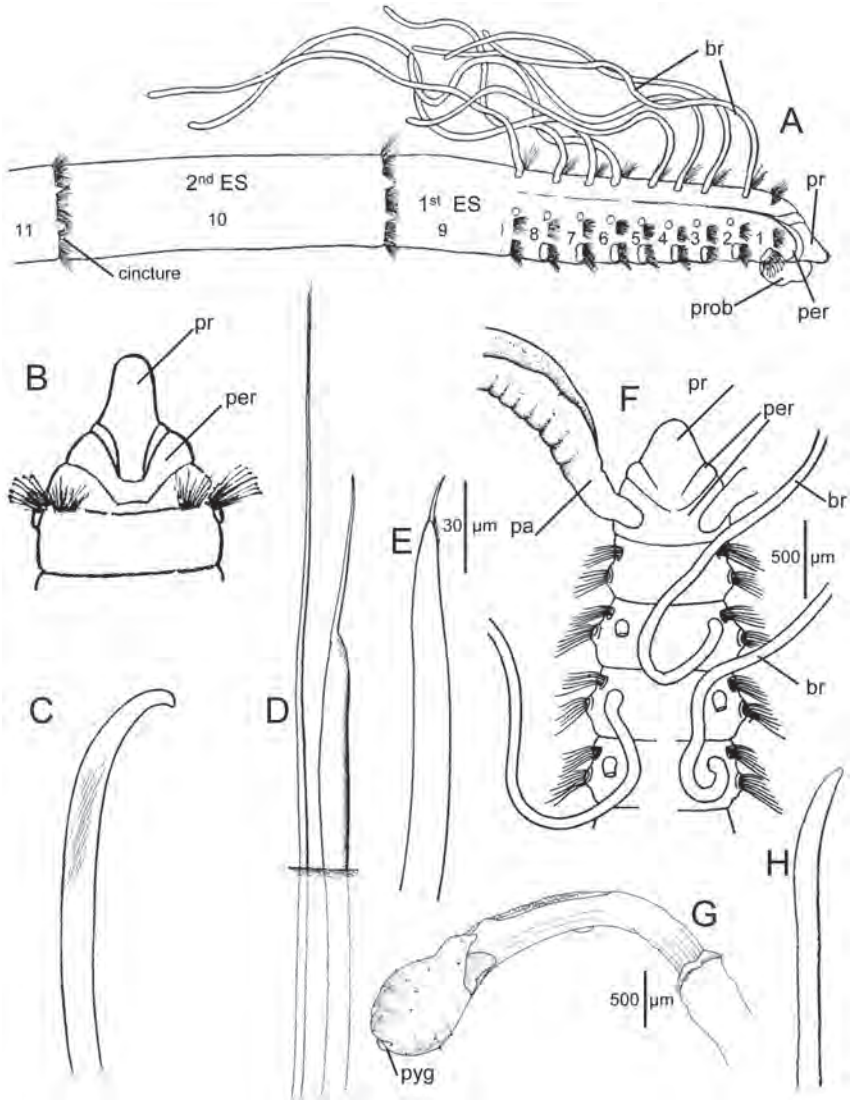


**Fig. 7.3.1.9.2:** *Heterospio* morphology. A–D, *Heterospio catalinensis*: A, anterior end, lateral view; B, anterior end, dorsal view; C, curved hook from neuropodium of chaetiger 1; D, capillary and aristate spine from middle body segment. E–F, *Heterospio sinica*: E, aristate spine from fourth elongated segment; F, anterior end dorsal view. G–H, *Heterospio longissima sensu* Hartman (1965): G, posterior end, lateral view; H, spine from posterior end. br, branchia; ES, elongated segment; pa, palp; per, peristomium; pr, prostomium; prob, proboscis; pyg, pygidium. A–D, H not to scale. A–C, After Hartman (1944); D, after Hartman (1957); E–F, after Wu and Chen (1966); G, original by the late Dr. Mary E. Petersen, of specimen originally identified as *H. longissima* by Kirkegaard (1980) from NE Atlantic (*Shackleton* Sta. 1903/2) in 4,120–4,065 m; H, after Hartman (1965).

become cylindrical in cross-section and are unusually elongated (Figs. 7.3.1.9.1 A, B, 7.3.1.9.2 A, and 7.3.1.9.3 C). The posterior end is enlarged, often bulbous (Figs. 7.3.1.9.2 G and 7.3.1.9.3 F) and bears a few hooked spines (Figs. 7.3.1.9.2 H and 7.3.1.9.3 F). The color of preserved specimens is pale, with distinct pigmentation not reported.

Juveniles of a species of *Heterospio* collected from slope sediments off North Carolina superficially resemble bitentaculate cirratulids in having expanded flattened thoracic segments and narrow elongated abdominal segments that appear to be moniliform (Blake personal observation).

**Head.** The head or prechaetigerous region consists of the prostomium and peristomium. The prostomium is conical, pointed, rounded, or slightly flattened on the anterior margin (Figs. 7.3.1.9.1 B and 7.3.1.9.2 B, F), sometimes also dorsoventrally flattened (Figs. 7.3.1.9.2 A and 7.3.1.9.3 B); ciliated nuchal grooves are located posterior and lateral to the prostomium (Fig. 7.3.1.9.3 B); eyes are absent. The peristomium typically surrounds the mouth ventrally and extends dorsally as a ridge behind the nuchal organs with a pair of palps arising from behind this ridge (Fig. 7.3.1.9.2 F); palp scars are visible with scanning electron microscopy (Parapar *et al*. 2016) and on specimens stained with Shirlastain A (Fig. 7.3.1.9.3 B). Palps are rarely observed intact but were reported by Wu and Chen (1966) as grooved, presumably similar to those of spionids and cirratulids; Parapar *et al*. (2014) also observed palps on *Heterospio indica*. Several specimens from deep water off North Carolina and SE Asia were collected with palps and branchiae intact (Blake & Maciolek unpublished) (Fig. 7.3.1.9.3 A). The pharynx is eversible (Hartman 1944, Parapar *et al*. 2016) (Fig. 7.3.1.9.2 A).

**Segmentation.** The anterior thoracic region consists of six to eight short segments with typical biramous

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parapodia (Figs. 7.3.1.9.1 B, C and 7.3.1.9.2 A). The posteriormost segment of the thoracic region may be slightly longer and is transitional between the thorax and the middle or abdominal segments. The abdominal segments consist of long, narrow segments where the parapodia are reduced but the numerous noto- and neurochaetae are arranged in a ring around each segment rather like the posterior cinctures of the cirratulid genus *Chaetozone* (Figs. 7.3.1.9.1 C, 7.3.1.9.2 A, and 7.3.1.9.3 E). Unique to *Heterospio* is that the chaetal fascicles emerge on the anterior end of each of the short anterior and elongated middle segments (Figs. 7.3.1.9.1 B and 7.3.1.9.2 A, B). In contrast, cirratulids have the chaetae arising from the middle or posterior end of each segment (Blake and Magalhães 2017).

The elongated middle abdominal segments of most species have the noto- and neuropodia surrounding each segment with the chaetae arranged as cinctures of spines and capillaries (Figs. 7.3.1.9.2 C and 7.3.1.9.3 E); in a few species, the biramous parapodia are retained on the elongated segments with cinctures absent, or cinctures are absent from a few of the anteriormost elongated segments.

The transition between the anterior thoracic segments and the middle elongated segments is usually not abrupt; there may be an intermediate segment between the two regions. The number of anterior short segments together with the location of the first elongated segment are important taxonomic characters. Therefore, it is important to decide which segment is the first elongated segment. In some species, a transitional segment has the same type of parapodia as the preceding ones but is simply longer. We therefore propose using a criterion that the first elongated segment should be at least twice as long as the previous short segments (Figs. 7.3.1.9.1 B and 7.3.1.9.2 A). In general, this criterion corresponds with current species descriptions (see Parapar *et al*. 2014).

Hartman (1944) noticed that the elongated segments of *H. catalinensis* were crossed by transverse wrinkles that she thought allowed individual segments to stretch and expand in length. In our observations of an undescribed species of *Heterospio* from offshore North Carolina, similar wrinkles were observed on the elongated segments. These appear to be associated with transverse muscle bands, suggesting that they are actually numerous minute annular rings. Similar rings on elongate segments are clearly illustrated in scanning electron micrographs for *H. longissima* and *Heterospio reducta* by Parapar *et al*. (2014; Figs. 7.3.1.9.3 A, C and 7.3.1.9.10 A–D) and *H. indica* by Parapar *et al*. (2016; Fig. 7.3.1.9.7 A).

Epidermal morphology, including the presence or absence of sense organs apart from the nuchal organs, is unknown.

**Branchiae.** The branchiae are long and filiform, as is typical for cirratuliform polychaetes (Figs. 7.3.1.9.2 A, F and 7.3.1.9.3 A, B). The actual branchiae or their scars are limited to some or all of the thoracic segments. The number of branchiae on the thoracic segments has been used as a character to separate species and ranges from two to about eight pairs depending on species (Parapar *et al*. 2014). The branchiae should be capable of extending into the overlying water in a manner similar to those of some cirratulids.

**Posterior segments.** Most observations of the posterior segments of *Heterospio* species come from isolated posterior fragments not connected to the rest of the worm. Complete specimens have rarely been observed. When observed, the elongate abdominal segments terminate in an enlarged bulbous far posterior piece that has two to five segments and bears pairs of hooked chaetae (Figs. 7.3.1.9.2 G and 7.3.1.9.3 F).

**Pygidium.** The actual pygidium is reduced to a ring surrounding the anal opening (Figs. 7.3.1.9.2 G and 7.3.1.9.3 F). The bulbous nature of the posterior end has been speculated to assist in burrowing (Jumars *et al*. 2015) but may serve as an anchoring device, which would explain the role of the hooked chaetae and why the posterior end is consistently detached during collection. Complete specimens have been collected for at least three of our provisional species, but these are rare (Blake & Maciolek unpublished).

**Chaetae.** Chaetae are all simple and include capillaries and acicular spines that may have aristate-like tips or curved hook-like spines. Apart from *H. catalinensis*, which has neuropodial spines in chaetiger 1 (Fig. 7.3.1.9.2 C), all other named species have only capillaries in the thoracic segments. Uebelacker (1984) reported spines in the neuropodia of chaetiger 1 in an undescribed species from the Gulf of Mexico; similar spines have been observed in an undescribed species from SE Asia (Blake & Maciolek unpublished).

The chaetae of the elongated segments are either all capillaries or a mixture of capillaries and spines in a double or triple row. Either the spines are pointed or blunt tipped or have a narrow aristate-like extension. The extension is either a tapering of the apex of the spine to a narrow capillary-like tip (chaetae termed subuluncini) (Fig. 7.3.1.9.2 D) or it is a definite arista that arises either from the tip of the spine (Fig. 7.3.1.9.2 E) or is subapical. The first use of the term subuluncini for these chaetae appears to be when Hartman (1957) redescribed *H. catalinensis*.

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A mixture of subuluncini and aristate spines occur in some species; the tips of spines or the aristae may have a fringe of fibrils (Borowski 1994). The chaetae of the expanded posterior end are few but may include pairs of curved acicular hooks (Figs. 7.3.1.9.2 H and 7.3.1.9.3 F) that appear to be directed in an anterior direction.

**Internal anatomy**

There are no published accounts of the internal morphology of any known species of *Heterospio*. There is a ventral proboscis (Wu and Chen 1966, Borowski 1995). Our observations of several specimens from off North Carolina suggest that the digestive tract is a simple tubular gut that extends from the eversible pharynx to the posterior end. It is narrower in the thoracic segments and may approximate an esophagus, while the thicker intestine of the elongated segments appears folded in some specimens.

The elongate segments of the middle region have prominent longitudinal muscles and bands of transverse or circular muscles that appear reflective in certain views (Figs. 7.3.1.9.1 A and 7.3.1.9.3 F). In some specimens, these transverse muscles are associated with minute annular rings on the elongate segments.

Numerous subdermal glands are present along the body of some species; these are usually present in patterns and stain with Methyl Green (Fig. 7.3.1.9.3 C, D). Different patterns among species may be important taxonomic characters but to date have not been described for any species. The function of these subdermal glands is unknown.

**Reproduction and development**

There is no information on the reproduction and development of *Heterospio*. Eggs have been observed in some specimens, and these are typically large and have a thick, reflective egg envelope. The eggs observed by Uebelacker (1984) for *H*. sp. A were ca. 170 µm in the longest dimension. The presence of large eggs suggests a direct or lecithotrophic type of development. Examination of numerous juveniles in samples from the North American Atlantic coast suggests that the morphology of the thoracic region, including the number of segments, develops early, whereas the elongated segments develop as long moniliform segments that continue to elongate during growth. The bulbous posterior region was observed in juveniles of one species to be only slightly larger than the posteriormost elongated segments; larger specimens, however, had distinctly larger posterior segments.

**Biology and ecology**

There are few direct observations on the biology and ecology of *Heterospio* species; and to date, no specimens have been collected and studied alive.

**Habitat**

Species of *Heterospio* are generally not common and are considered rare (Jumars *et al*. 2015); they have been collected from shallow subtidal to abyssal depths of over 4,000 m in sediments from fine sand to soft mud. We have never found *Heterospio* to be abundant in any of our North American or other benthic programs.

One exception to this generalization is the occurrence of an undescribed species of *Heterospio* in Marlborough Sound, New Zealand. This species was among the most frequently encountered invertebrate species in depths <60 m and in muddy sediments with <10% sand (Estcourt 1967).

**Burrowing and tube building**

Borowski (1994) observed that the detached posterior ends of the abyssal species, *Heterospio peruana*, were usually recovered >10 cm below the surface of the sediment. All specimens were recovered 5–20 cm below the surface. These results suggest that the species forms deep burrows and that upon collection the worms readily fragment because the enlarged posterior ends are deep within the sediment. Borowski (1994) also observed a mucoid sheath on one specimen, and this may suggest tube formation, but other investigators have not observed such a sheath.

Jumars *et al*. (2015) suggested that the enlarged posterior end of *Heterospio* might provide these polychaetes the ability to burrowing backward more often than burrowing forward. Presumably, the bulbous nature of the posterior end would serve in crack propagation as these authors have observed in other polychaetes. Another role for the enlarged posterior ends, however, is as an anchoring device where the paired hooks that are directed anteriorly serve to hold the worm in place.

As noted in the morphology section, numerous narrow annular rings are present on most of the elongated segments of several species, suggesting that these segments are capable of considerable stretching and contraction. How this capability works in burrowing and other activities is not known.

**Feeding**

Jumars *et al*. (2015: A149) indicated that if palps are present, *Heterospio* is likely discretely mobile and

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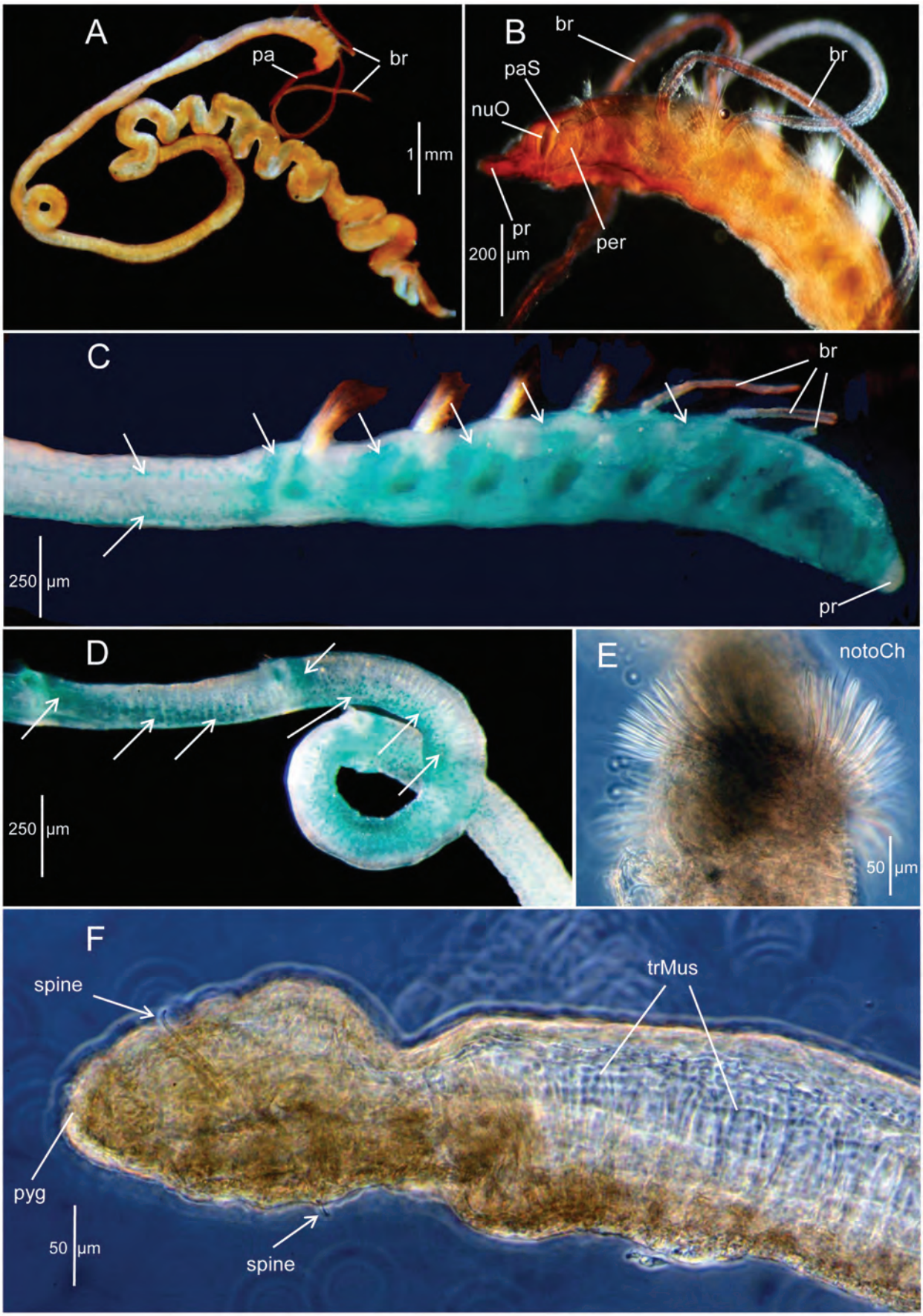


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potentially a subsurface deposit feeder similar to cirratulids. Parapar *et al*. (2016) confirmed that palps are present in *H. indica* and palps are present in several specimens of an undescribed species from off North Carolina (Fig. 7.3.1.9.3 A).

## Phylogeny and taxonomy

### Phylogeny

The first cladistic-based family-level phylogeny of polychaetes using morphological characters was by Rouse and Fauchald (1997). These authors arranged the polychaete families into six basic clades. A clade termed the Spionida included the families Spionidae, Apistobranchidae, Trochochaetidae, Longosomatidae (genus *Heterospio*), Magelonidae, Poecilochaetidae, and Chaetopteridae. *Heterospio* was closest to *Magelona* in this analysis. Rouse and Pleijel (2001) developed a "polychaete metatree" based on a variety of sources. In that effort, the same taxa, plus Uncispionidae, were again placed into Spionida. The Spionida was a sister group to the Terebellida, which included the cirratuliform and terebelliform families.

Blake and Arnofsky (1999), as part of a review of the reproduction and larval development of spioniform polychaetes, developed a preliminary phylogenetic analysis of 36 genera of Spionidae, Apistobranchidae, Trochochaetidae, Poecilochaetidae, Heterospionidae (=Longosomatidae), and Uncispionidae using 38 characters. *Cossura* and *Cirrophorus* were used as outgroups. Among the 38 characters, 14 were reproductive and developmental in nature. Largely based on egg morphology, *Heterospio* was grouped into a clade consisting of several spionid genera belonging to the subfamily Nerininae and the genera *Poecilochaetus*, *Trochochaeta*, and *Uncispio*. However, some of the egg membrane characters coded for *Heterospio* by Blake and Arnofsky (1999) were incorrect and they did not consider some morphological characters such as type of branchiae and position of nuchal organs. While the egg membranes are thick as in some Spionidae, they are not honeycombed and do not have cortical alveoli as coded. Our current opinion is that *Heterospio* species with their filiform branchiae and nuchal organs that are in deep grooves more closely resemble cirratuliform rather than spioniform polychaetes. Further, juveniles of several different *Heterospio* species in our collections superficially resemble bitentaculate cirratulids in having elongate abdominal segments that resemble moniliform segments of some *Aphelochaeta* species. Wilson (2000) also noted that *Heterospio* species share several characters with Cirratulidae, including filamentous branchiae and cinctures of chaetae similar to those the cirratulid genus *Chaetozone*.

There are no published phylogenies that include molecular data for *Heterospio*. However, as part of the description of *H. indica* from India, Parapar *et al*. (2016) collected COI and 18S rDNA sequence data, the first for this genus, and deposited the results in the GenBank database. Given the apparent close morphological similarity of *Heterospio* to cirratulids, we asked Dr. Ken Halanych, Auburn University, Auburn, AL, USA, to give an opinion regarding the similarity of these new *Heterospio* sequences to those from other polychaete families.

Dr. Halanych (personal communication) indicated that the 18S data, being from a short conserved region, does not work well for comparison between families. The COI, however, provided more information. Using an amino acid blast search, he compared sequences among over 100 taxa. The sequences most similar to *H. indica* were *Flabelligera*, *Tharyx*, *Chaetozone*, *Teuthidodrilus* (the acrocirrid squidworm), and *Diplocirrus*. These taxa are all Cirratuliformia; there were no spioniforms in the top 100 most similar blast hits. These molecular results are very sparse and preliminary but support our morphological observations that *Heterospio* species are more similar to cirratuliform rather than spioniform polychaetes.

### Taxonomic history

Ehlers (1874) first described the genus *Heterospio* and the type species, *H. longissima*, from deep water off SW Ireland with a brief Latin diagnosis and a more complete description in German with illustrations by Ehlers (1875). There were no subsequent collections or reports of *H. longissima* or any other species of *Heterospio* until 70 years later when Hartman (1944) described a new genus and species, *Longosoma catalinensis*, from south-

▸ **Fig. 7.3.1.9.3:** *Heterospio* sp. photomicrographs: A, mostly complete specimen, lateral view, with palp and branchiae, posterior elongated segments coiled. B, Anterior end, left lateral view of another specimen with long branchiae. C, Anterior end, right lateral view of a specimen stained with Methyl Green, arrows indicate concentrations of stain or rows of stained subdermal glands. D, Middle body segments of same specimen with arrows indicating concentrations of Methyl Green and numerous stained subdermal glands. E, Notochaetal capillaries and spines from elongated segment 14. F, Posterior end, lateral view, arrows indicate curved spines. All photographs originals of specimens of an undescribed species from the continental slope off North Carolina, 800 m. br, branchia; notoCh, notochaetae; nuO, nuchal organ; pa, palp; paS, palp scar; per, peristomium; pr, prostomium; pyg, pygidium; trMus, transverse muscle bands. A–B, E–F, Stained with Shirlastain A; C, D, stained with Methyl Green.

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ern California. In the same paper, Hartman also established a new family, Longosomidae, for this unusual polychaete. Hartman (1963) subsequently collected additional specimens of *L. catalinensis* and at that time recognized that the species was similar to *H. longissima* of Ehlers and thus referred *Longosoma* to synonymy with *Heterospio* and established the Heterospionidae as a new family. However, Petersen (1992) and Borowski (1995) both noted that Longosomatidae has priority (note change in spelling), and this family name has been used since.

Hartman (1965) next redescribed *H. longissima* from deep water in the Western North Atlantic as part of a rich polychaete collection obtained by the late Dr. Howard Sanders and Dr. Robert Hessler as part of their now classic deep-sea benthic investigations. As part of this report, Hartman (1965) also provided the first description of the unusual bulbous posterior end armed with pairs of curved hooks. Hartman's concept of *H. longissima* differed from that of Ehlers' in that her specimens had acicular spines in the elongated segments instead of lacking them (*fide* Laubier *et al*. 1973) and that the first elongated segment was shorter than that of Ehlers (*fide* Parapar *et al*. 2014).

Following Hartman (1965), additional species of *Heterospio* began to be discovered and described. Wu and Chen (1966) described *Heterospio sinica* from off China in 30–70 m. Laubier *et al*. (1973) described *Heterospio mediterranea* from off the French and Spanish Mediterranean coasts in 100–350 m and *H. reducta* from off Algeria in the Mediterranean Sea in deep water (2,355 m). Borowski (1994) described *H. peruana* from abyssal depths of 4,150 m in the SW Pacific. Bochert and Zettler (2009) described *Heterospio angolana* from off West Africa in 145–150 m. Parapar *et al*. (2016) recently described *H. indica* from shallow water off the west coast of India. These species raised the total number of named species of *Heterospio* to eight (see further in the chapter).

In addition to the eight known species, Uebelacker (1984) described and illustrated specimens of another species from the eastern Gulf of Mexico that she provisionally termed *Heterospio* sp. A. This species had neuropodial hooks on chaetiger 1 and was similar in this respect to *H. catalinensis* of Hartman (1944) from California. The two species apparently differ in details of the acicular spines of middle chaetigers and the number of segments with branchiae.

There have been several reports of the type species, *H. longissima*, from locations outside the North Atlantic that are likely different species. These include Imajima (1974: Japan), Hartman (1974: Arabian Sea, 34–88 m), Intes and Le Loeuff (1977: West Africa, Ivory Coast), and Rosenfeldt (1989: Red Sea, off Sudan). Imajima's specimens are likely an undescribed species that shares some characters with Hartman's (1965) account of *H. longissima* in having a short first elongated segment (ninth); unlike Hartman's (1965) account, Imajima's specimens lack spines and cinctures on the three elongated segments present. The brief description by Hartman (1974) does not contain sufficient information to compare her specimens from the Arabian Sea with known species. However, comparison with *H. indica* may be fruitful. The West African specimens from off the Ivory Coast reported by Intes and Le Loeuff (1977) are likely the same as *H. angolana* from off Angola described by Bochert and Zettler (2009), who were apparently unaware of the earlier work from an adjacent area of West Africa. Parapar *et al*. (2016) examined Rosenfeldt's (1989) specimen and referred it to their *H. indica*. It is likely that both versions of *H. longissima* by Ehlers (1874, 1875) and Hartman (1965) are limited to the North Atlantic.

## Taxonomy

### Family Longosomatidae Hartman, 1944

**Type genus**: *Heterospio* Ehlers, 1874
**Synonym**: Heterospionidae Hartman, 1963
**Diagnosis:** Same as genus (see further)
**Remarks**: Longosomatids are easily recognized by the unusually long segments of the middle body region; this character was considered a synapomorphy by Fauchald and Rouse (1997). Another unusual aspect of longosomatid segmentation is that the chaetal fascicles emerge on the anterior end of each of the short anterior and elongated middle segments. The enlarged and often bulbous posterior end with pairs of hooks is also unusual.

### Genus *Heterospio* Ehlers, 1874

**Type species:** *Heterospio longissima* Ehlers, 1874. By monotypy
**Synonym:** *Longosoma* Hartman, 1944. Type species: *Longosoma catalinensis* Hartman, 1944. By monotypy
**Diagnosis** (from Parapar *et al*. 2016): Body elongated, linear, divided into three regions. Anterior region with six to eight short chaetigers; median region with greatly elongated segments; posterior region with few short, inflated segments. Posterior part of prostomium with a pair of lateral nuchal organs. Proboscis eversible, epithelial pouch. One pair of grooved peristomial palps, easily lost, leaving scars on lateral surfaces. Anterior region with two to eight pairs of cirriform branchiae, usually very long, one pair per segment, arising above notopodia, beginning from chaetiger 2. Anterior region with biramous parapodia provided with simple capillaries, with or without acicular spines; elongated segments with chaetae usually forming a cincture near anterior margin; chaetae include simple

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capillaries, subuluncini, aristate chaetae, and acicular spines; posteriormost inflated chaetigers provided with strong acicular hooks.

**Remarks:** In addition to the eight known species given in the following list and reported in the "Taxonomic History" section earlier, there are indications that both the Hartman (1965) and Imajima (1974) accounts of *H. longissima* are actually separate species. Another species to be named is *H*. sp. A by Uebelacker (1984) from the Gulf of Mexico. The reports by Knox (1960), Estcourt (1967), and Wilson (2000) suggest that at least two undescribed species occur in New Zealand. As part of our studies, we have identified seven separate species from deep-water collections in the Gulf of Mexico (1), the western North Atlantic Ocean (3), and deep water in the South China Sea (3); these will be treated in a subsequent paper (Blake in preparation). Thus, at least another 10 species await description.

Geographically, seven of the eight currently described species of *Heterospio* are from the northern hemisphere; *H. peruana* is from the Peru Basin off western South America in the southern hemisphere.

### List of species

1. *Heterospio angolana* Bochert & Zettler, 2009. West Africa, off Angola, 145–150 m.
2. *Heterospio catalinensis* (Hartman, 1944). Southern California, 75 m.
3. *Heterospio indica* Parapar, Vijapure, Moreira & Sukumaran, 2016. India, west coast, 2.5–22 m; Red Sea, off Sudan, 507 m (Rosenfeldt 1989). *Fide* Parapar *et al*. (2016).
4. *Heterospio longissima* Ehlers, 1874. NE Atlantic, off SW Ireland, slope depths, 780–838 m.
5. *Heterospio mediterranea* Laubier, Picard & Ramos, 1973. Mediterranean coasts of France and Spain, 100–350 m.
6. *Heterospio peruana* Borowski, 1995. SE Pacific, Peru Basin, 4,150 m.
7. *Heterospio reducta* Laubier, Picard & Ramos, 1973. Mediterranean coast off Algeria, 2355 m; off Brittany coast of France, 400–500 m (Amoureux 1982); off Iceland, 270–922 m (Parapar *et al*. 2014).
8. *Heterospio sinica* Wu & Chen, 1966. East China Sea, 30 m.

### References


Amoureux, L. (1982): Annélides polychètes receillies sur la pente continentale de la Bretagne á l'Irelande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre espèces nouvelles pour la science. II. Inventaire taxonomique annoté de toutes les polychètes sédentaires. *Cahiers de Biologie Marine* 23: 179–214.

Blake, J.A. & Arnofsky, P.L. (1999): Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. In: Dorresteijn, A.W.C. & Westheide, W. (eds.). *Reproductive Strategies and Developmental Patterns in Annelids. Hydrobiologia* 402: 57–106. Kluwer, the Netherlands.

Blake, J.A. & Magalhães, W.F. (2017): Family Cirratulidae Ryckholt, 1851. In: Westheide, W. & Purschke, G. (eds.). *Handbook of Zoology, a Natural History of the Phyla of the Animal Kingdom*. Published on Line, 56 pp.

Bochert, R. & Zettler, M.L. (2009): A new species of *Heterospio* (Polychaeta, Longosomatidae) from offshore Angola. *Zoological Science* 26 (10): 735–737. http://dx.doi.org/10.2108/zsj.26.735

Borowski, C. (1995): New records of Longosomatidae (Heterospionidae) (Annelida, Polychaeta) from the abyssal Southeast Pacific, with the description of *Heterospio peruana* sp. nov. and a general remark on the family. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 92 (Suppl. 1): 129–144.

Ehlers, E. (1874): Annulata nova vel minus cognita in Expeditione "Porcupine" capta. *The Annals and Magazine of Natural history, Ser. 4*. 13: 292–298. Available online at: http://www.biodiversitylibrary.org/item/78506#page/306/mode/1up

Ehlers, E. (1875): Beiträge zur Kenntniss der Verticalverbreitung der Borstenwürmer im Meere. *Zeitschrift für wissenschaftliche Zoologie* 25: 1–102, 4 plates. Available online at: http://www.biodiversitylibrary.org/item/160682#page/9/mode/1up

Estcourt, I.N. (1967): Distribution and association of benthic invertebrates in a sheltered water soft bottom environment (Marlborough Sounds, New Zealand). *New Zealand Journal of Marine and Freshwater Research* 1: 352–370. http://dx.doi.org/10.1080/00288330.1967.9515211

Fauchald, K. & Rouse, G.D. (1997): Polychaete systematics: Past and present. *Zoologica Scripta* 26(2): 71–138.

Hartman, O. (1944): Polychaetous annelids. Part VI. Paraonidae, Magelonidae, Heterospionidae, Ctenodrilidae, and Sabellariidae. *Allan Hancock Pacific Expeditions* 10(3): 311–481.

Hartman, O. (1957): Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pacific Expeditions* 15(3): 211–393.

Hartman, O. (1963): Submarine canyons of Southern California. Part III. Systematics: Polychaetes. *Allan Hancock Pacific Expeditions* 27(3): 1–93.

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

Hartman, O. (1974): Polychaetous annelids of the Indian Ocean including an account of species collected by members of the international Indian Ocean Expeditions, 1963–64 and a catalogue and bibliography of the species from India. *Journal of the Marine Biological Association of India* 16: 191–252.

Imajima, M. (1974): Occurrence of species of three families, Eulepethidae, Apistobranchidae, and Heterospionidae (Polychaeta) from Japan. *Bulletin of the National Science Museum* 17(1): 57–64.

Intes, A. & Le Loeuff, P. (1977): Les annéides polychetes de Côte d'Ivoire. II. Polychètes sédentaires – Compte rendu systématique. *Cahiers ORSTOM, séries Océanographique* 15(3): 215–249.


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Jumars, P.A., Dorgan, K.M. & Lindsey, S.M. (2015): Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497–520 [+ Supplemental Appendix A. Family-by-Family Updates: A1–A350 + Supplemental Table of Guild Characteristics: 1–14].

Kirkegaard, J.B. (1980): Abyssal benthic polychaetes from the northeast Atlantic Ocean, southwest of the British Isles. *Steenstrupia* 6: 81–98.

Knox, G.A. (1960): The polychaete family Longosomatidae in New Zealand. *Nature* 187: 1131.

Laubier, L., Picard, C. & Ramos, J. (1973): Les Heterospionidae (Annélides polychaetes sédentaires) de Méditerranée Occidentale. *Vie et Milieu* 23: 243–254.

Parapar, J., Aguirrezabalaga, F. & Moreira, J. (2014): First record of Longosomatidae (Annelida: Polychaeta) from Iceland with a worldwide review of diagnostic characters of the family. *Journal of Natural History* 48: 983–998. http://dx.doi.org/10.1080/00222933.2013.859316

Parapar, J., Vijapure, T., Moreira, J. & Sukumara, S. (2016): A new species of *Heterospio* (Annelida, Longosomatidae) from the Indian Ocean. *European Journal of Taxonomy* 220: 1–17. http://dx.doi.org/10.5852/ejt.2016.220

Petersen, M.E. (1992): *Provisional review of the Cirratulidae from the Faroes, with comments on some other groups (Annelida, Polychaeta)*. Norðurlandahúsið i Føroyum, Yearbook for 1991–1992: 79–80.

Read, G. & Fauchald, K. (eds.) (2018): *World Polychaeta database. Longosomatidae Hartman*, 1944. Accessed through World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=22608 on 2018-04-13

Rosenfeldt, P. (1989): Die Polychaeta der Rotmeer-Expeditionen MESEDA I (1977) mit FS "SONNE" und MESEDA II (1979) mit FS "VALDIVIA". *Senckenbergiana Biologica* 69: 213–242.

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

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

Uebelacker, J.M. (1984): Family Heterospionidae Hartman, 1963. In: Uebelacker, J.M., Johnson, P.G., Vittor, B.A. & Associates (eds.) *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico, Vol. II*. U.S. Department of the Interior, Minerals Management Service, Metairie, AL, USA: 1–6.

Wilson, R.S. (2000): Family Longosomatidae. In: Beesley, P.L., Ross, G.J.B. & Glasby, C.J. (eds.) *Polychaetes and Allies: the Southern Synthesis:* 193–194. CSIRO Publishing, Melbourne.

Wu, B.L. & Chen, M. (1966): A new and interesting species of the genus *Heterospio* (Polychaeta, Heterospionidae). *Oceanology and Limnology Sinica* 8: 163–167.

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