Handbook of Zoology
Annelida

Volume 3:
Sedentaria III, Errantia I

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Annelida

Edited by Günter Purschke, Markus Böggemann
and Wilfried Westheide

DE GRUYTER

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Foreword

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

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

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

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

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

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

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

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

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and Markus Böggemann
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Volume 4: Annelida, Errantia II, ISBN 978-3-11-064531-6

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7.4 Sedentaria: Spionida/Sabellida

7.4.8 Fabriciidae Rioja, 1923

Introduction

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

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

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

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

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

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

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

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

Morphology

External morphology

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

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

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

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

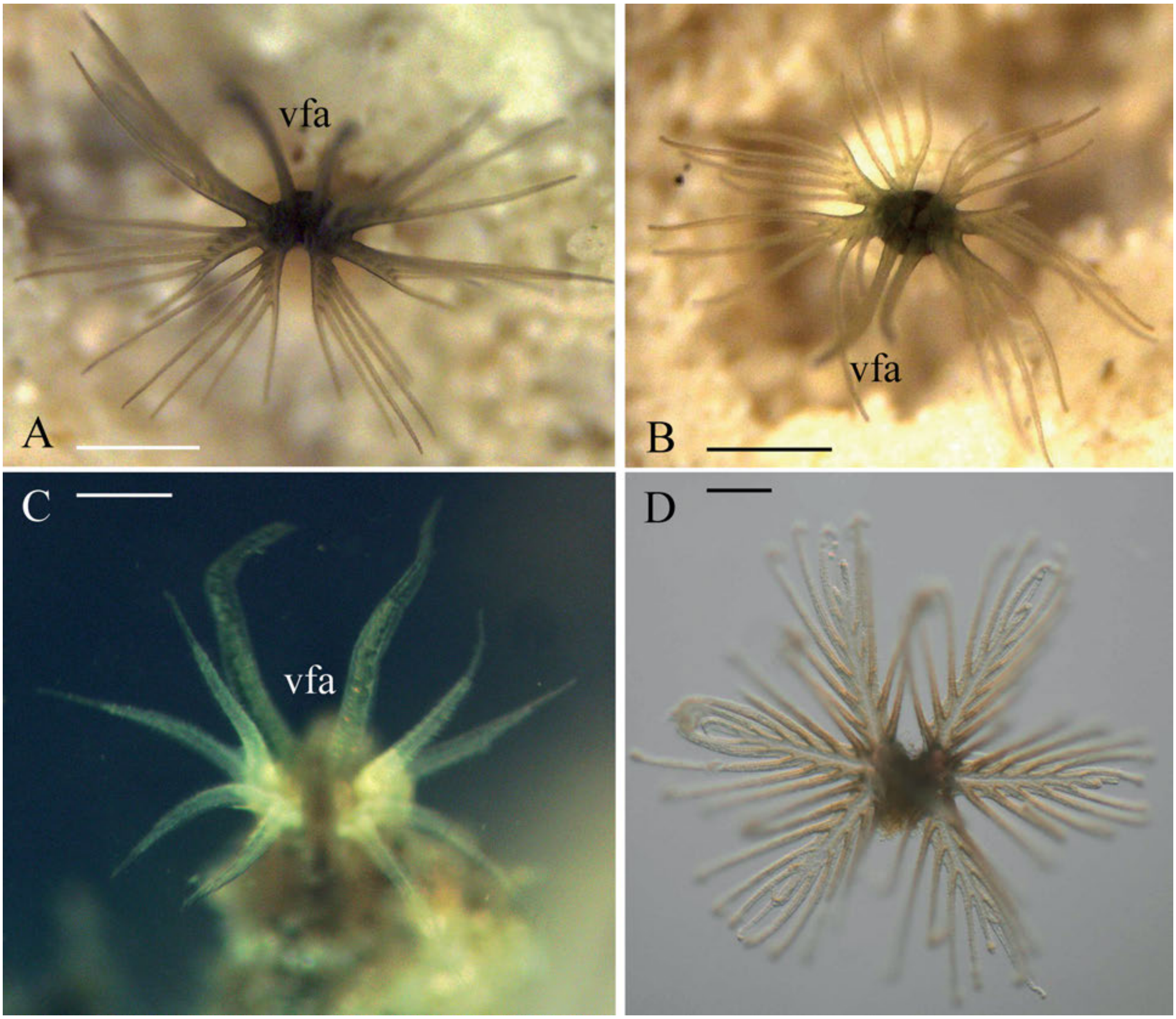
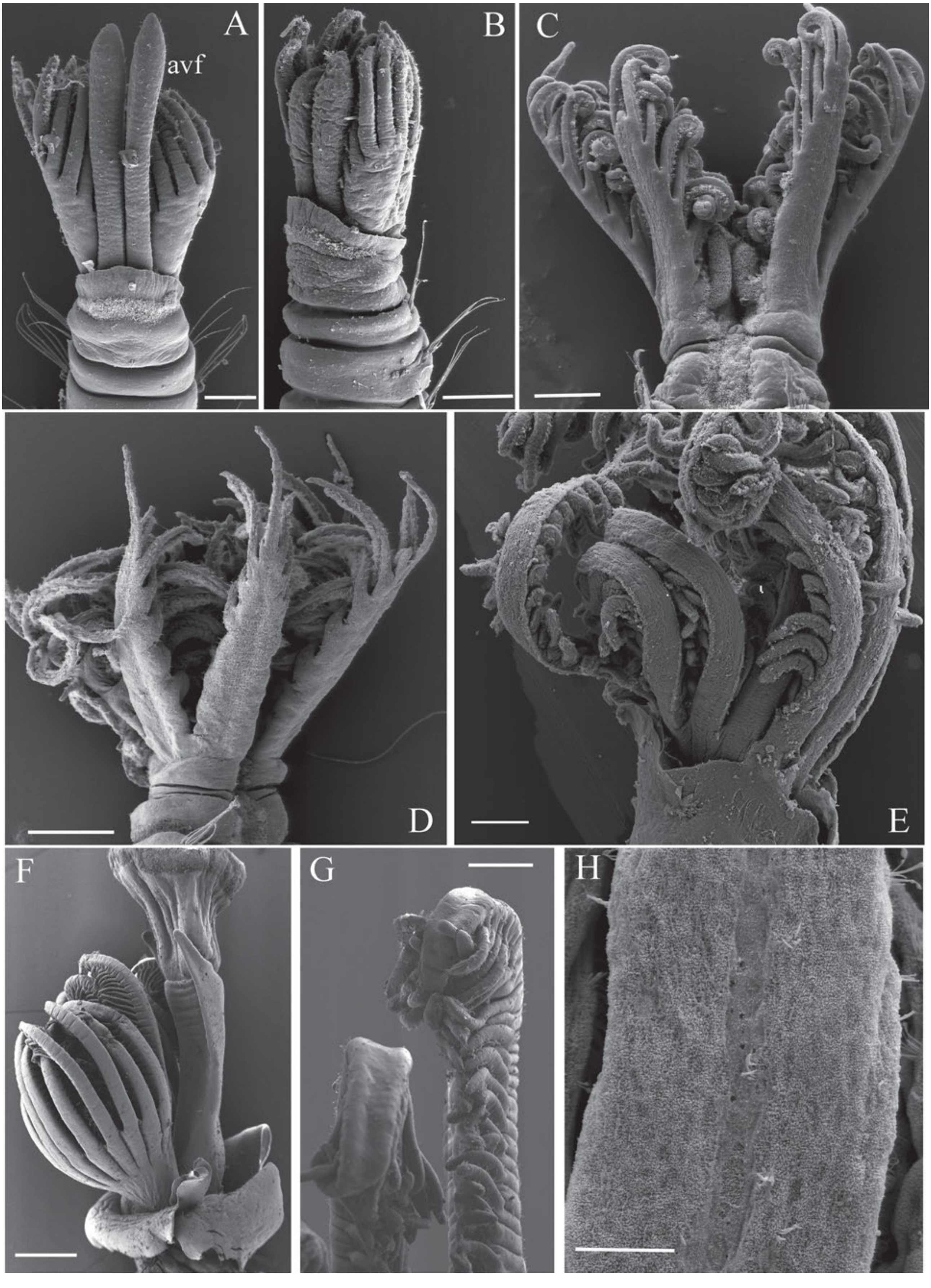


Fig. 7.4.8.2: Radiolar crown morphology of Fabriciidae (micrographs of live specimens). A, B, Asymmetrical branching and pectinate radioles in *Manayunkia athalassia* Hutchings, Deckker & Geddes, 1981; C, Asymmetrical branching and pectinate radioles in *Manayunkia aestuarina* (Bourne, 1883); D, Symmetrical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

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

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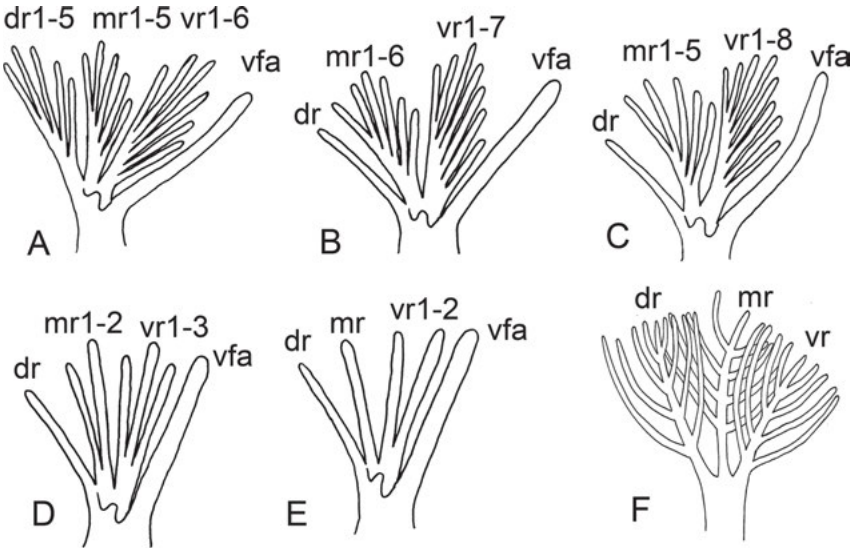

Fig. 7.4.8.4: Schematic view branching of the radiolar crown in *Manayunkia* species and *Fabricia stellaris* (Müller, 1774). A–E, Asymmetrical branching and pectinate radioles; A, *M. athalassia* Hutchings, Deckker & Geddes, 1981; B, *M. caspica* Annenkova, 1928; C, *M. zenkewitschii* Sitnikova, Shcherbakov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

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

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

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

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

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

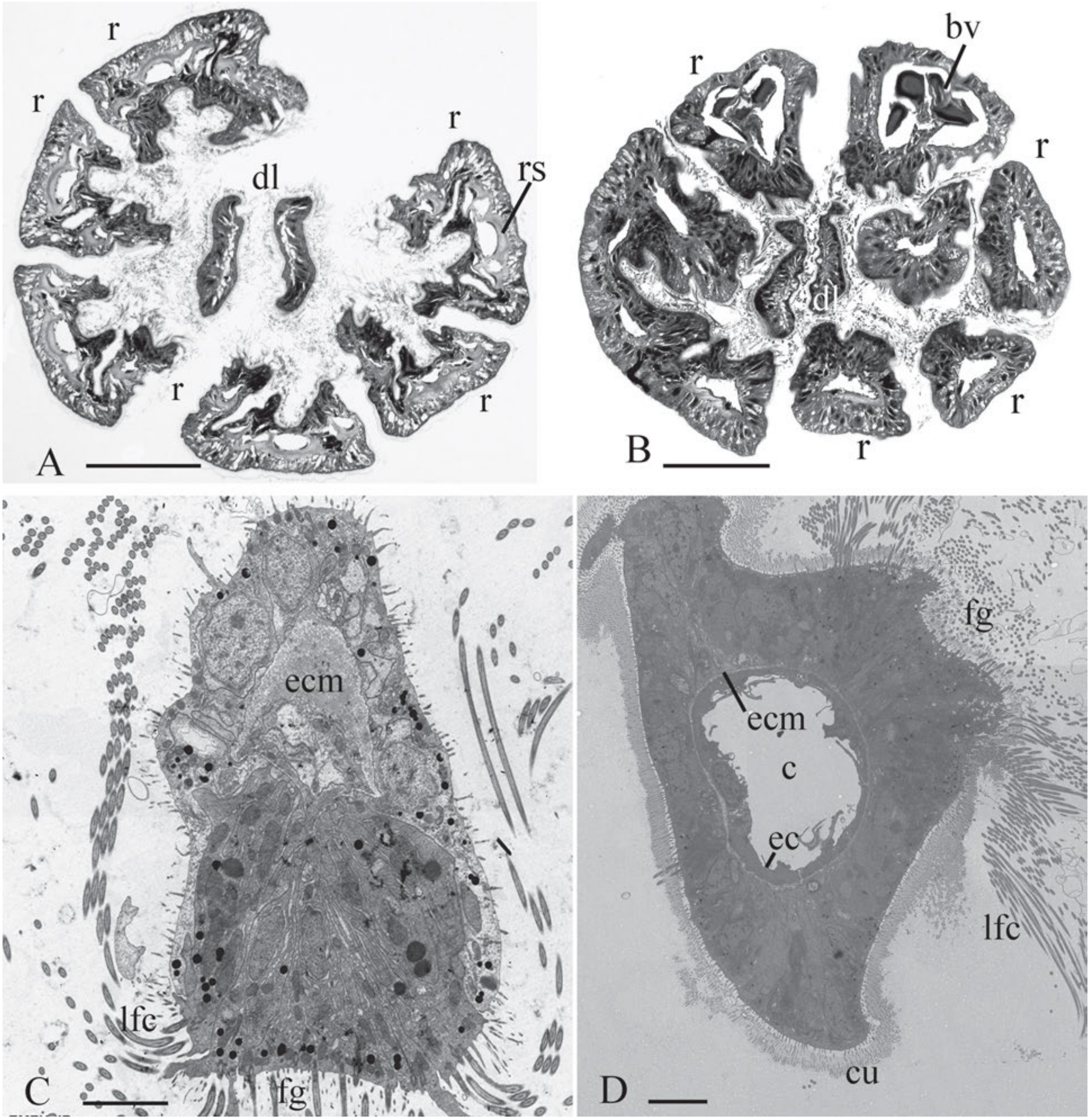

Fig. 7.4.8.5: Transverse section of the radiolar crown and radioles of *Fabricia stellaris* (Müller, 1774) and *Manayunkia aestuarina* (Bourne, 1883). A, Semithick section of the radiolar crown of *F. stellaris*; B, Semithick section of the radiolar crown of *M. aestuarina*; C, Ultrathin section of a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

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

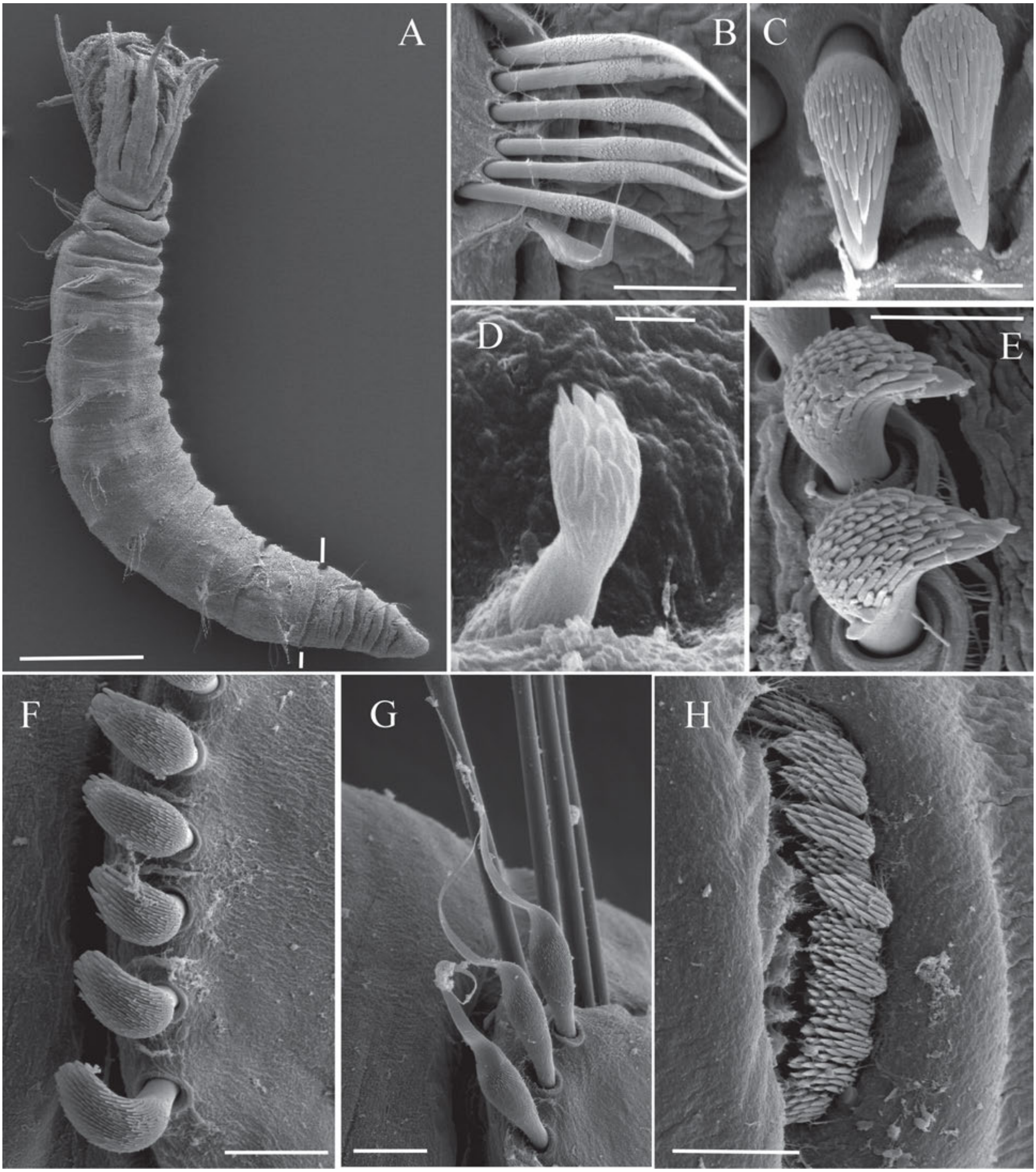

Fig. 7.4.8.6: Chaetae and uncini of Fabriciidae (SEM micrographs). A–C, *Fabricia stellaris* (Müller, 1774); A, Lateral view with thoracic and abdominal regions; B, Six narrowly hooded and one pseudospatulate chaetae of thoracic region; C, Thoracic uncini with a single larger tooth above the main fang;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

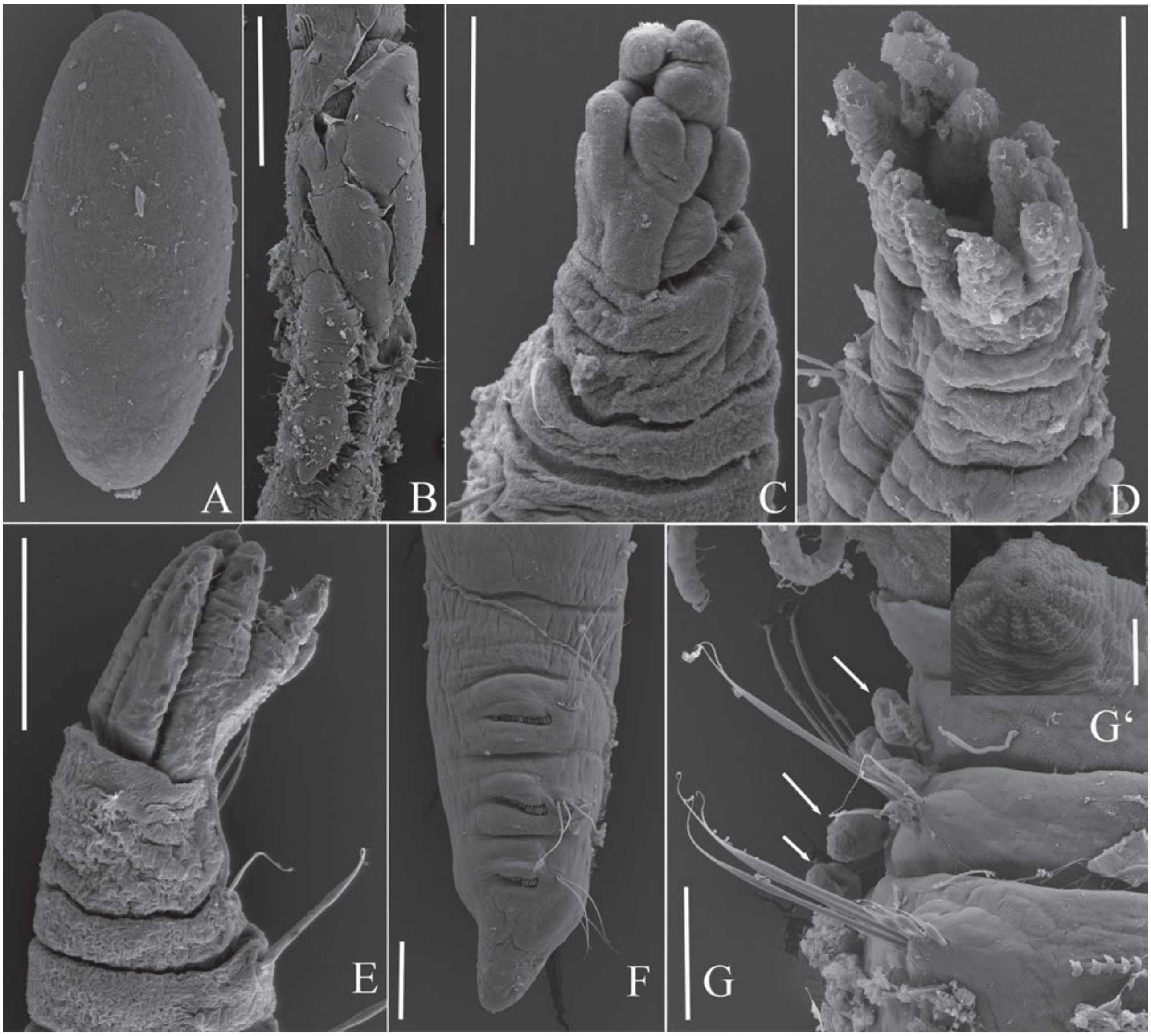

Fig. 7.4.8.7: Larval development and epibiosis in *Manayunkia aestuarina* (Bourne, 1883) (SEM micrographs). A, Egg; B, Clutch from a tube with several larvae; C, D, Larvae with three pairs of radioles and short ventral filamentous appendages; E, Larva with completely developed radiolar crown and first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

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

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

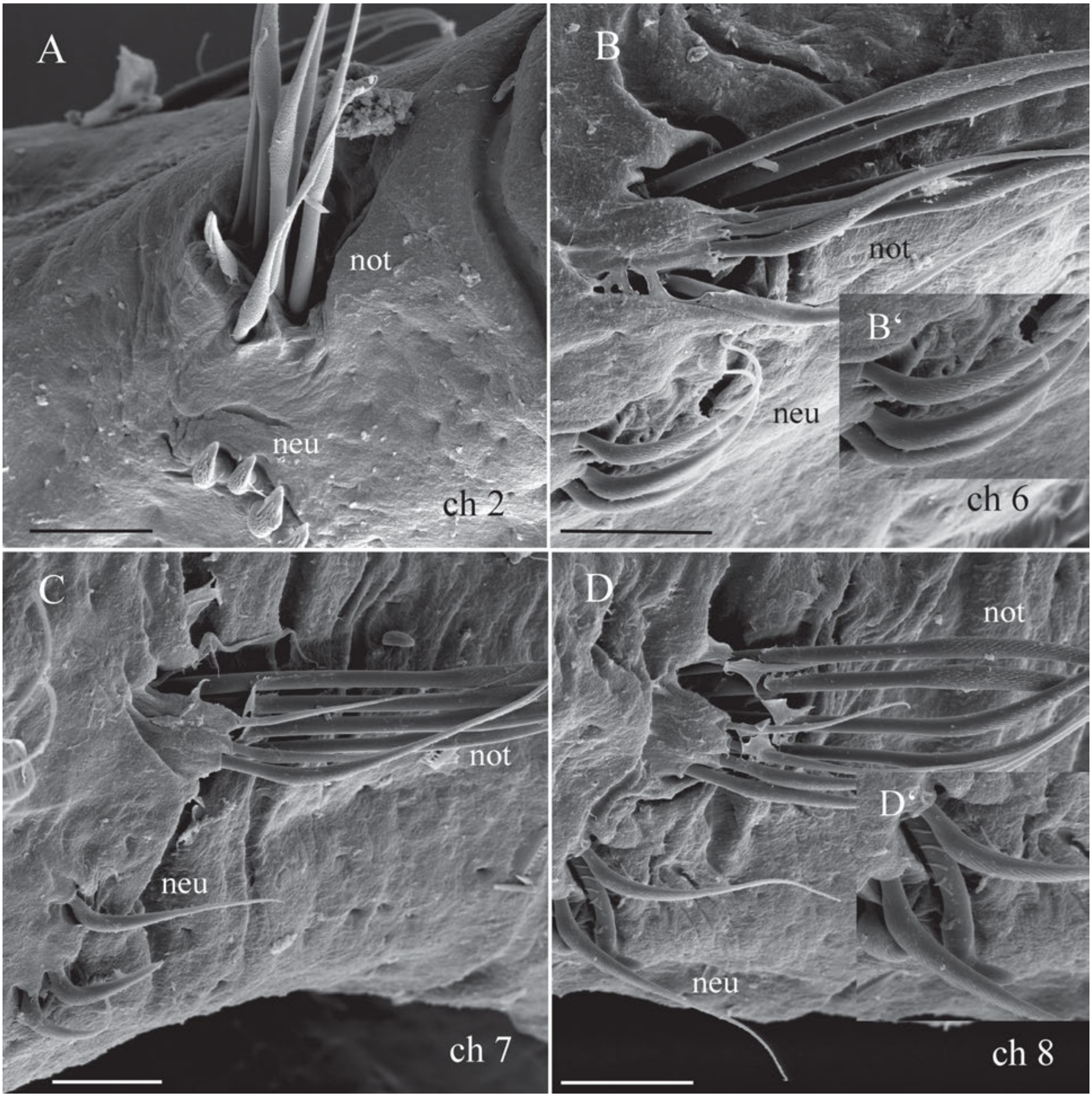

Fig. 7.4.8.8: Pattern of thoracic neuropodial chaetae in *Manayunkia zenkewitschii* Sitnikova, Shcherbakov & Kharchenko, 1997 (SEM micrographs). A, Chaetiger 2, normal shape of neuropodial thoracic uncini (also present on chaetigers 3–5); B, Chaetiger 6 with three strongly bent neuropodial narrowly hooded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

a long manubrium and a main fang surmounted by a series of smaller teeth (Fig. 7.4.8.6C, E, F). A slightly offset medium-sized tooth occurs between the large main fang and the smaller apical teeth in several genera (Fig. 7.4.8.6C) (e.g., in *Augeneriella*, *Fabricia*, *Fabricinuda*, *Monroika*, *Novafabricia*, and *Pseudoaugeneriella*). The apical teeth can also exhibit about the same size (Fig. 7.4.8.6F) (e.g., in *Echinofabricia* species) or may gradually decrease in size away from the main fang (Fig. 7.4.8.6E). A layer of less electron-dense material on the adrostral side that appears translucent has usually been referred to as a hood. The dentate distal end is bent toward the manubrium. The abdominal uncini are arranged side by side in a torus. Their dentate region is anteriorly directed (Figs. 7.4.8.6H, 7.4.8.7F). They usually exhibit multiple rows of equal-sized teeth. Only *Novafabricia chilensis* (Hartmann-Schröder, 1962) and *Novafabricia gerdi* (Hartmann-Schröder, 1974) are known to have a single row of teeth. The length of the manubrium is as long as the dentate region or up to two to three times longer.

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

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

Internal morphology

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

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

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

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

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

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

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

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

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

Reproduction and development

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

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

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

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

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

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

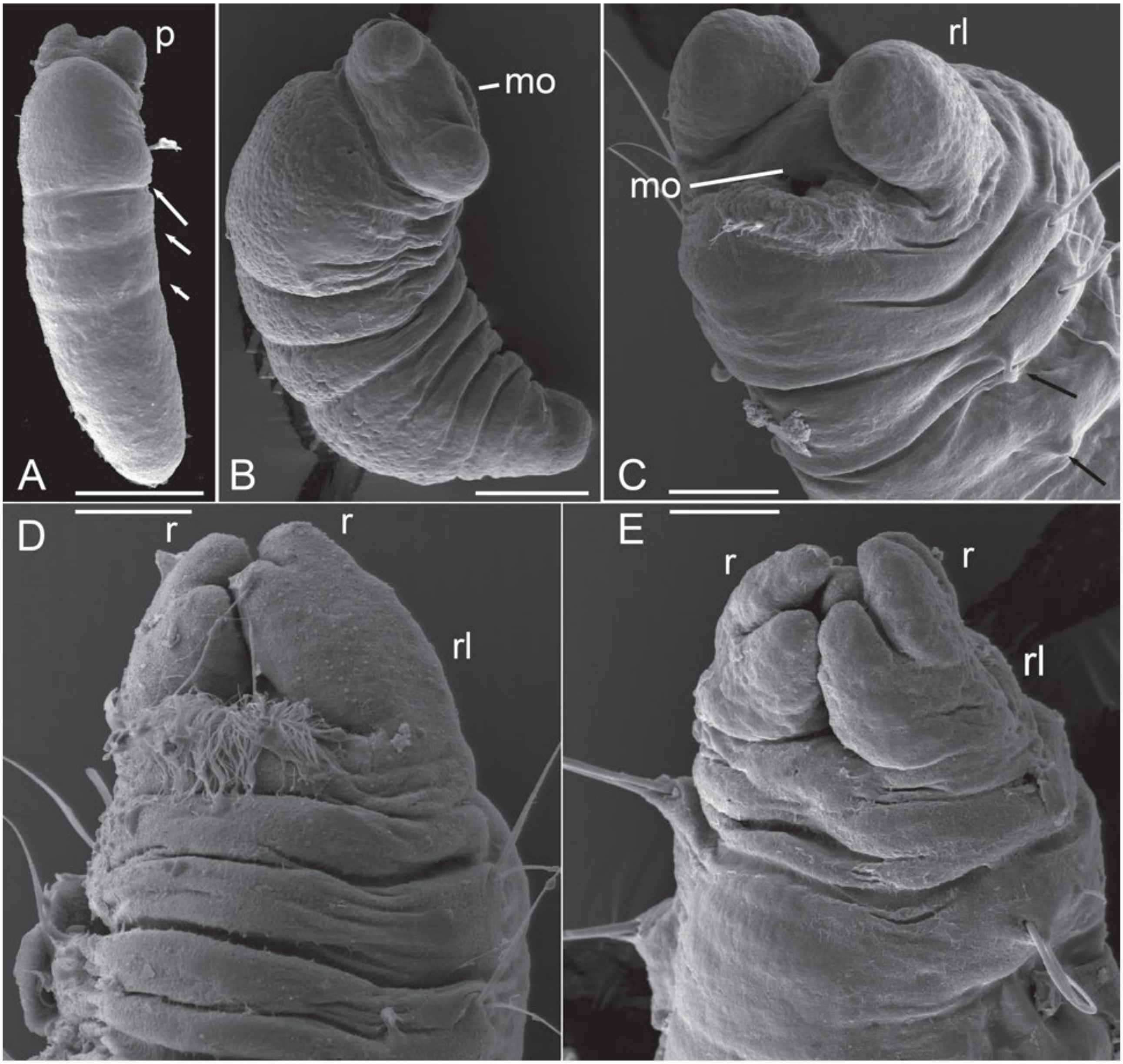

Fig. 7.4.8.9: Larval stages of *Fabricia stellaris* (Müller, 1774) (SEM micrographs). A, Barely segmented (arrows) juvenile with protuberances on anterior end; B, Juvenile with mouth opening, eight thoracic segments and one capillary on chaetigers 1 to 3 each; C, Anterior end of a six-chaetiger juvenile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

tubes of females was described by Randel and Bick (2012). Before the initiation of segmentation, a pair of protuberances appears at the anterior end, which represents the branchial lobes of the radiolar crown (Fig. 7.4.8.9A). Thereafter, three thoracic segments are formed. On the first chaetiger, one narrowly hooded notochaetae develops. One of the next stages is characterized by the existence of eight thoracic segments with one narrowly hooded chaeta on each of the first three segments, whereas the mouth opening is still located ventrally, and abdominal chaetigers are still absent (Fig. 7.4.8.9B). In the next stage, there are two narrowly hooded notochaetae on the first six thoracic chaetigers and one uncinus on the second and third chaetigers (Fig. 7.4.8.9C). The mouth opening is displaced more terminally; a patch of cilia is located ventral to the mouth. Three pairs of short, unbranched radioles are present on larvae with eight thoracic chaetigers (Fig. 7.4.8.9D, E). The mouth opening is now located between the branchial lobes. Only at this stage do abdominal chaetigers appear. In the final stages of larval development, characterized by the presence of eight thoracic and one to three abdominal chaetigers and an incompletely developed radiolar crown, the larvae leave the maternal tube, crawl on the surface for a short time, and construct their own tubes adjacent to the maternal tube (Randel and Bick 2012). The resultant sex ratio is 1 male to 4 to 5 females (Forsman 1956).

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

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

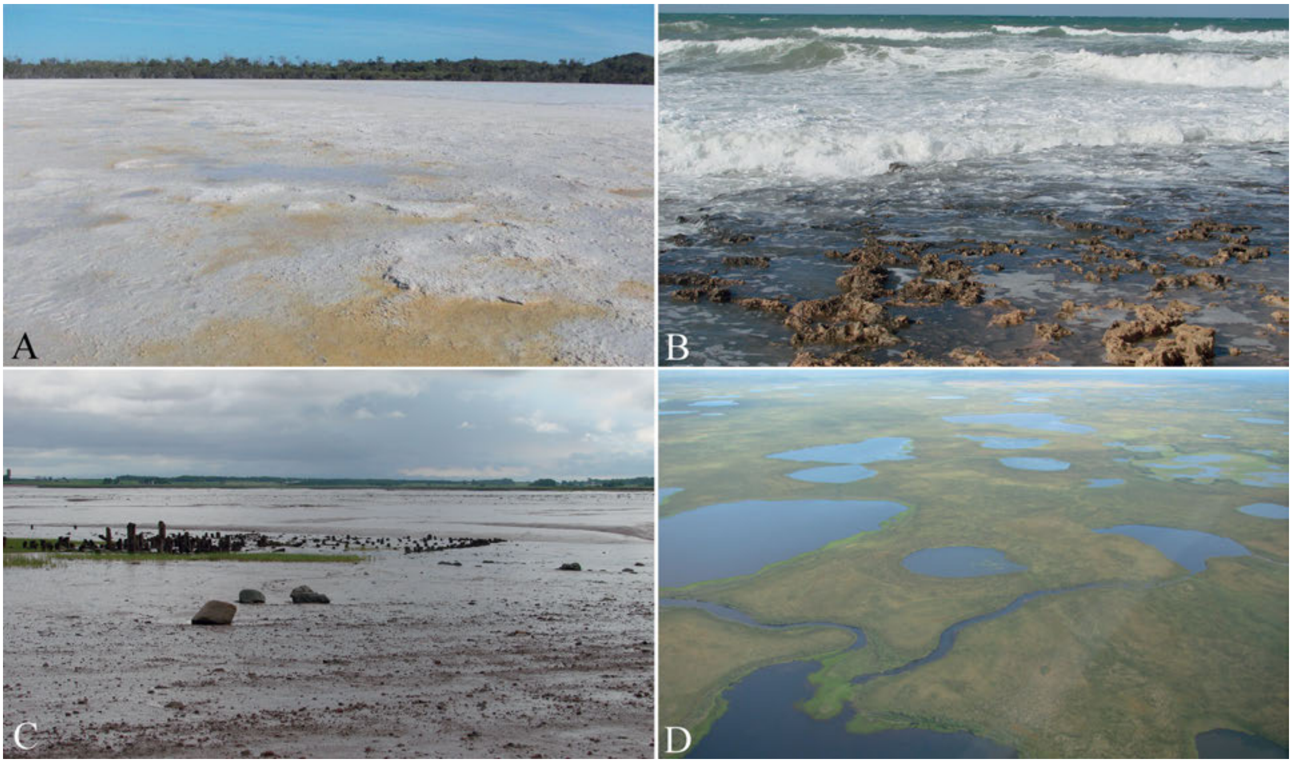

Fig. 7.4.8.10: Characteristic habitats of Fabriciidae species. A, Hypersaline salt lakes (Yalgorup Lake System, Swan Pond, Western Australia); B, Marine intertidal and subtidal hard bottoms (Mediterranean Sea); C, Mudflat areas (northeast America); D, Freshwater lakes (Canadian Arctic). Images by G.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

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

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

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

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

Distribution, ecology, and biology

Distribution and ecology

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

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

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

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

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

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

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

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

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

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

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

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

Fabriciidae species are usually found in sheltered areas on sandy, muddy, or hard bottoms, in mangroves, on red and green algal mats, and in seagrass beds, always where there is a large amount of fine particulate matter present in the water column (Fig. 7.4.8.10B) (e.g., Muus 1967, Lewis 1968b, Bick 1996). Some species do not show a preference for a particular substrate type. *Fabricia stellaris* is known from hard (Gillandt 1979), sandy (Sicinski 1982), and soft (Berger et al. 2001, Cacabelos et al. 2008) bottoms in addition to occurring among algae (Weslawski et al. 2010), as an epizoan on algae (Muus 1967), and on corallines (Southern 1914) and forming tubes within sponges and *Lithothamnion* (Southern 1914). Two other species, *Rubifabriciola tonerella* and *Novafabricia infratorquata*, are found on the shells of *Stramonita haemastoma* inhabited by hermit crabs in the Mediterranean Sea. Both species have been characterized as facultative symbionts of *Calcinus tubularis* (Linnaeus, 1767) (see Bick 2006). They use the cavities formed by boring species in the encrusting calcareous algae that cover the shells. *R. tonerella* was first described from submarine caves in the Mediterranean Sea (Banse 1956, 1959b) but has since been found in infralittoral polychaete assemblages associated with the brown algae *Cystoseira amentacea* and with Demospongiae (Bick 2006). *N. infratorquata* was first found in mats of green algae and *Caulerpa verticillata* as well as rootmats of *Rhizophora mangle* from Belize (Fitzhugh 1983) and later identified on photophilic algae in the Adriatic Sea (Licciano and Giangrande 2006).

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

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

Tube building

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

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

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

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

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

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

Biology and behavior

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

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

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

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

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

Symbiosis

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

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

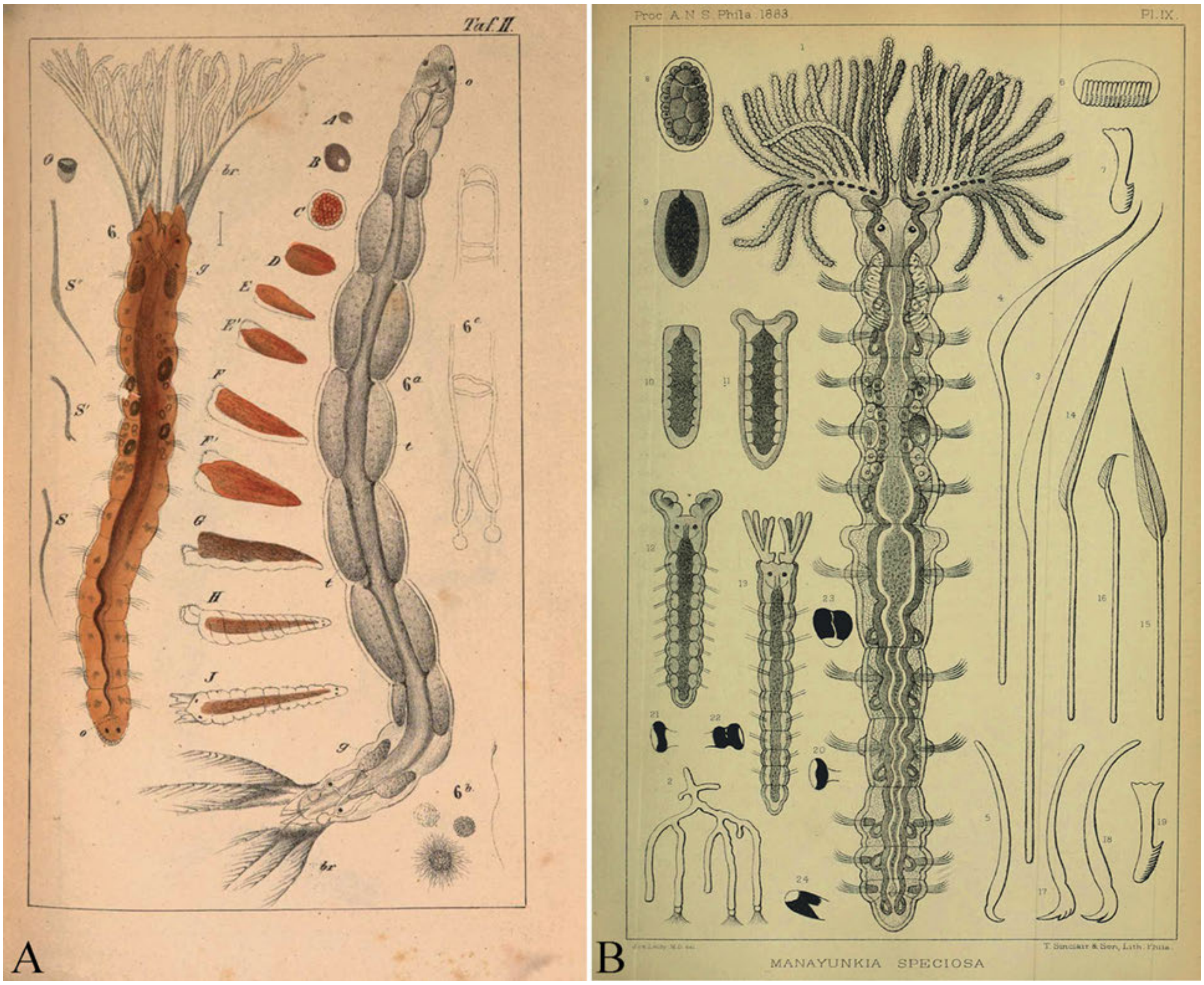

Fig. 7.4.8.11: Original plates of the morphology and development of the first described species of Fabriciidae from the nineteenth century. A, B, figures 14–24, *Fabricia stellaris* (Müller, 1774); B, figures 1–13, *Manayunkia speciosa* Leidy, 1858. Both original plates show the external and internal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

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

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

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

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

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

Phylogeny and taxonomy

Taxonomic history

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

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

All fabriciid species have long been included within Sabellidae Latreille, 1825 based on the shared presence of a radiolar crown on a reduced prostomium, a thorax region with notopodial chaetae and neuropodial uncini, and an abdominal region with neuropodial chaetae and notopodia uncini. The tube of fabriciids is usually formed from mucus combined with mud or sand, as also observed in all Sabellidae, whereas nearly all species of Serpulidae, the sister taxon, inhabit calcareous tubes. Rioja (1923) established the subfamily Fabriciinae based on the presence of thoracic acicular uncini in several genera of Sabellidae.

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

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

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

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

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

Phylogeny

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

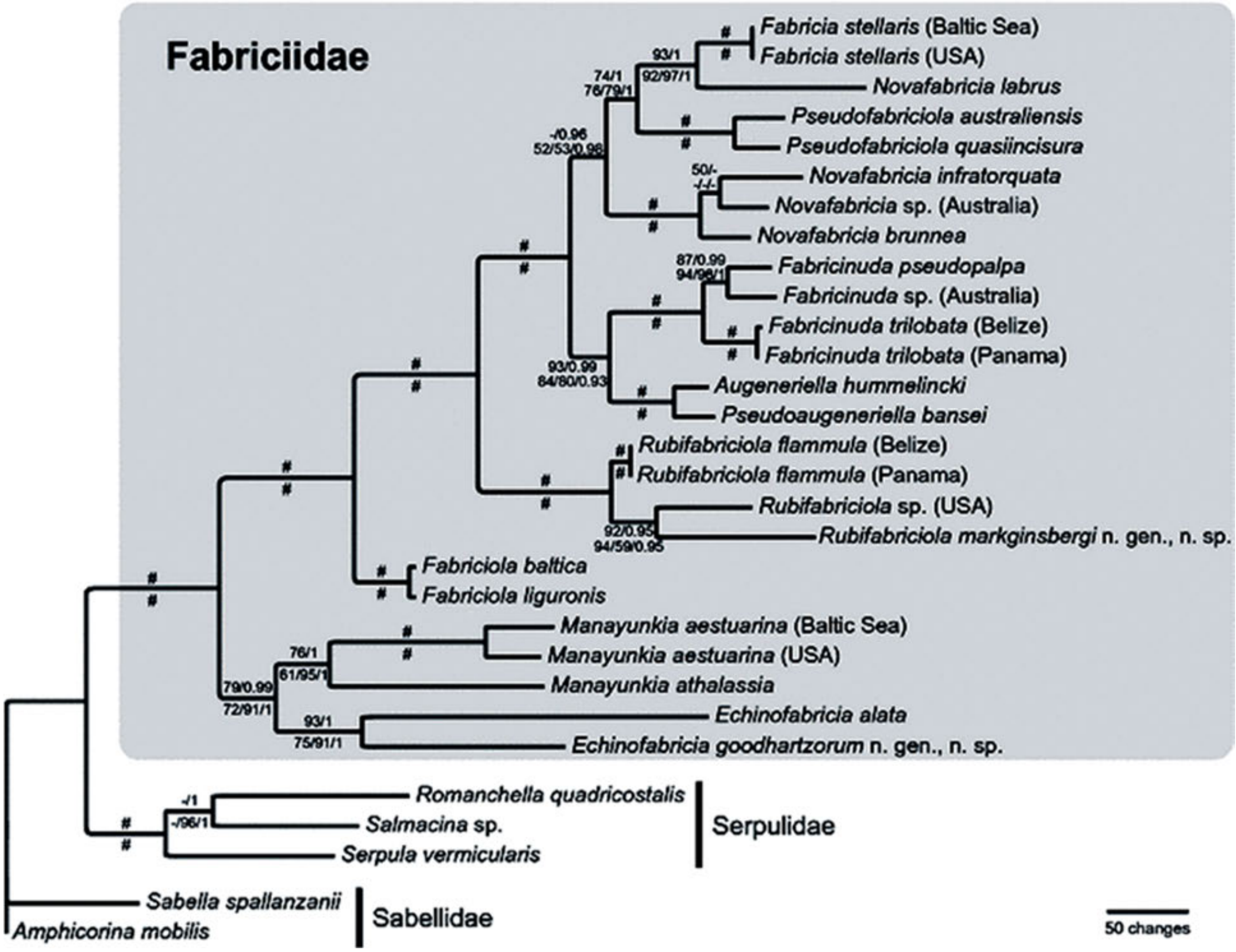

Fig. 7.4.8.13: Most parsimonious (MP) tree from analysis of combined molecular and morphological data. Numbers adjacent to branches are support values from various analyses. Those above are from the combined data analyses (MP jack-knife ≥50 followed by Bayesian posterior probability ≥0.9), whereas the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

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

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

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

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

In any case, the distribution of species and genera suggests that Fabriciidae is a very ancient polychaete taxon widespread in the oceans of the Palaeozoic or Mesozoic at least 250 to 200 million years b.p. [However, fossils attributed to spirorbids (Serpulidae) are known from as early as the Ordovician (505–438 million years b.p.) (Knight-Jones 1981).] With the development of the branchial crown with radioles and pinnules in Sabellidae and Serpulidae (see External morphology section), highly specialized filter feeders developed, which displaced the less specialized and less competitive fabriciids. At present, fabriciids are mainly found in habitats with low species numbers. Therefore, their occurrence in tidal zones under different stress conditions may not be a common character within Fabriciidae but may be the result of low competitiveness.

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

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

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

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

Fabriciidae Rioja, 1923

Type genus: *Fabricia* Blainville, 1828.

About 80 species.

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

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

Distribution: Marine, brackish, and freshwater benthic ecosystems; from intertidal to deep sea; worldwide.

Augeneriella Banse, 1957

Type species: *Augeneriella hummelincki* Banse, 1957, by monotypy.

6 species.

Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages present, vascularized, dichotomously branched, nonciliated; dorsal lips erect, well developed. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a low ridge laterally and dorsally; a rounded, conical lobe ventrally; annulation between anterior and posterior peristomial rings distinct all around, except middorsally. Inferior thoracic notochaetae on chaetigers 2 and 8, sometimes on chaetiger 7, elongated, narrowly hooded and on chaetigers 3 to 7 or 3 to 6 pseudospatulate; thoracic uncini with single large tooth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about same length and width as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 4 to 8.

Distribution: Caribbean Sea; Mediterranean Sea; Indian Ocean: Mozambique, Picard Island; South Australia (Day 1957, Gitay 1970, Hartmann-Schröder 1986, Fitzhugh 1990e, 1991a).

Bansella Fitzhugh, 2010

Type species: *Fabricia oregonica* Banse, 1956, by subsequent designation.

1 species.

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

Distribution: Pacific Ocean: Oregon (Banse 1956, 1979, Hobson and Banse 1981, Fitzhugh 2010).

Brandtika Jones, 1974

Type species: *Brandtika asiatica* Jones, 1974, by original designation.

1 species (plus another undescribed species).

Diagnosis: Eight thoracic and two abdominal chaetigers. Anterior peristomial ring collar present; margin entire but with deep middorsal incision; annulation between anterior and posterior peristomial rings distinct. Inferior thoracic notochaetae on chaetigers 2 to 8 pseudospatulate; thoracic uncini on chaetigers 2 to 5 with single large tooth slightly offset over main fang followed by a series of smaller teeth; on chaetigers 6 to 8, short and geniculated (sharply bent) chaetae with pilose end (transitional chaetae) replaced the thoracic uncini; abdominal uncini with a single, proximal large central tooth surmounted distally by rows of equal-sized teeth.

Remarks: Characters of the radiolar crown are unknown due to the dried condition of the collected specimens (Jones 1974).

Distribution: Southeast Asia: Laos, Mekong River; Thailand, Salween River; Burma, Thoungyin River (Jones 1974).

Brifacia Fitzhugh, 1998

Type species: *Brifacia metastellaris* Fitzhugh, 1998, by original designation.

2 species.

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

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

Echinofabricia Huang, Fitzhugh & Rouse, 2011

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

Fabricia Blainville, 1828

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

Fabricinuda Fitzhugh, 1990

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

Fabriciola Friedrich, 1939

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

nonvascularized, unbranched, slender; dorsal lips well developed, distal end rounded. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a low membranous collar, except for middorsal gap; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct dorsally. Inferior thoracic notochaetae on all chaetigers short, narrowly hooded; thoracic uncini with two or three larger teeth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium at least twice as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8 or 4 to 8.
Distribution: North Atlantic Ocean: Baltic Sea, Maine; White Sea; Barents Sea; Pacific Ocean: Commander Islands, Papua New Guinea; Caribbean Sea: Belize; India, Chilka Lake (Southern 1921, Annenkova 1934, Friedrich 1939, Fitzhugh 1990c, Rouse 1993, 1996a, Sarma et al. 1994, Fateev 1997, 1999).

***Manayunkia* Leidy, 1858**
Type species: *Manayunkia speciosa* Leidy, 1858, by monotypy.
10 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles asymmetrically branched, slightly wrinkled; acellular radiolar skeleton absent; unbranched vascularized ventral filamentous appendages present, slightly wrinkled; dorsal lips erect, broadly rounded. Anterior margin of anterior peristomial ring developed as a membranous collar with rectangular ventral lobe, narrowly separated middorsally. Inferior thoracic notochaetae on chaetigers 5 to 8 or 6 to 8 elongated, narrowly hooded and on chaetigers 2 to 5 or 2 to 6 pseudospatulate; thoracic uncini with one or two larger teeth above main fang followed by a series of smaller teeth, sometimes with transitional chaetae on chaetigers 6 to 8; abdominal uncini with multiple rows of equal-sized teeth, manubrium longer than dentate region. Peristomial eyes present, pygidial eyes absent. Spermiogenesis on chaetigers 6 to 8.
Remarks: Based on the description of Annenkova (1938), *M. siaukhu* does not belong to this genus, as it has pygidial eyes. Already, Zenkevitsch (1935) and Hartman (1951) assumed a synonymy of *M. polaris* with *M. aestuarina*, and Banse (1956) assumed a synonymy of *M. balticus*, described as *Haplobranchus balticus* by Karling (1933), with *M. aestuarina*.
Distribution: North Atlantic Ocean: North America; North Sea; Baltic Sea; southwest Atlantic Ocean: Brazil; Pacific Ocean: Papua New Guinea; South Australia; Caspian Sea; Lake Baikal (Leidy 1858, Bourne 1883, Nusbaum 1901a, b, Annenkova 1929, Dybowski 1929, Zenkevitsch 1935, Banse 1956, Hutchings et al. 1981, Rouse 1996a, b, Sitnikova et al. 1997).

***Monroika* Hartman, 1951**
Type species: *Manayunkia africana* Monro, 1939, by original designation.
1 species (plus another undescribed species).
Diagnosis: Eight thoracic and two abdominal chaetigers. Radioles asymmetrically branched; acellular radiolar skeleton absent; unbranched vascularized ventral filamentous appendages present; dorsal lips erect, broadly rounded. Anterior margin of anterior peristomial ring developed as a membranous collar with rectangular ventral lobe, narrowly separated middorsally. Inferior thoracic notochaetae on chaetigers 2 and 6 to 8 elongated, narrowly hooded and on chaetigers 2 to 5 pseudospatulate; thoracic uncini with one larger teeth above main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of equal-sized teeth, manubrium about twice as long as dentate region. Peristomial eyes black, pygidial eyes absent.
Remarks: A second *Monroika* species has been found in Uruguay River. This will be described elsewhere (Bick in preparation).
Distribution: West Africa, Congo River; South America, Uruguay River (Bick own unpublished data).

***Novafabricia* Fitzhugh, 1990**
Type species: *Fabriciola chilensis* Hartmann-Schröder, 1962, by original designation.
11 species.
Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages absent; dorsal lips reduced to low, narrow ridges. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring developed as low ridge laterally and dorsally and a rounded lobe ventrally; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct middorsally. Inferior thoracic notochaetae on chaetigers 2 and 6 to 8 or 7 to 8 narrowly hooded and on chaetigers 3 to 5 or 3 to 6 pseudospatulate chaetae; thoracic uncini with a single large tooth slightly offset over main fang followed by a series of smaller teeth; abdominal uncini with multiple rows of one to several teeth per row, manubrium as long as dentate region or twice as long. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 3 to 8 or 4 to 8.
Distribution: Atlantic Ocean: southwest Africa; Pacific Ocean: Australia, California, Chile, Papua New Guinea;

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

***Parafabricia* Fitzhugh, 1992**

Type species: *Parafabricia ventricingulata* Fitzhugh, 1992, by original designation.

2 species.

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

Distribution: Pacific Ocean: northwest Australia; Mediterranean Sea, Tyrrhenian Sea (Fitzhugh 1992a, b, Giangrande et al. 2014).

***Pseudoaugeneriella* Fitzhugh, 1998**

Type species: *Pseudoaugeneriella unirama* Fitzhugh, 1998, by original designation.

3 species.

Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; vascularized ventral filamentous present, slightly shorter than radioles, surface smooth or slightly wrinkled; dorsal lips low or slightly erect, broadly rounded distally or a low ridge, distinct from radioles. Anterior peristomial ring wider than long, shorter than posterior peristomial ring; anterior margin of anterior peristomial ring a low ridge laterally and dorsally; ventrally developed as an low, triangular lobe; annulation between anterior and posterior peristomial rings visible only ventrally. Inferior thoracic notochaetae on chaetigers 2 and 7 to 8 narrowly hooded and on chaetigers 3 to 6 each with two pseudospatulate chaetae; thoracic uncini with a large tooth slightly offset over main fang surmounted distally by progressively shorter teeth; abdominal uncini with multiple rows of equal-sized teeth; manubrium longer than dentate region, slightly expanded proximally. Peristomial and pygidial eyes black.

Distribution: Atlantic Ocean: Madeira, Canary, and Selvagem islands; Indian Ocean: Andaman Sea, Thailand; Pacific Ocean: Okinawa Island (Langerhans 1880, *Núñez* and Talavera 1995, Fitzhugh 1998, 1999, *Núñez* et al. 2001, Bick 2004).

***Pseudofabricia* Cantone, 1972**

Type species: *Pseudofabricia aberrans* Cantone, 1972, by monotypy.

1 species.

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

Distribution: Mediterranean Sea: Tyrrhenian and Adriatic seas (Cantone 1972, Giangrande and Cantone 1990, Fitzhugh 1995a, b).

***Pseudofabriciola* Fitzhugh, 1990**

Type species: *Pseudofabriciola incisura* Fitzhugh, 1990, by original designation.

12 species.

Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; ventral filamentous appendages unbranched, slender and vascularized, or absent; dorsal lips erect, well developed, triangular or reduced to low, narrow ridges. Anterior peristomial ring wider than long; anterior margin of anterior peristomial ring a well-developed, high, entire membranous collar; even high all around; middorsal region of collar not split along its entire length; annulations between anterior and posterior peristomial rings distinct ventrally and laterally and indistinct middorsally. Inferior thoracic notochaetae on chaetigers 2 to 8 narrowly hooded; thoracic uncini with small subequal teeth above main fang; abdominal uncini with multiple rows of equal-sized teeth, manubrium as long as dentate region. Peristomial and pygidial eyes black. Spermiogenesis on chaetigers 4 to 8.

Distribution: Mediterranean Sea: Adriatic Sea, Aegean Sea, Ionian Sea; Pacific Ocean: California, Gulf of Thailand, Papua New Guinea; South Africa; Caribbean Sea: Belize; Gulf of Mexico, Florida; Indian Ocean: Picard Island, Western Australia (Monro 1937, Day 1963, Hartmann-Schröder 1981, 1986, Giangrande and Castelli 1986, Simboura 1989, Fitzhugh 1990b, 1991a, 1996, Fitzhugh et al. 1994, 1995a, b, 2002).

Raficiba Fitzhugh, 2001

Type species: *Raficiba* Fitzhugh, 2001, by original designation.

1 species.

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

Distribution: Antarctica, Ross Sea (Fitzhugh 2001).

Rubifabriciola Huang, Fitzhugh & Rouse, 2011

Type species: *Rubifabriciola markginsbergi* Huang, Fitzhugh & Rouse, 2011, by original designation.

10 species.

Diagnosis: Eight thoracic and three abdominal chaetigers. Radioles symmetrically branched; acellular radiolar skeleton present; unbranched unvascularized ventral filamentous appendages present; dorsal lips as triangular ridges; radiolar lobes wide and short, with an even ventral margin. Anterior peristomial ring wider than long, shorter than posterior peristomial ring; anterior margin of anterior peristomial ring a low membranous collar and with middorsal gap. Inferior thoracic notochaetae elongated, narrowly hooded; thoracic uncini with several rows of progressively shorter teeth above main fang; abdominal uncini with multiple rows of equal-sized teeth, proximal end of manubrium two or more times wider than dentate region; abdominal neuropodia with pinhead chaetae (in most species). Peristomial and pygidial eyes red (persisting after fixation). Spermiogenesis on chaetigers 3 to 8 or 4 to 8.

Distribution: Caribbean Sea, Belize; South Australia; Indian Ocean: Picard Island, Phuket Island; Pacific Ocean: California, Papua New Guinea, Okinawa Island; Red Sea; Mediterranean Sea, Adriatic Sea (Banse 1956, 1959a, Hartman 1969, Fitzhugh 1990c, 1992a, 1998, 1999, Rouse 1993, 1996a, b, Giangrande and Montanaro 1999, Huang et al. 2011).

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7.7 Sedentaria: Terebellida/ Arenicolida

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

7.7.1 Pectinariidae Quatrefages, 1866

Introduction

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

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

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

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

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

Morphology

External morphology

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

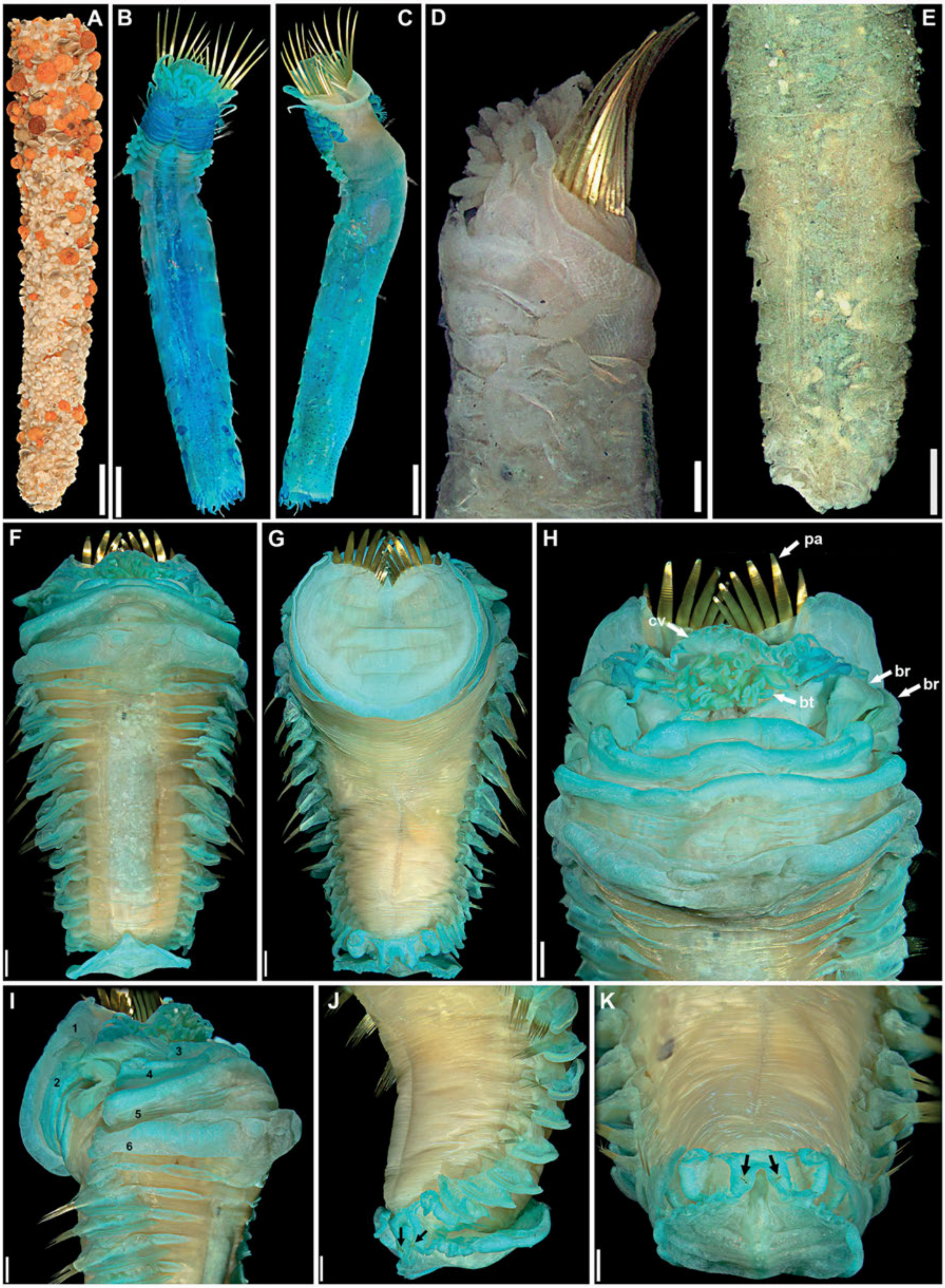

Fig. 7.7.1.1: *Petta investigatoris*: A, tube; B, C, entire worm, ventral and dorsal views, respectively, stained in methyl green. *Petta alissoni*: D, anterior end, left lateral view; E, posterior end, ventral view. *Pectinaria carnosa*, stained in methyl green: F, G, entire worm, ventral and dorsal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

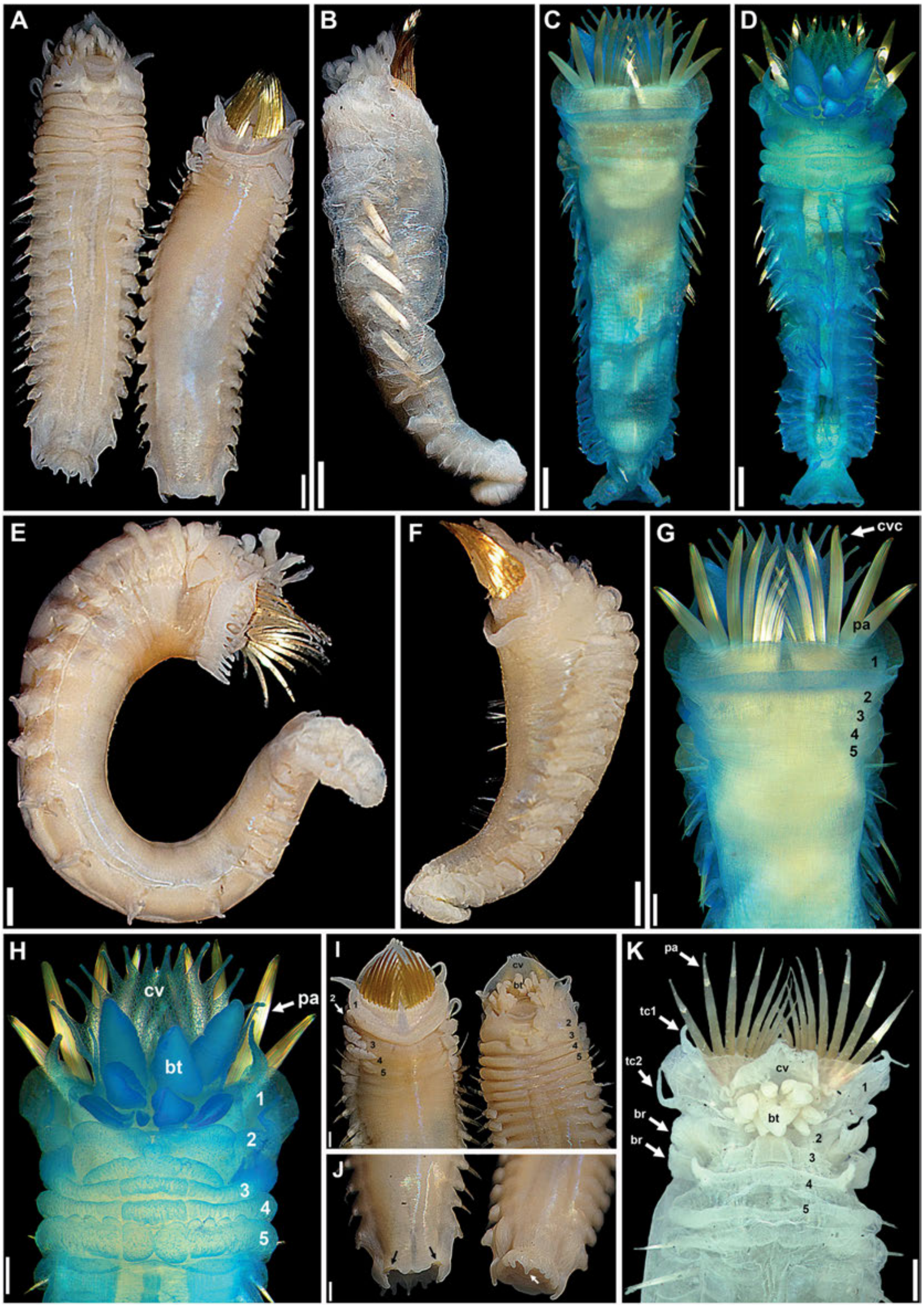

Fig. 7.7.1.2: *Petta pusilla*: A, entire worms, ventral (left) and dorsal (right) views; I, anterior end, dorsal (left) and ventral (right) views; J, posterior end, dorsal (right) and ventral (left) views. Black arrows point to scaphal hooks; white arrow points to anal flap. *Lagis koreni*: B, entire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

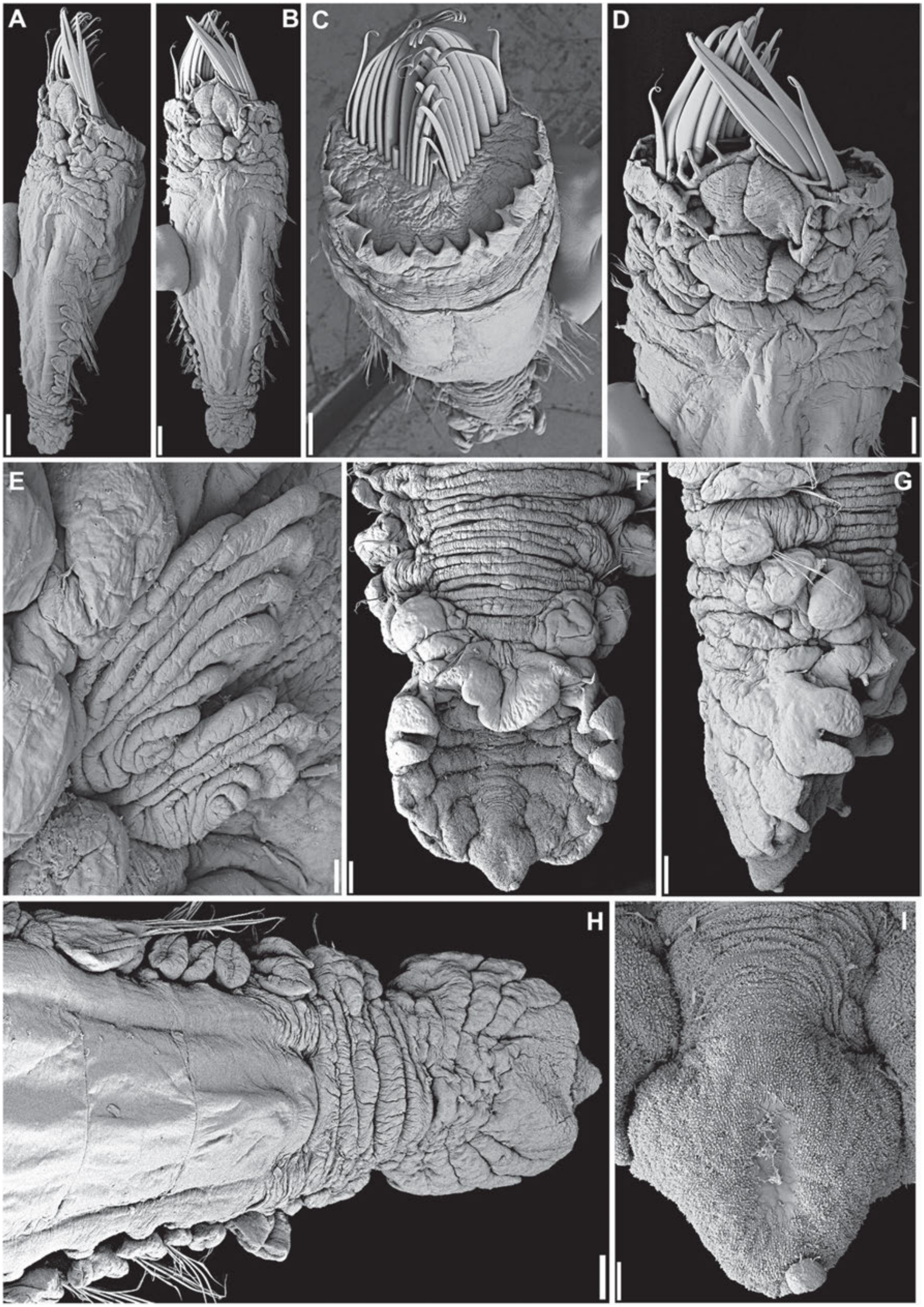

Fig. 7.7.1.3: *Amphictene lizardensis*: A, B, entire worm, left lateral and ventral views, respectively; C, D, anterior end, dorsal and ventral views, respectively; E, branchiae; F–H, posterior end, dorsal, left lateral and ventral views, respectively; I, close-up of ciliated foliaceous process of anal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

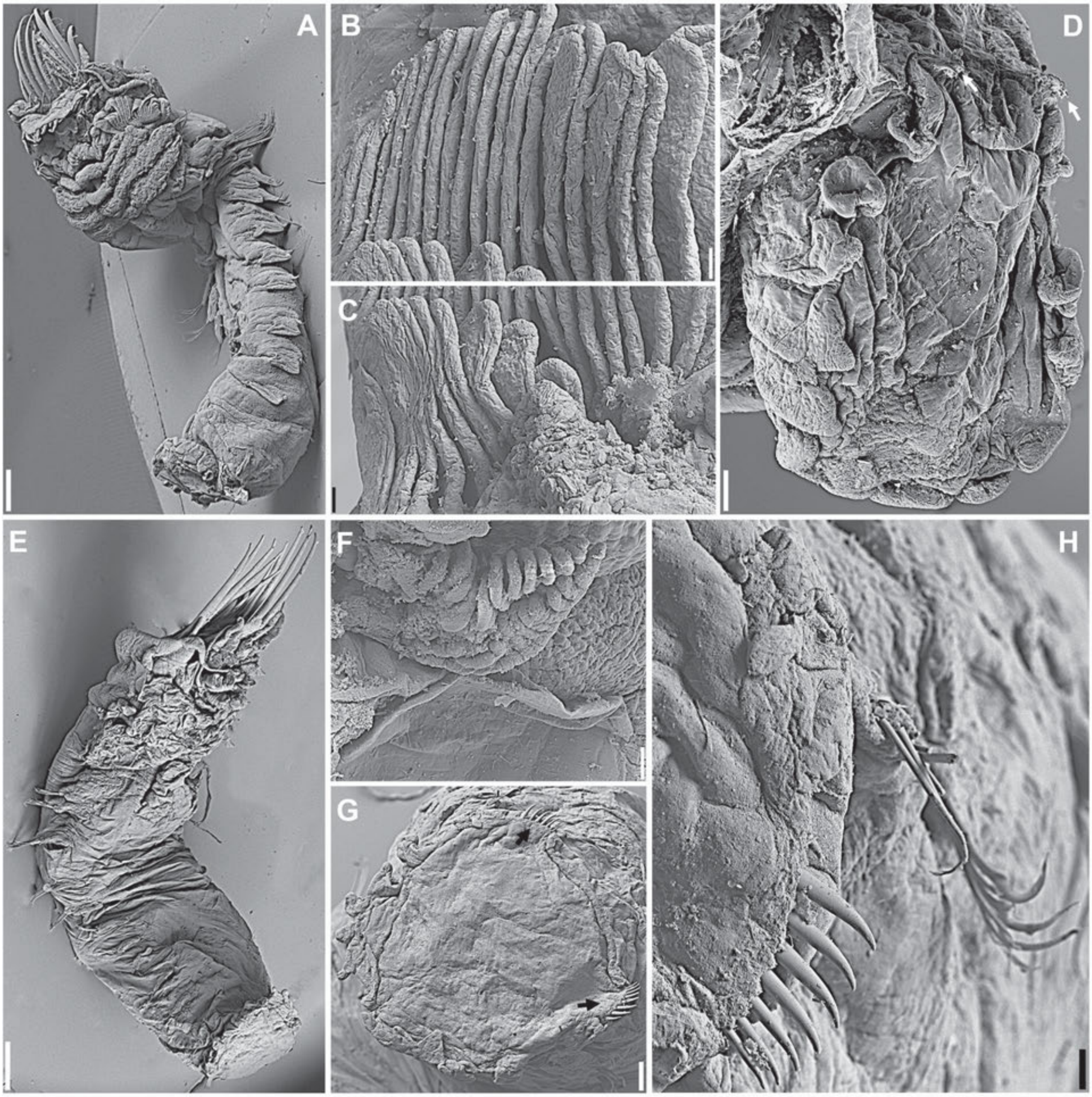

Fig. 7.7.1.4: *Pectinaria nonatoi*: A, entire worm, left ventrolateral view; B, C, branchiae; D, scaphe, dorsal view. *Petta alissoni*: E, entire worm, right ventrolateral view; F, branchiae; G, scaphe, dorsal view. Arrows point to scaphal hooks. H, last notopodium and scaphal hooks, left side of body.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

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

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