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Handbook of Zoology

A Natural History of the Phyla of the Animal Kingdom

Annelida: Polychaetes

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Sabellidae Latreille, 1825

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Introduction

Sabellidae is one of the most diverse and ubiquitous polychaete families with over 400 nominal species described to date, classified in 40 genera. They are found from fresh waters to full marine conditions, and from intertidal to abyssal depths all over the world.

Sabellids inhabit the tubes they build with secreted mucus and attached mud or sand particles. *Glomerula piloseta* (Perkins 1991) represents an exception as it builds a calcareous tube. They are able to move inside this tube, extending their radiolar crown out of it for fulfilling their feeding needs or withdraw into it for protection. The radiolar crown is a residue of the prostomium after its reduction during metamorphosis (Wilson 1936, Schroeder & Hermans 1975, Fitzhugh 1989). It is formed by numerous feathery-like appendages, responsible for these animals being commonly known as feather-duster worms. It is vascularized, allowing the gas exchange with the water, and is also provided with cilia to capture particles from the water column for feeding and tube building. Sabellids have biramous parapodia where each ramus bears either capillary chaetae or uncini. The body is divided in two regions, the thorax and the abdomen. Thoracic chaetigers bear capillary chaetae on notopodia and uncini on neuropodia, whereas abdominal chaetigers show the opposite arrangement, with uncini present on the notopodia and capillary chaetae on the neuropodia (chaetal inversion).

Sabellids generally withdraw in their tubes when disturbed, but in some small species inhabiting unstable environments (intertidal habitats, fluctuating estuarine conditions or under strong currents where tubes are detached from the substrate) the worms are able to leave the tubes and build a new one fairly quickly (e.g., Bonar 1972). Some larger species, with slower tube building processes, can live permanently in the same tube (Fitzsimons 1965), but still have the capability of rebuilding a new tube if excessively agitated or removed from old one (Nicol 1930, Fitzsimons 1965, Licciano et al. 2012, Murray et al. 2013, pers. obs.).

Some species are capable of boring into calcium carbonate of shells and are considered as parasites of marine and fresh water mollusks or active bioeroders of coral reefs (e. g., Goldberg 1913, Jones 1974, Chughtai & Knight-Jones 1988, Culver et al. 1997, Fitzhugh & Rouse 1999). Several species have been unintentionally translocated on ships hulls, in ballast water or associated to mariculture species cultivated outside of the natural distribution range, generating in some cases ecological and economic negative impacts in the arrival localities (e. g., Clapin & Evans 1995, Patti & Gambi 2001, Tovar-Hernández et al. 2009a, b, Read et al. 2011, Capa et al. 2013a).

Although there have been several attempts of generating phylogenetic hypothesis about their relationships with other polychaetes and within the group, results are still not fully stable and resolved. It is mostly accepted that the Sabellidae does not include the previously considered subfamily Fabriciinae (Kupriyanova & Rouse 2008, Capa et al. 2011a) and some groups of genera form well established clades (e. g., Fitzhugh 1989, 2003, Rouse & Fitzhugh 1994, Fitzhugh & Rouse 1999, Capa 2007, 2008, Capa et al. 2011a), but further effort is still required to resolve the sabellid phylogeny.

Due to lack of hard body parts or solid tubes, sabellids have not left fossil records besides a few exceptions. Only members attributed to the genus *Glomerula* Nielsen, 1931, with calcium carbonate tubes, have been found from the Hettangian (around 200 Million years ago) to the Recent, most common and geographically widespread from the Upper Toarcian until the Eocene (Kočí 2012). In fact, calcification in Sabellidae had apparently originated in the early Mesozoic and tube ultrastructure has remained unchanged since then (Vinn et al. 2008).

Morphology

External morphology

Sabellids are tube dwelling annelids that project an often colourful radiolar crown (= branchial crown) (Fig. 1A-D) out of their tubes (Fig. 1A). *Sabella spallanzanii* (Gmelin 1791) can reach up to 40 cm in length (Knight-Jones & Perkins 1998), but species of *Amphicorina* Claparède 1864, *Amphiglana* Claparède 1864 (Fig. 1E) or *Desdemona* Banse, 1957 (Fig. 1F, G) do not grow over 4 mm (Hutchings & Murray 1984, Giangrande et al. 1999, Capa & Rouse 2007). The length of the tubes often reaches twice the length of the worms.

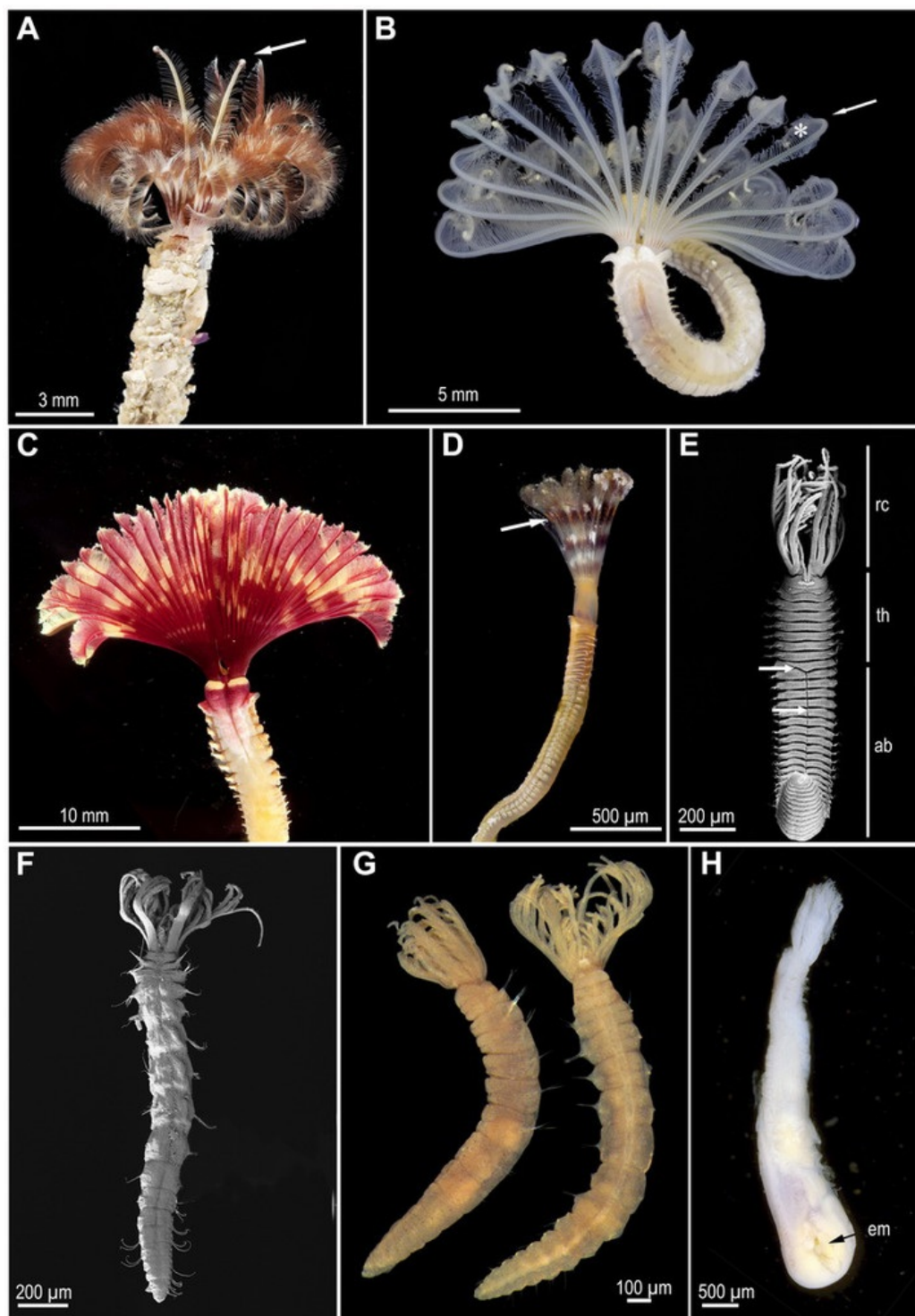


Fig. 1

General morphology of members of Sabellidae. A, *Megalomma* sp. from Australia, within its tube, embedded with sand grains, showing two distal compound radiolar eyes sticking out of the radiolar crown (arrow); B, *Parasabella* sp. from Australia, dorsal view with opened radiolar crown showing the radioles (arrow) and pinnules (asterisk); C, *Bispira porifera* from Australia, dorsal view, showing the characteristic spongy cushion outgrowth in anterior thoracic chaetigers; D, *Notaulax* sp. from Australia, lateral view, with groups of orange radiolar eyespots (arrow); E, *Amphiglana nishi* from Japan, ventral view (arrow points to faecal groove), showing different body regions; F, *Desdemona ornata* from Australia, dorsal view; G, *Desdemona aniara* from Australia, lateral and ventral views, respectively; H, *Caobangia* sp. from Vietnam. - em embryos, rc radiolar crown, th thorax, ab abdomen. A-D, life specimens; E-F, SEM photographs; G-H, light microscopy photographs of preserved material. Images by A-B, D, A. Semevov; C, E, H, M. Capa; F-G, E. Wong.

In members of Sabellidae, the prostomium and peristomium are fused and highly modified due to the presence of the characteristic radiolar crown, which is homologous to the palps of other polychaetes (Orrhage 1980). The radiolar crown is provided with a base formed by two generally semi-circular radiolar lobes (surrounding the mouth and that are fused dorsally) and distal anterior projections known as the radioles (Figs. 1A-H, 2A-D). The radioles bear two longitudinal rows of small ciliated pinnules on their inner edges (Figs. 1A-B, 2A-D). Moreover, in members of *Branchiomma* Kölliker, 1858, radioles also bear

paired appendages along the outer edge, known as stylodes (Fig. 3D), which are considered as an autapomorphy for the genus. The radiolar crown, similarly present in Fabriciidae Rioja 1923 and Serpulidae Rafinesque 1818, shows some differences on its internal morphology among members of these three families (Fitzhugh 1989, 1991, Rouse & Fitzhugh 1994, Fitzhugh & Rouse 1999, Cochrane 2003, Capa et al. 2011b). The ventral edge of the radiolar lobes can grow resulting in spiral crowns like in some members of *Bispira* Krøyer, 1856, *Sabella* Linnaeus, 1767, and *Sabellastarte* Krøyer, 1856 (Knight-Jones & Perkins 1998, Knight-Jones & Mackie 2003, Capa 2008, Capa et al. 2010, Fig. 3A). Some sabellids have a membrane joining the radioles at their bases, named as the basal membrane (= radiolar membrane or palmate membrane) (Figs. 3B, 4A). The condition of its maximum development is shown in *Myxicola* Renier in Meneghini, 1847. The basal membrane can continue as a narrow sheath of tissue on both lateral sides of the radioles, the radiolar flanges (Figs. 3C, 4E-F), or as dorsal and/or ventral extensions at the base of crown, in between radiolar lobes, the dorsal and ventral radiolar basal flanges (Fig. 4B) (Perkins 1984, Capa 2008, Capa et al. 2011b). External margins of radioles can be quadrangular (Fig. 4C), or rounded (Fig. 4D) (e. g., Fitzhugh 1989; Capa 2007). Radiolar rachis is generally smooth, but in some species of *Branchiommata*, such as *B. nigromaculatum* (Baird 1865) and, at least, Brazilian specimens of *B. luctuosum*, it has a segmented appearance due to regular obtuse indentations (Nogueira et al. 2006, Tovar-Hernández & Knight-Jones 2006).

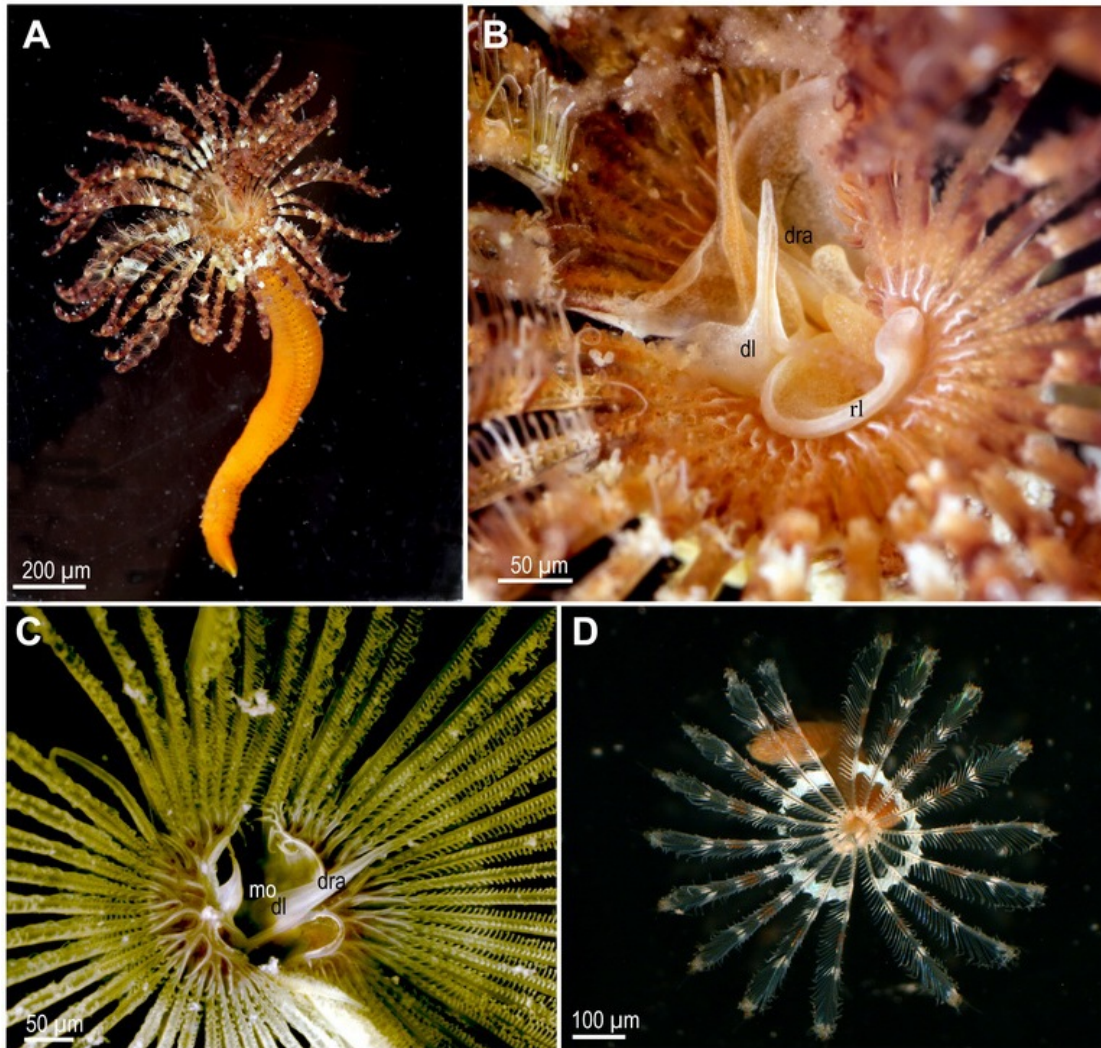


Fig. 2

Opened radiolar crowns showing associated structures. A, *Branchiommata* sp. from Australia with naturally opened radiolar crown; B, Detail of the radiolar crown's internal structures, including radiolar lobes, dorsal lips and dorsal radiolar appendages, same specimen; C, *Bispira porifera* from Australia, base of radioles, each with a double longitudinal row of pinnules, dorsal lips and radiolar appendages; D, Opened radiolar crown and internal structures, *Notaulax* sp. from Australia. - dl dorsal lip, dra dorsal radiolar appendages, mo mouth, rl radiolar lobe. A-D, life specimens. Images by: A-B, A. Semenov; C-D, M. Capa.

Several other structures associated with the radiolar crown are the dorsal and ventral lips (Fig. 2B-D), the parallel lamellae and ventral sacs (Fig. 3E-G), the dorsal and ventral radiolar appendages, and the pinnular appendages of the dorsal lips. The dorsal lips are ciliated lappets on the dorsal edge of the mouth, in some cases fused to a modified radiole, called dorsal radiolar appendage. Dorsal lips are considered as extensions of the dorsal margins of the radiolar lobes (Banse 1956, 1957, Fitzhugh 1989, Figs. 2B-D, 3H). The ventral lips are also lappets that extend from the ventral margin of the radiolar lobes towards the dorsal lips (Nicol 1931, Perkins 1984, Fitzhugh 1989) with the exception of *Myxicola*, where dorsal lips are surrounded by the ventral lips (Fitzhugh 2003). Many sabellids present ventral extensions of the ventral lips, the parallel lamellae, continuing towards the collar ventral incision and terminating by a pair of ventral sacs, where sediment for tube building is stored (Nicol 1931, Perkins 1984, Fitzhugh 1989). Ventral radiolar appendages are present in several genera, such as *Amphicorina*, *Chone* Krøyer, 1856, *Euchone* Malmgren, 1866 and *Jasmineira* Langerhans, 1880; these structures are considered as reduced radioles (Fitzhugh 1989, Tovar-Hernández 2008, Capa et al. 2011a, b). A remarkable organ recently found in some *Megalomma* species is the caruncle, a prostomial projection placed dorsally above the mouth, between the dorsal lips, supported with vacuolated skeletal cells and innervated directly from the cerebral ganglion (Tovar-Hernández & Salazar-Vallejo 2008, Tovar-Hernández & Carrera-Parra 2011, Fig. 4G, H).

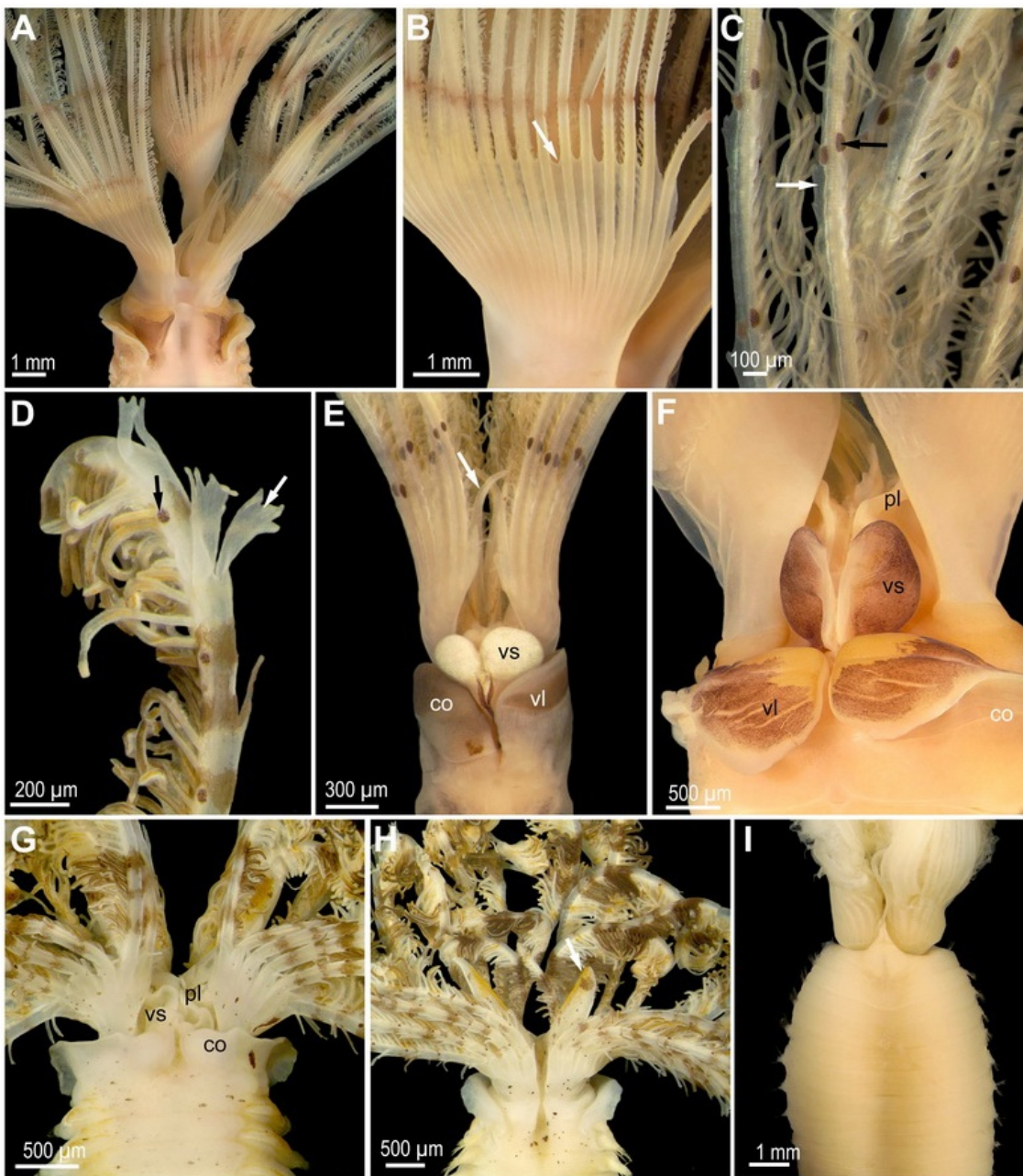


Fig. 3

Radiolar crown and associated structures. A, Radiolar crown with right radiolar lobe spirals, dorsal view, *Sabella spallanzanii* from Australia; B, Basal membrane joining radioles (arrow), same species; C, Radioles with radiolar flanges (white arrow) and paired compound eyes (black arrow), *Bispira serrata* from Australia; D, Radioles with stylodes (white arrow) and paired compound eyes (black arrow), *Branchiomma bairdi* from Australia; E, Base of radiolar crown with incipient growing radioles (white arrow), ventral sacs and collar ventral lappets, *Bispira serrata* from Australia; F, Detail of base of radiolar crown, ventral view, showing ventral sacs, parallel lamellae and folded collar ventral lappets, *Sabella spallanzanii* from Australia; G, Base of radiolar crown and anterior thoracic segments, ventral view, showing peristomial collar, ventral sacs and parallel lamellae, *Branchiomma bairdi* from Australia; H, Same, dorsal view, with dorsal lips and dorsal radiolar appendages (white arrow); I, Base of radiolar crown and anterior thoracic segments, ventral view, *Myxicola infundibulum* from Australia. - co collar, pl parallel lamellae, vs ventral sacs, vl ventral lappets. A-I, Light microscopy photographs. Images by: A-I, E. Wong.

Sabellids have a two-ring peristomium. The anterior ring and its associated ventral lobe can be reduced in some taxa (Fitzhugh 1989). The posterior ring is often provided with a membranous collar with a variable degree of development (Figs. 3G, 4B, G), but the collar is absent in some taxa (Fig. 3I). The dorsal margins of this collar can be widely separated (Fig. 3H), fused to the faecal groove (Fig. 4B), or form a continuous structure dorsally (Fig. 4A-B). Collar dorsal margins can be as long as the rest of collar (Fig. 4B) or developed as dorsal lappets (Fig. 4C), and they can form pockets at either side of faecal groove (Fig. 4C, G). Mid-ventral and latero-dorsal incisions of the posterior peristomial ring collar may be present in some species, the presence of the former one creates more or less developed ventral lappets (e. g., Fig. 3E, F).

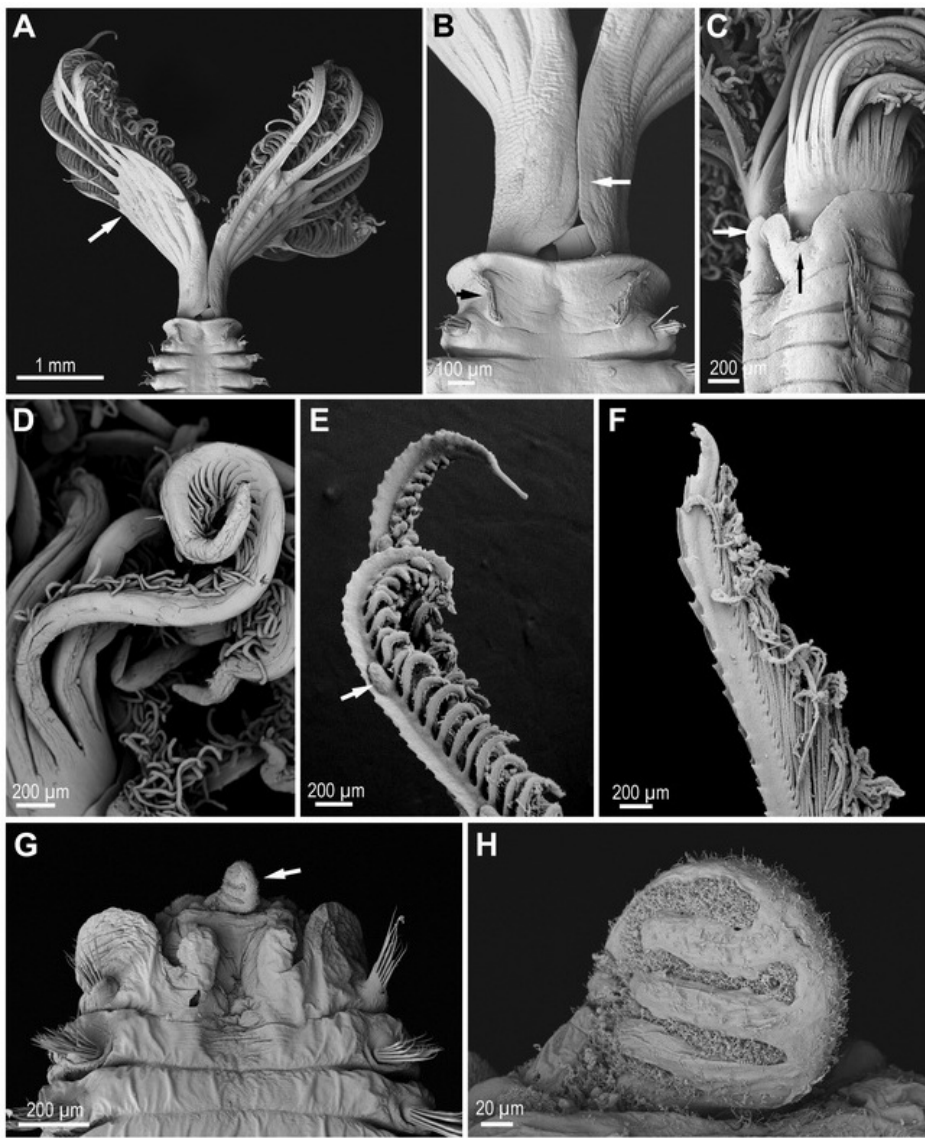


Fig. 4

Radiolar crown and caruncle. A, Radiolar crown with radioles joined by a well developed basal membrane (arrow) and anterior chaetigers, dorsal view, *Notaulax* sp. from Australia; B, Detail of base of radiolar crown showing dorsal radiolar flanges (arrow) and collar chaetae with oblique arrangement (black arrow), same specimen; C, Junction of thorax and radiolar crown, showing well developed dorsal margins of collar (arrow) and collar "pockets" (black arrow), *Megalomma* cf. *acrophthalmos* from Australia; D, Radioles with rounded and smooth edges, *Parasabella* sp. from Australia; E, Radiole with serrated radiolar flanges and compound eyes (arrow), *Bispira serrata* from Australia; F, Radiole with serrated radiolar flanges, without eyes, *Stylomma juani* from Australia; G, Anterior thoracic segments with detached radiolar crown, showing a caruncle (arrow), *Megalomma* sp. from Australia; H, Detail of caruncle with four transverse ciliated rows, same specimen. A-H, Scanning electron micrographs. Images by: A-H, M. Capa.

The body is divided in two regions, the thorax, consisting typically of eight chaetigers. There are, however, some species showing a different pattern, being the most remarkable exception *Anamobaea* Krøyer, 1856 with remarkably long thorax consisting in 32–74 segments. In turn, shorter thoracic regions can be found in species with asexual reproduction, as explained below. The number of abdominal chaetigers generally varies between and within species except for some species of *Amphicorina*, *Desdemonia* and *Terebrasabella* Fitzhugh & Rouse, 1999 with fixed number of segments. The boundary between thorax and abdomen is clearly distinct by the chaetal inversion and the shift of the position of the faecal groove. The chaetal inversion refers to the condition where thoracic notopodia have capillary chaetae (long slender bristles gradually tapering to a fine tip) and the neuropodia bear uncini (stout-handled simple chaetae generally curved and distally toothed), but the opposite condition is found in abdominal segments, which bear notopodial uncini and neuropodial capillary chaetae (Fig. 5A). The inversion of the faecal groove is the deviation of this ciliated path from the ventral midline in the abdomen, running along the side between the first abdominal neuropodia and last thoracic notopodia and continuing along the dorsal midline along the thorax (Figs. 1E, 5A). Both chaetal and faecal groove inversions are features shared by all members of Sabellidae, Fabriciidae and Serpulidae and unique among annelids (Kieselbach & Hausen 2008, Capa et al. 2011a).

Ventral shields are spongy cushions composed by glandular columnar epithelium present mid ventrally (Fig. 5A, C, E) (Evenkamp 1931, Tovar-Hernández & Sosa-Rodríguez 2006). In each thoracic chaetiger shields are entire whereas in abdominal segments, shields are longitudinal divided in two by faecal groove.

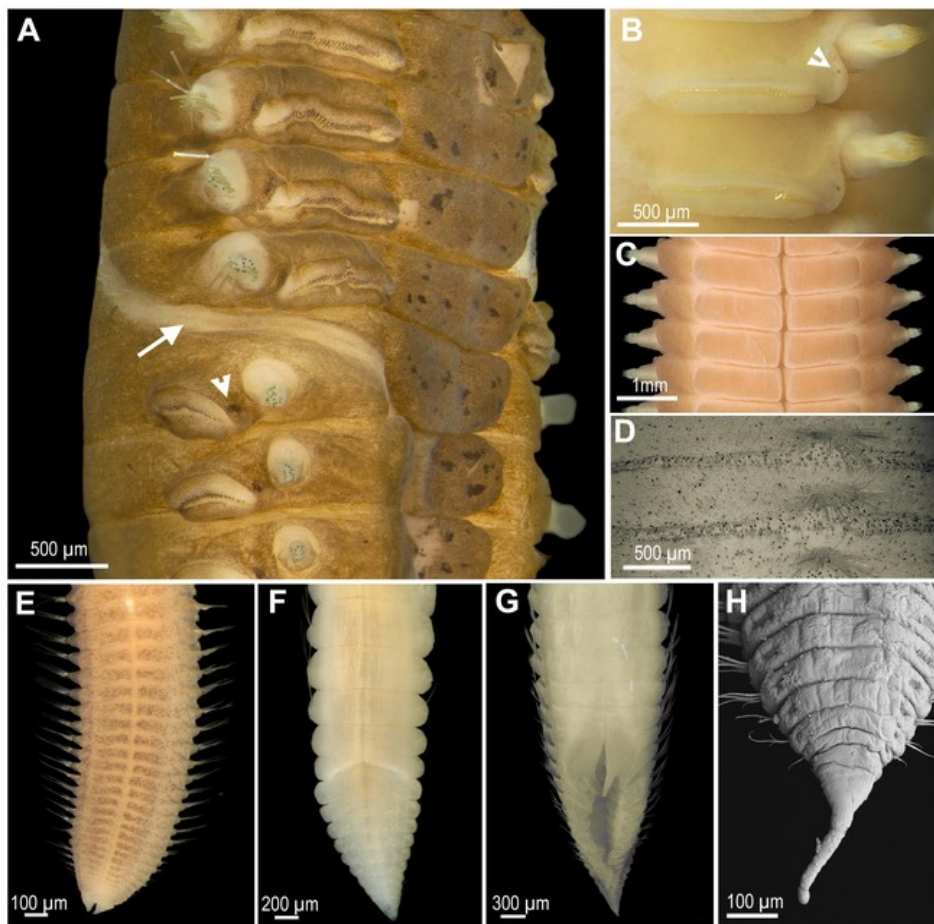


Fig. 5

Thoracic and abdominal segments and pygidia. A, Posterior thoracic and anterior abdominal chaetigers, lateral view, showing the faecal groove running between body regions (arrow) and inter-ramal eyespots (arrowhead), *Branchiomma bairdi* from Australia; B, Abdominal parapodia, ventral view, *Bispira porifera* from Australia (arrowhead, interramal eyes); C, Abdominal chaetigers with conspicuous ventral shields divided by the longitudinal faecal groove, *Sabella spallanzanii* from Australia; D, Thoracic parapodia, *Myxicola infundibulum* from Australia, lateral view; E, Posterior abdominal segments and pygidium, ventral view, *Bispira serrata* from Australia; F, Posterior abdominal segments showing pre-pygidial depression and pygidium, dorsal view, *Euchone limnicola* from Australia; G, Posterior abdominal segments showing with pre-pygidial depression and lateral wings, dorsal view, *Euchone variabilis* from Australia; H, Posterior abdominal segments and pygidium provided with pygidial cirrus, ventral view, *Jasmineira* sp. from Australia. A-G, micrographs; H, scanning electron micrograph. Images by: A-G, E. Wong; H, M. Capa.

As mentioned above, sabellids have biramous parapodia, with the exception of the first chaetiger that only bears chaetae in the notopodia, known as the collar chaetae. Rami bearing capillary chaetae show a variety of shapes, such as well-developed conical lobes, transverse ridges, or inconspicuous rami, where chaetae appear to protrude directly from body wall (Figs. 5B, D, 6A, C-F). Rami bearing uncini are more or less conspicuous transverse ridges, often referred to as tori, and show more uniformity between taxa and body regions. Thoracic and abdominal capillary chaetal fascicles generally present two groups of chaetae, originated in independent formation sites (Kryvi 1989, Kieselbach & Hausen 2008, Fig. 6A, C-F). In some cases one of the groups may be absent. Both groups may show similar or different chaetal morphologies (Fitzhugh 1989, Capa et al. 2011a). In the abdominal region, the chaetae are generally arranged in transverse rows (anterior and posterior) protruding from conical tori or ridges (Fig. 6F). Exceptions are the *Branchiomma-Sabellastarte* clade (Capa 2008), with well-developed conical neuropodia with chaetae of the anterior group in a C-shape to spiral arrangement, and chaetae of posterior group enclosed in this arc (Fig. 5A-C) and *Myxicola* with chaetae protruding directly from the body wall in irregular bundles (Fig. 5D).

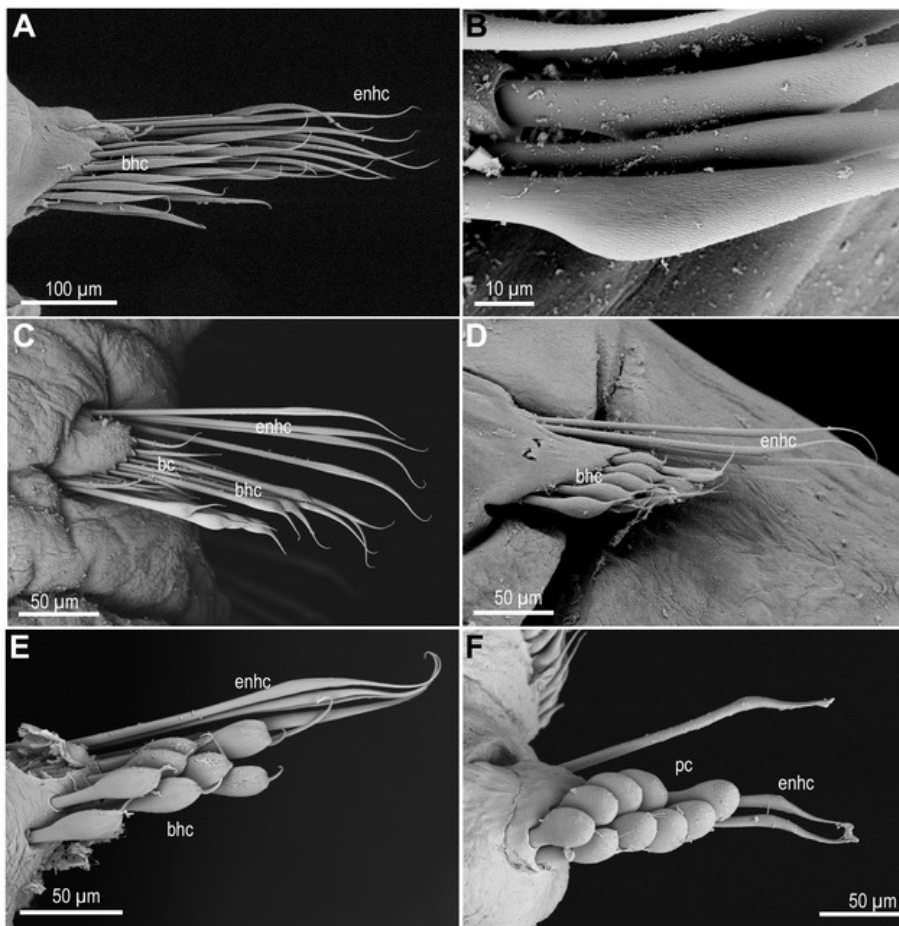


Fig. 6

Thoracic capillary chaetae. A, Superior thoracic chaetae elongate narrowly hooded, inferior broadly hooded, *Parasabella* sp. from Australia; B, Inferior thoracic chaetae, spine-like (narrowly hooded), *Bispira* sp. from Australia; C, Superior thoracic chaetae, elongate narrowly hooded, inferior broadly hooded, bayonet chaetae, *Jasmineira* sp. from Australia; D, Superior thoracic chaetae elongate narrowly hooded, inferior broadly hooded, *Parasabella* sp. from Australia; E, Broadly hooded chaetae, *Amphiglena bondi* from Australia; F, Superior thoracic chaetae elongate narrowly hooded, inferior paleate, *Notaulax* sp. from Australia. - bc bayonet chaetae, nhc narrowly hooded chaetae, bhc broadly hooded chaetae, pc paleate chaetae. A-F, Scanning electron micrographs. Images by A-F, M. Capa.

Sabellid capillary chaetae, like those present in some other polychaetes, are not simple cylindrical or tapering bristles. Instead, they show a midlength enlargement that narrows progressively towards the distal tip, sometimes resembling a thin arrow tip. They have commonly been referred to as winged or limbed capillary chaetae although detailed studies showed that there is no such limbation (Perkins 1984, Kryvi & Sørvig 1990, Hausen 2005). The emergent part of the chaetae is composed of a core with tightly packed, narrow rods or canals, continuation of the shaft from the proximal part of the chaetae, surrounded distally by a hood composed of a thin layer of loosely packed microtubules and a series of irregular lacunar spaces in between the shaft and the hood (Perkins 1984, Kryvi & Sørvig 1990, e.g., Fig. 7B, C). Chaetal terminology, according to their shape and ultrastructure, has been reviewed (see Perkins 1984, Fitzhugh 1989, Capa et al. 2011a for details). Chaetae with a hood visible on both sides of the shaft are termed broadly hooded (Perkins 1984, Fitzhugh 1989, Knight-Jones & Perkins 1998, Capa et al. 2011a, Figs. 6A, C-E, 7C). Paleate chaetae resemble externally the broadly hooded chaetae but they lack a shaft running inside the distal hood, generally observed under the compound microscope (Perkins 1984, Fitzhugh 1989, Knight-Jones & Perkins 1998, Capa et al. 2011a, Figs. 6F, 7A, B). Chaetae with a narrow hood only on one side of the shaft, perceptible under the compound microscope have been defined as narrowly hooded (Figs. 6A, C-F, 7D-E). When the hood is observed on one side of the shaft but it is wide, such as those present the collar chaetae or *Notaulax* and *Anamobaea* or the inferior row in the *Branchiomma-Sabellastarte* clade, chaetae have been referred to as spine-like chaetae (Perkins 1984, Knight-Jones & Perkins 1998, Capa et al. 2011a, Figs. 6B, 7D). Other subtypes of narrowly hooded chaetae, as defined by Perkins (1984) and Fitzhugh (1989), are referred to as elongate or modified, elongate narrowly hooded chaetae depending on their proportions, terms that not often have been followed in subsequent studies. Members of some genera, such as *Amphicorina*, *Jasmineira*, *Chone*, and *Euchone*, possess a tier of small chaetae parallel to the inferior thoracic chaetae, with a thin hood and termed bayonet chaetae (Fitzhugh 1989, Capa et al. 2011a, Fig. 6C).

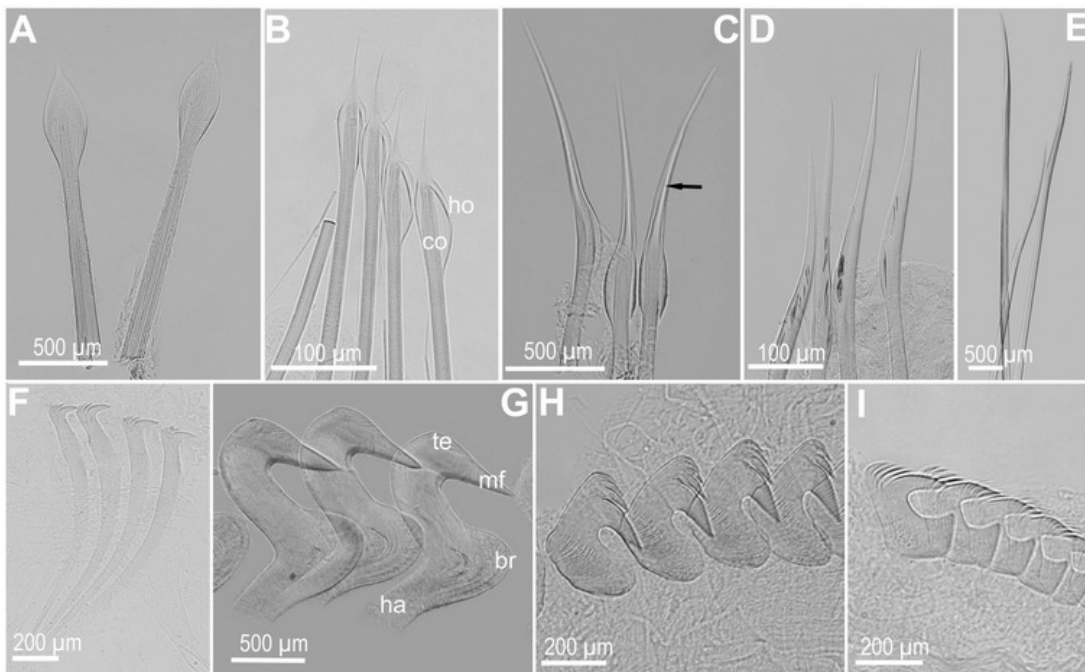


Fig. 7

Capillary chaetae and uncini. A, Paleate chaetae, first chaetiger, *Laonome triangularis* from Australia; B, Paleate, mid thoracic chaetae, *Euchone limnicola* from Australia (core absent in tip of the hood); C, Broadly hooded, anterior abdominal chaetae, *L. triangularis* (core present in tip of hood, arrow); D, Spine-like (narrowly hooded), inferior thoracic chaetae, *Sabellastarte australiensis* from Australia; E, Elongated narrowly hooded, superior thoracic chaetae, same species; F, Acicular uncini from thoracic segments, with well developed handles and narrow breasts, *Euchone limnicola*; G, Avicular uncini from abdominal segments, with well developed handles and breasts, *S. australiensis*; H, Avicular uncini from thoracic segments lacking handles, *L. triangularis*; I, Uncini with squared breasts and reduced handle, abdominal segments, *Euchone variabilis* from Australia. - br breast, co core, ha handle, ho hood, mf main fang, te distal teeth. A-I, Compound microscopic photographs. Images by: A-I, E. Won.

Sabellids uncini (= hooks) are arranged side by side forming a transverse line embedded in the tori, with the dentate distal end directed anteriorly (Fig. 6E). These uncini have a well-developed main fang (= rostrum) on their distal end, usually surmounted by a series of smaller teeth (= capitium) generally arranged in an imbricated pattern (Figs. 7F-I, 8A-C). The proximal end, known as handle (= shaft), varies greatly in length among taxa. It is secondarily reduced in *Laonome* Malmgren, 1866 (Fig. 7H) and also in the abdominal uncini of *Chone*, *Dialychone* Claparède 1870, *Paradialychone* Tovar-Hernández, 2008, *Euchone*, and *Myxicola* (Fitzhugh 1989, Capa et al. 2011a, Fig. 7I). Handles can be straight or gently curved (acicular, Fig. 7F) or bent in a z-shape (avicular, Fig. 7G-I). They show a high variability in length among taxa, feature that has frequently been used in genus and species diagnoses. The avicular uncini have an inflated area below the main fang referred to as a breast (e. g., Fitzhugh 1989). Breasts are well developed in most genera, usually swollen, distally rounded (Fig. 7G, H), but they are reduced to a narrow swelling in species of *Fabrisabella*, *Potamethus* and *Jasmineira* (Fitzhugh 1989, Fig. 7F). Abdominal uncini of members of *Amphicorina*, *Chone*, *Dialychone*, *Euchone* and *Paradialychone* have a square or rectangular breast (Fig. 7I). Most genera have uncini with teeth above main fang of nearly uniform sized. In *Paradialychone*, however, abdominal uncini have a large tooth above the main fang at midline, followed by a series of smaller teeth. The extension of dentition above main fangs varies among and within genera (Figs. 7F-I, 8A-D, F-G) being the extreme condition found uncini on posterior abdomen of *Amphicorina*, *Dialychone*, *Euchone* and *Paradialychone*, in which teeth cover the entire length of main fang, giving it a rasp-shaped appearance (Tovar-Hernández 2008). In the region behind the teeth and directly opposite the main fang, thoracic uncini of some *Chone*, *Dialychone*, *Paradialychone*, *Euchone* and *Jasmineira* species have a hyaline structure which was referred to as a hood (Uebelacker 1984, Tovar-Hernández et al. 2007, Tovar-Hernández 2008), probably composed by loosely packed microtubules, as in other sabellids. A special type of uncini is present on the anterior chaetigers of members of *Caobangia* Giard, 1893 and *Terebrasabella*, in which uncini are distally palmate (Jones 1974, Fitzhugh 1989, Fitzhugh & Rouse 1999, Murray & Rouse 2007, Fig. 8E).

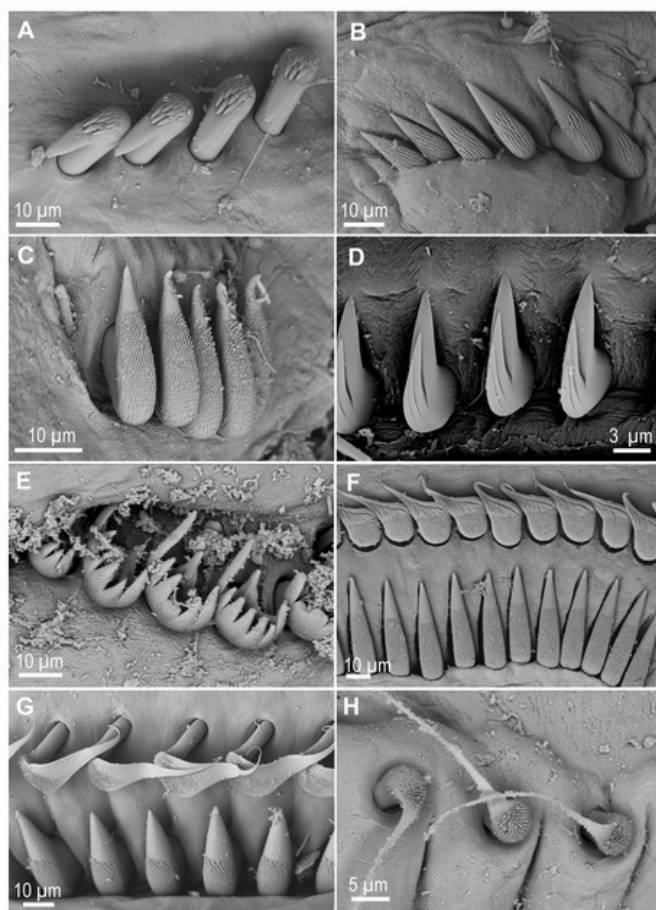


Fig. 8

Uncini and companion chaetae. A, Thoracic uncini with teeth different in size over main fang, *Jasmineira* sp. from Australia; B, Thoracic uncini with similar sized teeth over main fang, *Sabellastarte* sp. from Australia; C, Abdominal uncini with high number of small teeth covering most of length of main fang, *Notaulax* sp. from Australia; D, Thoracic uncini, with teeth over main fang arranged in a single line, *Laonome triangularis* from Australia; E, Thoracic uncini, distally palmate, *Caobangia* sp. from Vietnam; F, Thoracic uncini and companion chaetae with asymmetrical hoods, *Notaulax* sp. from Australia; G, Thoracic uncini and companion chaetae with asymmetrical hoods, *Megalomma* sp. from Australia; H, Companion chaetae with enlarged mucro and distal tip, *Parasabella* sp. from Australia. A-H, Scanning electron micrographs. Images by: A-H, M. Capa.

Some genera bear another kind of thoracic uncinal chaetae, referred to as companion chaetae, with a long shaft embedded in the tissue and a head with a distal hyaline structure or hood (e. g., *Amphiglena*, *Bispira*, *Eudistylia* Bush 1905, *Notaulax* Tauber 1879, *Perkinsiana* Knight-Jones 1983, *Potaspina* Hartman 1969, *Pseudobranchiomma* Jones 1962 and *Sabella* (Fig. 8F-G) or mucro (*Parasabella* Bush 1905, Fig. 8H). Usually companion chaetae form a row parallel to that of the thoracic uncini.

The pygidium can be rounded, conical, bilobed, or resembling a rim around the anus (Figs. 1F-G, 5E-G), and in some *Dialychone*, *Jasmineira* and *Paradialychone* species it is provided with a cirrus (Tovar-Hernández 2008, Fig. 5H). Pygidial eyespots are frequently present (see below), especially in juveniles but also adults of species. The segments preceding the pygidium in some species of *Euchone*, *Euchoneira* Licciano et al., 2009, *Dialychone*, *Paradialychone*, and *Chone* are flattened ventrally forming a pre-pygidial depression (= anal depression) (Tovar-Hernández 2007, 2008, Fig. 5F-G).

Ventral patches of cilia in the peristomial segment is typical of *Amphiglena* (Fig. 1E). Similar patches, but on the collar have been recorded in *Laonome*, *Amphicorina*, *Paradialychone ecaudata* (Moore 1903), *Dialychone trilineata* (Tovar-Hernández 2007) and *Pseudobranchiomma schizogenica* (Tovar-Hernández & Dean 2014). Besides, in *P. schizogenica* the thoracic and abdominal segments also have patches of typical cilia (kinocilia-type), distributed in pairs. Cilia may be of different kinds and not all they are necessarily sensory, since some seem to have different functions such as to generate water currents inside tubes (Tovar-Hernández 2008, Tovar-Hernández & Dean 2014).

Sabellidae holds the largest variation of type and arrangement of eyes of the Annelida. A great diversity is found not only among species but also several types of eyes can be found in a single individual since they can have radiolar, peristomial, segmental and pygidial eyes. Radiolar eyes can be arranged in different positions along the radioles and appear as single ocelli (e. g., *Parasabella*), compound eyes consisting of numerous repetitive units (e. g., *Bispira*, *Branchiomma*, *Megalomma* and *Pseudopotamilla*; Krasne & Lawrence 1966, Verger-Bocquet 1992, Nilsson 1994; Figs. 3C-E, 9B-F), or as an intermediate state between compound eyes and groups of individual ocelli, like in the case of *Notaulax* (Nilsson 1994, Fig. 9A). Peristomial eyespots are present in small or medium size sabellids and are considered to be cerebral eyes due to proximity to the brain (Purschke 2005, Purschke et al. 2006). Members of *Branchiomma*, *Pseudobranchiomma*, *Bispira*, *Sabella*, *Sabellastarte*, *Sabellomma* Nogueira et al. 2010, and *Stylomma* Knight-Jones, 1997 bear simple, pigmented eyes between the noto- and neuropodia, called interramal eyes (Fitzhugh 1989, Capa 2008, Nogueira et al. 2010, Fig. 5A-B). Some authors have also described interramal eyespots in *Megalomma*, *Parasabella* and *Perkinsiana* species (Tovar-Hernández & Salazar-Vallejo 2006, Capa et al. 2011a, Tovar-Hernández et al. 2012), although further studies have to be undertaken to determine their ultrastructure and similarity with previous taxa. Pygidial eyes are present in some species, generally those sabellids with the ability of leaving the tube and building new ones (Purschke 2005). Out of the tube, they crawl with the pygidium in front and the radiolar crown folded up.



Fig. 9

Radiolar eyes. A, Eyespots (arrow) on lateral edges of radioles, *Notaulax* sp. from Australia; B, Paired compound eyes, *Branchiomma* sp. from Australia (arrow); C, Paired compound eyes in another *Branchiomma* species from Australia; D, Unpaired compound eyes (arrow), *Pseudopotamilla* sp. from Australia; E, Distal compound eye, *Megalomma phyllisae* from Australia; F, Same in *Megalomma* sp. from Australia. A-F, Light microscopy photographs. Images by: A-B, D-F, M. Capa; C, R. Springthorpe.

Internal morphology

The radiolar crown of the sabellids is supported by hyaline cartilage (Person & Mathews 1967, Tovar-Hernández & Sosa-Rodríguez 2006, Capa et al. 2011a, Fig. 10A) where chondrocytes and chondroblasts secrete a homogeneous matrix made of granules and fibers (Kryvy 1977). Some chondrocytes have a large vacuole and run along the radiolar lobes, radioles, pinnules, and in some cases the radiolar appendages in packed rows, which has been often referred to as the 'skeleton' (Nicol 1931, Fitzharris 1976, Kryvy 1977, Knight-Jones 1983, Perkins 1984, Fitzhugh 1989, Capa et al. 2011a, Fig. 10A, B). The presence of vacuolated cells is an autapomorphy of Sabellidae, being absent from fabriciids and serpulids (Hanson 1949, Orrhage 1980, Cole & Hall 2004, Capa et al. 2011b).

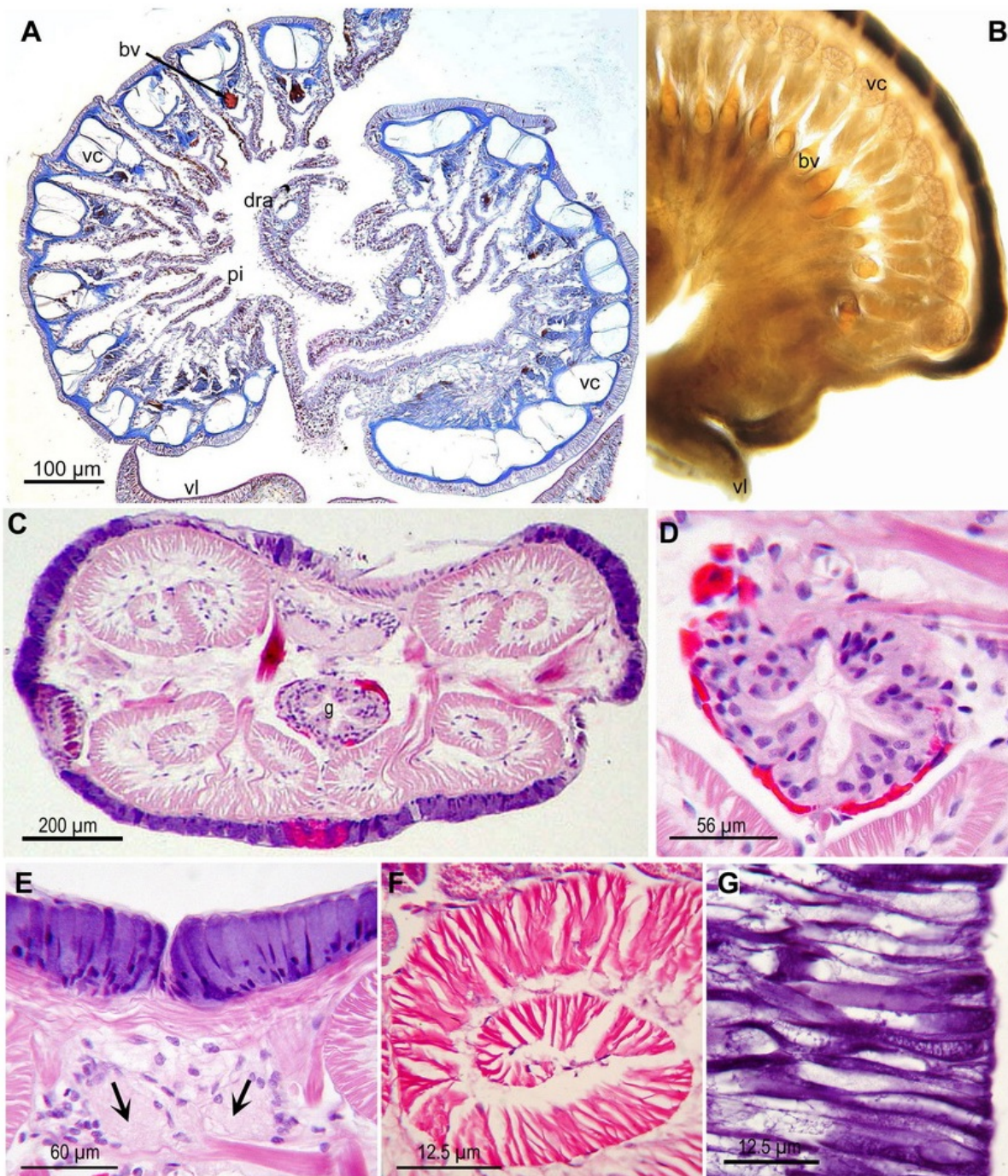


Fig. 10
 Internal anatomy and histology A, Cross section at base of radioles, *Laonome triangularis* from Australia; B, Cross section at the base of radioles, *Megalomma carunculata* from Mexico; C, Abdomen in cross section, *Dialychone quebecensis* from Canada (dorsal in upper side of picture); D, Gut, *Dialychone quebecensis*; E, Detail of C showing ventral nerve chord (arrows), *Dialychone quebecensis*; F, Muscular package, *Dialychone quebecensis*; G, Glandular epithelium, *Chone infundibuliformis* from Greenland. - bv blood vessel, dra dorsal radiolar appendage, g gut, pi pinnules, vc vacuolated cells (chondrocytes) supporting radioles in upright position, vl collar ventral lappets, tissue dyed in blue is hyaline cartilage. A-G, Micrographs. Images by: A, original from Capa et al. 2011; B, Tovar-Hernández, C-F, original from Tovar-Hernández 2007; G, original from Tovar-Hernández and Sosa-Rodríguez 2006.

Epidermal glandular regions in sabellids are extensive and may be diffuse or clearly limited as ventral glandular shields (Chughtai & Knight-Jones 1988, Fitzhugh 1989, Cochrane 2003, Tovar-Hernández 2007, 2008, Fig. 10C, G). Staining worms with methyl green solution is useful to reveal epidermal glandular patterns (Fig. 11A-C). In addition, *Amphicorina*, *Chone*, *Desdemona*, *Euchone*, *Euchoneira*, *Jasmineira*, *Myxicola* and *Potamethus* Chamberlin, 1919 have a pale transverse ridge located on the second chaetiger (glandular ridge on chaetiger 2) (Tovar-Hernández & Sosa-Rodríguez 2006, Tovar-Hernández 2007, Fig. 11 B). Members of some of these groups also present glandular ridges on posterior thoracic chaetigers (Tovar-Hernández 2007, 2008), as well as some species of *Megalomma* Johansson, 1925 (Tovar-Hernández & Carrera-Parra 2011).

Longitudinal muscles run along the length and usually form four discrete bands two running ventrally and two larger ones running dorsally (Evenkamp 1931, Kryvi 1971, Tzetlin & Filippova 2005, Tovar-Hernández 2007, Figs. 3C, 11D-E). The fibers making up these bands are arranged as two reverse helices with each coil tightly adjoining the previous one (Johansson 1925, Tzetlin & Filippova 2005, Fig. 3C, F). Circular and other transverse fibers are poorly developed compared to the longitudinal muscles.

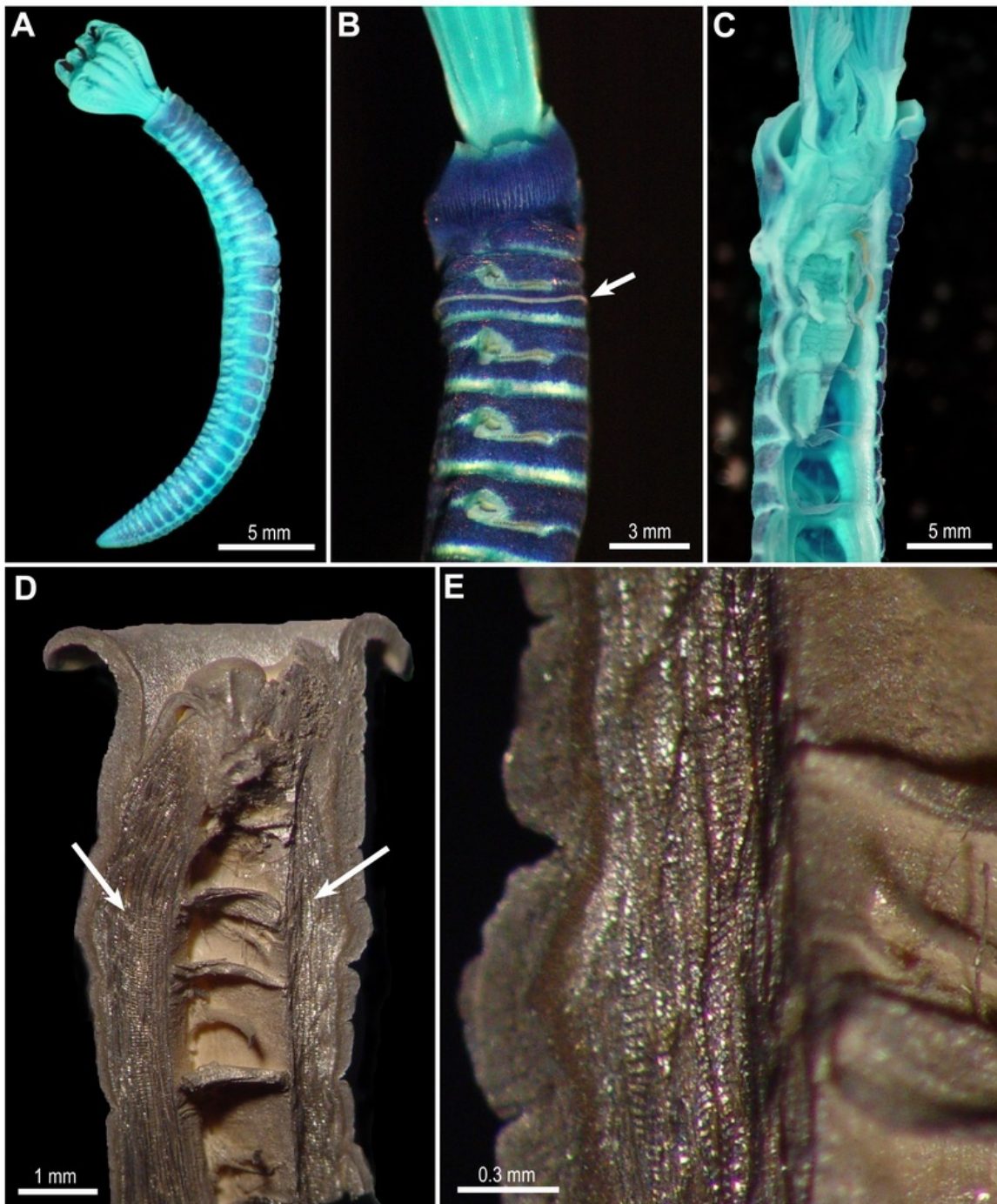


Fig. 11
 Glandular patterns revealed using methyl green and internal anatomy. A, Glandular epithelium along the entire body of *Paradialychone ecaudata* from USA; B, Glandular epithelium in collar and thoracic segments, *Paradialychone paramollis* from USA, glandular ridge as indicated by arrow; C, Internal view of thorax, longitudinal section, *Chone mollis* from USA; D, Longitudinal muscles as indicated by arrows, and septa, *Chone aurantiaca* from USA; E, Detail of longitudinal muscular fibers, *Chone aurantiaca*. A-C, stained with methyl green, D-E, coated with gold. Images by: A-E, M. A. Tovar-Hernández.

The alimentary canal in Sabellidae is a straight, ciliated tube (Fig. 10C-D). The foregut is simple and lacks a buccal organ (Tzetlin & Purschke 2005), the midgut consists of a stomach and an intestine (Dales 1962), and the posterior part is the rectum (Nicol 1931). The anterior portion of the gut is greatly constricted by the mesenteries, and swells out between them into a series of almost spherical chambers, while the intestine is often distended with faeces and bent from one side to another on each segment (Nicol 1931). The walls of the gut consist typically of four layers: an outer peritoneal layer, the lining of the body cavity, a muscular coat of circular and longitudinal fibers, a vascular sinus surrounding completely the gut from segment two to the posterior end of the body and a ciliated and glandular epithelium resting on a well-developed basal membrane (Nicol 1931).

The circulatory system is closed and lacks a heart (Hanson 1951). A ventral blood vessel runs from the second segment to the pygidium and connects to segmental ring vessels and the sinus around the gut. In the anterior end this ventral vessel continues forward as two latero-dorsal vessels and a perioesophageal plexus. In the peristomium, the latero-dorsal vessels join to form a median dorsal vessel, which opens into a transverse vessel just behind the cerebral ganglia. The latter also irrigates the radiolar crown and other prostomial structures (Ewer 1941, Hanson 1950, 1951). A pair of lateral vessels run along each side of the body in most sabellids examined from pygidium back to the second thoracic segment. The blood supply of the the body-wall and parapodia shows variation among taxa. In some species it is derived from these lateral vessels in addition to the segmental ring vessels and in other just from the ring vessels. Branching patterns and distribution of these vessels also shows variation within the family (Hanson 1950). The blood lacks blood cells and it is green in most studied sabellids due to the presence of chlorocruorin (Hanson 1951, Imai & Yoshikawa 1985, de Hass et al. 1996).

There is no evidence of lateral organs, densely ciliated areas, pits or small papillae present segmentally between the neuro- and notopodia with sensory function, in Sabellidae (Purschke & Hausen 2007). A single pair of nephridia opens into the first segment (Goodrich 1945, Orrhage 1980, Schulze 2001, Bartolomaeus & Quast 2005). These are classified as metanephridia with podocytes (Goodrich 1945, Koechlin 1966, 1981, Orrhage 1980, Smith & Ruppert 1988, Bartolomaeus 1993). In *Sabella pavonina* Savigny, 1822, the nephridia are giant and fill almost all the coelomic space between the digestive tract and the body walls in the 8–11 anterior segments (Koechlin 1981).

The brain is located on the peristomium due to the reduction of prostomium after metamorphosis (Schroeder & Hermans 1975). Like in most polychaetes, the brain of Sabellidae contains four transverse commissures. A pair of dorsal and a ventral commissures contact with an anterior circumesophageal root, while another pair of comisures is connected to a posterior root of the connectives (Orrhage & Müller 2005). The innervation of the radiolar crown is equivalent to that of the palps of other groups of polychaetes and is consequently considered to be homologous (Orrhage 1980, Orrhage & Müller 2005). The ventral nerve cord is double in the first four thoracic segments and single posteriorly (Nicol 1948a, Fig. 10E). A single giant axon, up to 1 mm in diameter, is found in *Myxicola infundibulum* (Montagu 1808) (Nicol & Young 1946, Nicol 1948b) whereas other sabellids possess two giant axons (Nicol 1948a, Hagiwara et al. 1964, Mellon et al. 1980).

The nuchal organs, paired ciliated sensory structures generally appearing as ciliated patches or bands, pits or grooves on the head, have an anomalous position in sabellids, serpulids and fabriciids. They have become internalized, probably due to the development of the radiolar crown and form a pair of pouches arising from the dorsal epithelium of the mouth cavity (Orrhage 1980, Purschke 1997, 2005).

The diversity of eyes found in members of this family does not only concern to their arrangement and external morphology but also at cellular level. Sabellids eyes can hold either ciliary or rhabdomeric photoreceptors. In compound radiolar eyes each ocellus or unit contains a photoreceptor cell provided with stacks of parallel and modified cilia, known as ciliary photoreceptor (Purschke 2005). Moreover, a lens-like structure formed by supportive cells other than the pigment cells is also present, with a field of view of about 10°. Peristomial, segmental and pygidial ocelli are composed of several pigment and few sensory cells (rhabdomeric photoreceptors) forming a follicle-like epidermal invagination filled with a cuticular lens (Ermak & Eakin 1976, Dragesco-Kernéis 1980, Purschke 2005, Purschke et al. 2006).

Statocysts, structures that act as gravity detectors, have been found in the peristomium of *Amphicorina* (Rouse 1990, 1992, Yoshihara et al. 2012) and other small Sabellidae (Rouse 2001), but no ultrastructural studies have been conducted to date (Purschke 2005). Other characteristic peristomial structures are the vascular loops (= vascular coil), that are circular cavities situated dorso-laterally on the peristomium and containing an S- or C-shaped vessel. In Sabellidae, they can be observed in *Euchone analis* (Krøyer 1856), some species of *Jasmineira* and *Fabrisabella* Hartman, 1969 (Hartman 1969, Fitzhugh 2002, Tovar-Hernández 2008).

Tube morphology

The structure of tubes can be very different and often is a useful feature in taxonomic identification, at least at genus level (Tovar-Hernández & Carrera-Parra 2011). Some species, such as *Sabella spallanzanii* and *Sabellastarte spectabilis* (Grube 1878), combine mucus with feces to build a flexible and pergamentaceous tube (Giangrande et al., 2014, Fig. 12B). In *Branchiomma* and *Bispira* a thin-walled tube is formed of mucus combined with sand sediment, giving a parchment-like appearance is produced (Fig. 12C). In this case the opening of the tube can be closed when the worm withdraws. Species of *Anamobaea*, *Notaulax*, *Perkinsiana* and *Pseudopotamilla* Bush, 1905 construct thick and horny mucous tubes, leathery in appearance, inside dead coral blocks or limestone (Chughtai & Knight-Jones 1988). *Megalomma* species build tubes by attaching gravel of different sizes, echinoderms spines, and shell fragments to a very thin layer of mucus and sometimes the tube is completely buried in the soft substrate (Giangrande et al., 2014, Fig. 12E-F). *Bispira serrata* Capa, 2007 constructs tubes with an additional outer lining covering the muddy sediment (Fig. 12D). *Panousea* sp. has translucent tubes, covered with scattered sand grains and shell fragments (Fig. 12G). Soft-bottom species, such as *Chone*, *Euchone* and *Jasmineira*, produce very flexible tubes formed by fine sand. In some cases, the worms can incorporate algae, shell fragments, detritus, ascidians, sponges and hydrozoans within the tube (Fig. 12A, F). The calcareous tubes of *Glomerula piloseta* is circular in cross section, coiled, plain or with anterior end erect (Perkins 1991). Its wall is composed of subparallel lamellae of aragonitic, irregular spherulitic prisms in the inner layer, and spherulites in the outer layer, and calcified lamellae are separated by organic films of different thickness (Vinn et al. 2008).

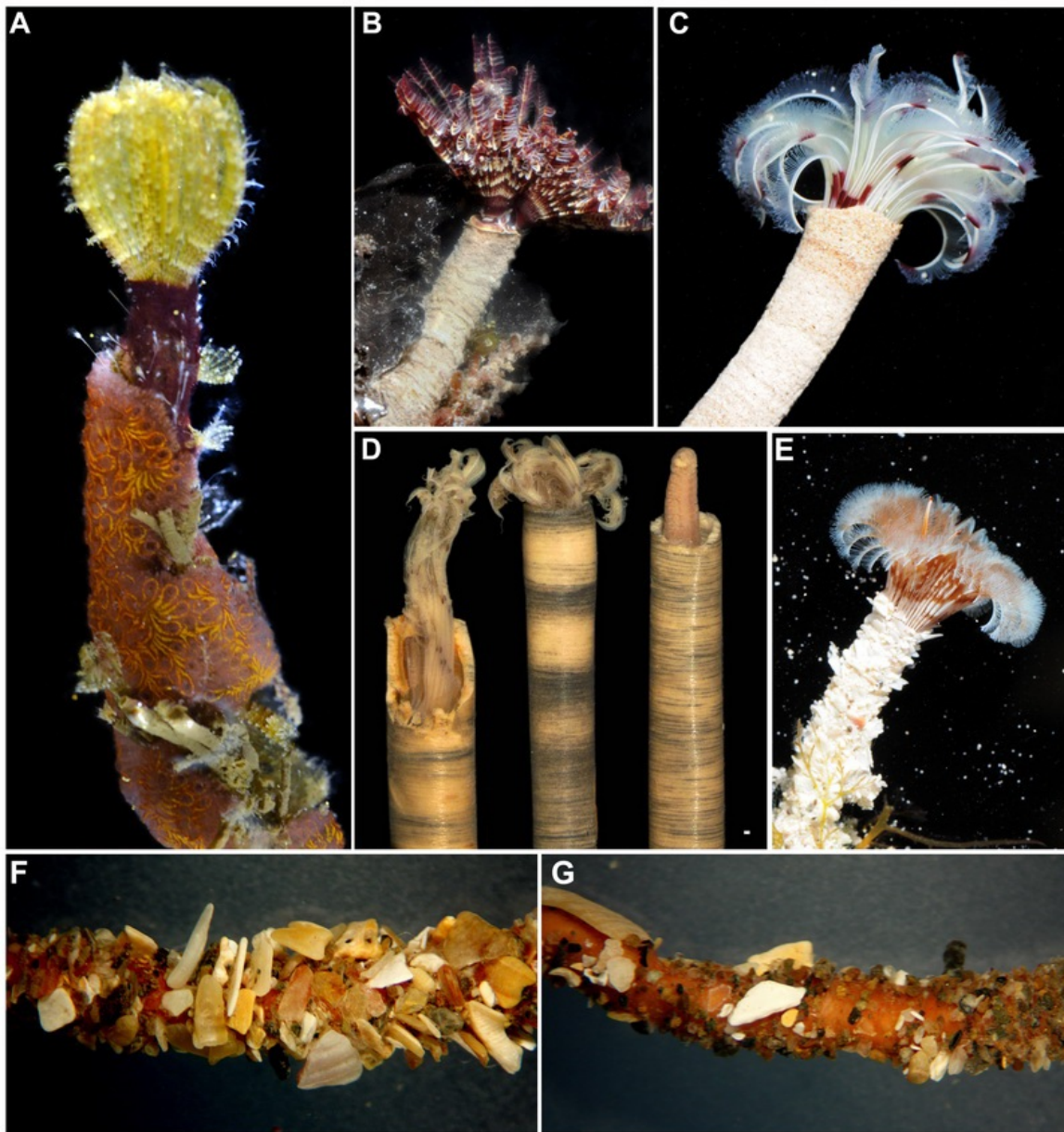


Fig. 12
 Sabellid tubes. A, Tube covered with botryllid ascidians, *Branchiomma bairdi* from Mexico; B, *Sabellastarte* sp. from Australia, with a muddy tube; C, *Bispira manicata*'s tube covered in fine sand; D, Unusual tube of *Bispira serrata*, with a ringed and shiny outer lining; E, *Megalomma* sp. from Australia, with rests of shells attached to the sandy tube; F, Tube of *Megalomma pacifica* from Panama; G, *Panousea* sp. from Panama, tube with leathery appearance. A-C, E, live specimens. Images by: A, H. Bahena-Basave; B, M. Capa; C, E, C. Granich; D, E. Wong; F-G, M. A. Tovar-Hernández.

Reproduction, Development and Regeneration

Sabellidae is among the best-understood polychaetes families in terms of reproduction (Rouse & Fitzhugh 1994, Giangrande 1997, Rouse et al. 2006). Sexual reproduction was reviewed by Rouse & Fitzhugh (1994) and compilations of reproductive features for several sabellid species were provided by McEuen et al. (1983) and Giangrande (1997). Subsequently, many studies have been published about reproduction issues of 25 species (Tab. 1). Sabellids display a range of sexual reproductive modes, from broadcast spawning to ovoviviparity. They are mainly gonochoric, but some taxa show simultaneous or protandric hermaphroditism.

Species	Referentes
<i>Aracia heterobranchiata</i> (Nogueira, López and Rossi, 2010)	Nogueira et al. 2004
<i>Aracia riwo</i> (Rouse, 1996)	Rouse 1996a
<i>Aracia sinaloae</i> Tovar-Hernández, 2014	Tovar-Hernández 2014
<i>Amphiglena lindae</i> Rouse and Gambi, 1997	Rouse & Gambi 1998b
<i>Amphiglena mediterranea</i> (Leydig 1851)	Rouse & Gambi 1998a, b
<i>Amphiglena nathae</i> Rouse, 1994	Rouse & Gambi 1998a, b
<i>Amphiglena pacifica</i> Annenkova, 1934	Rouse & Gambi 1998b
<i>Bispira brunnea</i> (Treadwell 1917)	Tovar-Hernández & Pineda-Vera 2008
<i>Bispira volutacornis</i> (Montagu 1804)	Nash & Keegan 2003
<i>Branchiomma bairdi</i> (McIntosh 1885)	Tovar-Hernández et al. 2011; Arias et al. 2013
<i>Branchiomma luctuosum</i> (Grube 1870)	Licciano et al. 2002
<i>Euchone pallida</i> Ehlers, 1908	Gambi et al. 2001
<i>Myxicola</i> cf. <i>Sulcata</i>	Gambi et al. 2001
<i>Parasabella polarsterni</i> Gambi, Patti, Micaletto and Giangrande, 2001	Gambi et al. 2001
<i>Perkinsiana antarctica</i> (Kinberg 1866)	Gambi & Patti 1999; Gambi et al. 2000
<i>Perkinsiana littoralis</i> (Hartman 1967)	Gambi et al. 2000
<i>Perkinsiana borsibrunoi</i> Giangrande and Gambi, 1997	Gambi et al. 2000
<i>Perkinsiana milae</i> Giangrande and Gambi, 1997	Gambi et al. 2000

<i>Pseudopotamilla reniformis</i> (Bruguière 1789)	Kolbasova et al. 2013
<i>Pseudobranchiomma schizogenica</i> Tovar-Hernández and Dean, 2014	Tovar-Hernández & Dean 2014
<i>Sabella pavonina</i> Savigny, 1822	Murray et al. 2011, 2013
<i>Sabella spallanzanii</i> (Gmelin 1791)	Giangrande et al. 2000
<i>Sabellastarte spectabilis</i> (Grube 1878)	Bybee et al. 2006a, b, 2007
<i>Sabellastarte</i> sp.	Murray et al. 2013
<i>Terebrasabella heterouncinata</i> Fitzhugh and Rouse, 1999	Fitzhugh & Rouse, 1999; Gray & Kaiser 2007

Tab. 1

Studies about reproductive issues in Sabellidae after Giangrande (1997).

Sabellids lack permanent gonads, but there are dispersed ovaries in which packets of germ cells, previtelogenic oocytes and mature oocytes float in the coelom of mainly the abdominal region (Rouse & Fitzhugh 1994, Currie et al. 2000, Bybee et al. 2007) although *Amphicorina*, *Branchiomma*, *Chone*, *Dialychone*, *Euchone*, *Jasmineira* and *Paradialychone* also contain gametes in the thorax (e. g., Rouse & Fitzhugh 1994, Nogueira & Amaral 2000, Tovar-Hernández et al. 2011). Primary gametes of both sexes appear to be derived from peritoneal cells. Maturation of gametes happens along the entire length of the coelom and mature eggs and sperm are expelled through paired lateral gonoducts that extend from the coelom of each chaetiger and open at the neuropodia of the next posterior segment (e. g., Currie et al. 2000, Giangrande et al. 2000, Fig. 13A-B). Simultaneous hermaphrodites can have eggs and sperm in the same segments, as in *Caobangia*, *Sabellastarte magnifica*, *Branchiomma luctuosum*, *Parasabella* (Rouse & Fitzhugh 1994, Licciano et al. 2002), and *B. bairdi* (Tovar-Hernández et al. 2009a), or in different segments, as in some members of *Amphiglena*, *Laonome*, and *Perkinsiana* (Rouse & Fitzhugh 1994). Protandric hermaphroditism has been described only in *Sabellastarte spectabilis* (Bybee et al. 2006a), and is supposed to occur in *Sabella spallanzanii* (Giangrande & Petraroli 1994), which was found to be gonochoric in further investigations (Giangrande et al. 2000). Lastly, *Laonome albicingillum* Hsieh, 1995 is also simultaneous hermaphrodite (Hsieh 1995) but the distribution of its gametes is unknown.

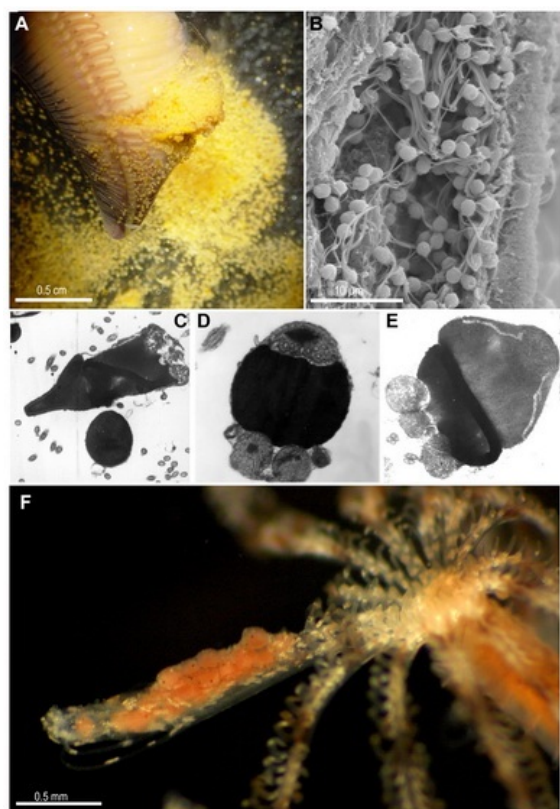


Fig. 13

Oocytes, spermatozoa and brooding. A, *Megalomma carunculata* from Mexico, a gravid female releasing oocytes previous body wall rupture; B, Sperm of *Branchiomma bairdi* from Mexico; C-E, Acrosome development and internal structure in broadcasting sabellids; C, *Myxicola infundibulum* from Italy (x 12000); D, *Branchiomma luctuosum* from Italy (x 28000); E, *Eudistylia vancouveri* (x 20000); F, Embryos of *Aracia sinaloae* from Mexico attached to the dorsalmost pair of radioles. A, F, Light microscopy photograph, B, SEM photograph, C-E, TEM photographs. Images by: A-B, F, M. A. Tovar-Hernández; C-E, A. Giangrande.

Oogenesis has been studied in *Sabella spallanzanii* (Giangrande et al. 2000), *Sabella pavonina* (Murray et al. 2011), *Branchiomma luctuosum* (Licciano et al. 2002), *Bispira volutacornis* (Nash & Keegan 2003), *Terebrasabella heterouncinata* (Simon 2004), *Sabellastarte spectabilis* (Bybee et al. 2007), and *Branchiomma bairdi* (Tovar-Hernández et al. 2011, Arias et al. 2013). Spermatogenesis happens in tetrads in most of Sabellinae, but clusters of spermatids attached to a cytophore can be found in several genera. The clusters can be composed of more than 100 spermatids, as in *Caobangia* and *Potamilla*, or of less than 100 spermatids, as in *Amphiglena* and *Laonome* (Rouse & Fitzhugh 1994, Fitzhugh & Rouse 1999, Rouse et al. 2006).

Mature sperm have spherical heads and mitochondria and a free flagellum (e. g., *Bispira*, *Sabella*, *Branchiomma*, *Parasabella*, *Perkinsiana*, *Eudistylia*, and *Pseudopotamilla*, Fig. 13D-E), cylindrical head and spherical mitochondria and free flagellum (e. g., *Myxicola*, *Chone*, *Euchone*, *Potamethus*, Fig. 13C), or elongate heads with elongate mitochondria forming a long mid-piece and free flagellum (e. g., *Caobangia*, *Amphicorina*, and *Amphiglena*) (Giangrande & Petraroli 1994, Rouse & Fitzhugh 1994, Giangrande et al. 2000).

Spermathecae have been described only in *Amphicorina*, *Amphiglena* and *Terebrasabella*. *Terebrasabella* is unusual in having a single spermatheca, with blind-ending and extending along the ventral epidermis from the basal part of the crown to at least the first chaetiger (Simon & Rouse 2005), whereas in *Amphicorina* and *Amphiglena* spermatheca are always paired (Rouse 1992, Rouse & Gambi 1998b).

Based on the classification system of sperm defined by Jamieson & Rouse (1989), ect-aquasperm type is found in broadcasting species with external fertilization, in which sperm are released into the water and fertilize similarly released eggs, as in *Branchiomma luctuosum* (Sordino & Gambi 1994, Licciano et al. 2002, Fig. 13D) and *Sabellastarte spectabilis* (Bybee et al. 2006a). In turn, ent-aquasperm type is found in species with in situ fertilization, in which sperm are also released freely into the water but are gathered by or in some other way reach the female prior to fertilization that never happens in the water column. Ent-aquasperm have been reported in *Amphicorina* spp. (Rouse 1992), *Amphiglena* spp. (Rouse 1993, Rouse & Gambi 1998a, b), *Perkinsiana antarctica* (Kinberg 1866) (Gambi & Patti 1999), *Aracia riwo* (Rouse 1996) (Rouse 1996a) and *Terebrasabella heterouncinata* (Fitzhugh & Rouse 1999, Simon & Rouse 2005).

The egg size varies from very small size, as 82 µm diameter in *Amphicorina brevicollaris* (Rouse 1990) and *Jasmineira regularis* Hartman, 1978 (Giangrande 1997) or 110 µm in *Branchiomma bairdi* (Tovar-Hernández et al. 2009a), to larger size as 250 µm as in *Parasabella microphthalmia* (Verrill 1883) and *Sabella spallanzanii* (Giangrande 1997), with the largest eggs being 500 µm in diameter in *Potamilla torelli* (Malmgren 1866, Rouse & Fitzhugh 1994) and 600 µm in *Amphiglena marita* (Chlebovitsch 1959). However, most of the species have eggs measuring from 120 to 150 µm (Giangrande 1997). Estimates of egg numbers ranged from a minimum of one per body in *Caobangia* (Rouse & Fitzhugh 1994) to nearly 660000 in *Eudistylia vancouveri* (Kinberg 1866, Rouse & Fitzhugh 1994), with intermediate numbers such as 2500 in *Chone duneri* (Yun & Kikuchi 1991a) or 1300 in *B. bairdi* (Tovar-Hernández et al. 2011). There is no information about male fecundity in sabellids.

Natural spawning has been detailed for *Megalomma vesiculosum* by Hornell (1893). In laboratory, spawning and fertilization is not easy to observe. It was obtained for some broadcasting species such as *Myxicola infundibulum* (Dean et al. 1987), *Bispira volutacornis* (Yun & Kikuchi 1991a), *Sabella spallanzanii* (Giangrande et al. 2000), *Branchiomma luctuosum* (Licciano et al. 2002) and *Sabellastarte spectabilis* (Bybee et al. 2007). In the last species fertilization probably does not happen in the water column but takes place in the tube just after the egg are released from the coelomic cavity, and the produced mucus would act as a medium were eggs are released and fertilized (Stabili et al. 2011). *Bispira volutacornis* releases all its gametes in a single large batch, surviving to breed again. Gravid specimens have a bloated appearance prior to spawning, with the coelom filled to its maximum capacity with gametes. Gametes are released through gonoducts located segmentally and mid-laterally to the parapodia. The deeply segmented ventral shields aid in the organized passage of the gametes. The gametes travel along the transverse furrows, in a stream-like fashion, reach the midline of faecal groove, follow this groove anteriorly. The flow of gametes is assisted by rapid muscular contractions of the abdomen, which continue for the duration of spawning. In the crown, the gametes enter upward flowing rejection current (Nash & Keegan 2003). Also under lab conditions, many adults of *Chone duneri* were seen to emerge anterior half of the body from their tubes during spawning (Yun & Kikuchi 1991a).

Most large sabellids are iteroparous (able to reproduce more than once, often annually or semi-annually), devoting considerable amounts of energy and body space to the reproduction of copious numbers of gametes seasonally (Giangrande 1997, Patti et al. 2003). *Chone duneri* is semelparous, it spawns only once and dies soon after discharging the gametes (Yun & Kikuchi 1991a). *Sabellastarte spectabilis* has a broad maturation period with clear evidence of one peak in October (annual producers) in which wild-caught worms were induced to spawn (Bybee et al. 2007). Small worms generally have semi-continuous reproduction (reproduce continuously over an extended season) due to limitations in body volume as seen in *Amphiglena mediterranea* (Rouse & Fitzhugh 1994).

In *Sabella spallanzanii*, males were recorded to account for more than 80% of the reproductive population in the Mediterranean Sea (Giangrande & Petraroli 1994); however further investigations revealed an actual sex ratio of 1:1 (Giangrande et al. 2000). A sex ratio of 1:1 also was described for *Chone duneri* (Yun & Kikuchi 1991a), *Branchiomma luctuosum* (AG, unpublished data), and *Sabellastarte spectabilis* (Bybee et al. 2006a).

Protection of larvae (brooding) is present in some sabellids, be it intratubular or extratubular, although the first pattern is more common in the group (e.g., *Amphicorina*, *Amphiglena*, *Caobangia* and *Potamilla* (Rouse & Fitzhugh 1994). Three types of extratubular brooding have been documented. One consists in keeping the larvae in a jelly ring located around the mouth of the tube (McEuen et al. 1983) and was observed in *Parasabella media* Bush, 1905 and *Branchiomma lucullanum* (Delle Chiaje 1828). In another type, larvae form a mass attached to a single radiole, as seen in *Perkinsiana antarctica* (Knight-Jones & Bowden 1984, Gambi & Patti 1999, Gambi et al. 2000); on ventral-most radiolar pair, as in *Aracia riwo* (Rouse 1996a); or on the modified dorsal-most pair of radioles, as in *Aracia heterobranchiata* (Nogueira et al. 2004) and *Aracia sinaloae* (Tovar-Hernández 2014, Fig. 13F). A third type consists in brooding the larvae embedded in a jelly mass attached to the mouth of the tube and is only known for *Chone infundibuliformis* (Okuda 1946).

All sabellids present lecithotrophic larvae (Rouse & Fitzhugh 1994) with a short planktonic phase (Fig. 14A-C), lasting only 1–2 days in *Laonome albicingillum* (Hsieh 1995, 1997), three days in *Branchiomma luctuosum* (Licciano et al. 2002), six days in *Branchiomma nigromaculatum* (Berrill 1978), seven days in *Megalomma infundibulum* (Dean et al. 1987), and nine days in *Megalomma vesiculosum* (Wilson 1936) and *Parasabella media* (McEuen et al. 1983). The longest period, 2 weeks, was recorded for *Sabella spallanzanii* (Giangrande et al. 2000, Pernet et al. 2002). Detailed accounts of the complete sequences of larval development through metamorphosis are known for *Chone infundibuliformis*, *Chone duneri* (Yun & Kikuchi 1991b), *Terebrasabella heterouncinata* (Gray & Kaiser 2007), and *Sabellastarte spectabilis* (Bybee et al. 2006b). Larvae of *Parasabella media* settle nine days after spawning and metamorphosis begins with emergence of branchial buds and loss of prototroch and neurotroch; however, metamorphosis is only completed at day 15 (McEuen et al. 1983). In *Sabellastarte spectabilis* settlement occurs 6–7 days after spawning, when prototroch is lost and larvae drop out of the water column, no longer able to swim, and settles on the bottom (Bybee et al. 2006b).

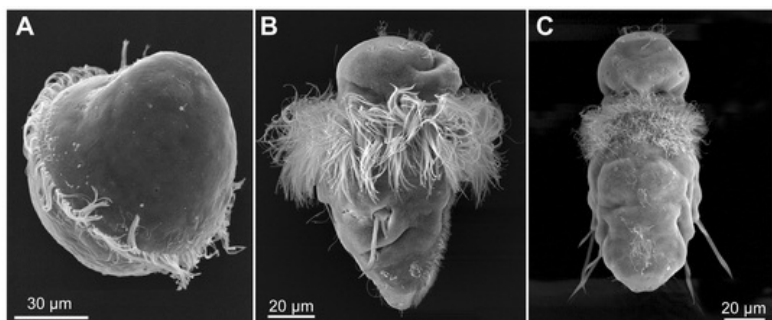


Fig. 14
Larvae of *Sabellastarte spectabilis* from Hawaii. A, 24 h after hatching; B, 5 days after hatching; C, Settled larva, 7 days old. Images by D. Bybee.

Very little is known about sabellid longevity. The largest species, *Sabella spallanzanii*, can live for more than five years and attain a very large size (50 cm) (Giangrande & Petraroili 1994), but *Branchiomma luctuosum* can reach a large size (40 cm) in only 2 years. The former species reproduces at the second year of its life, while the latter reproduces during the first year of its life and oogenesis starts at just third month (Mastrotodaro et al. 2014). Small-sized species live for only one year, e. g., as *Chone duneri* (Yun & Kikuchi 1991a), or even less than one year, as *Amphiglena mediterranea* (AG, unpublished data).

Sabella pavonina (as *S. penicillus*), *Myxicola infundibulum* and *Chone infundibuliformis* have a diploid count of 28 chromosomes (Christensen 1980).

Asexual reproduction in sabellids takes the form of architomy (spontaneous fission or autotomy followed by subsequent regeneration). Thus, natural fission or autotomy, has been recorded in 14 species (Tab. 2). Among these species, *S. discifera*, *B. bairdi*, *B. brunnea*, *P. reniformis* and *Pseudobranchiomma* spp. form dense aggregations and natural fission seems a process that leads to the formation of colonial forms as in some serpulids (Nishi & Nishihara 1994; Pernet 2001). *Megalomma cinctum*, *Pseudopotamilla reniformis*, *Bispira manicata*, *B. brunnea* and *Branchiomma bairdi* reproduces also sexually (all are gonochoric, except for hermaphrodite *B. bairdi*). In *Megalomma cinctum*, a small portion of the population (4–13% of individuals) exhibited scissiparity (Yuan 1992) and in *Bispira brunnea*, 20–50% of the population reproduce asexually (Tovar-Hernández & Pineda-Vera 2008). In the Gulf of California, 82% of the population of *Pseudobranchiomma schizogenica* was found to be undergoing architomy during summer (Tovar-Hernández & Dean 2014). In the White Sea, 95% of the entire population of *Pseudopotamilla reniformis* reproduce asexually during winter (Kolbasova et al. 2013) and asexual reproduction happens throughout the year in *Branchiomma bairdi*, with an annual mean around 11% (Tovar-Hernández et al. 2011).

Species	References
* <i>Bispira brunnea</i> (Treadwell 1917)	Tovar-Hernández & Pineda-Vera 2008
* <i>Bispira manicata</i> Capa, 2008	Capa 2008
* <i>Branchiomma bairdi</i> (McIntosh 1885)	Tovar-Hernández et al. 2009b; Arias et al. 2013
<i>Branchiomma curtum</i> (Ehlers 1901)	Tovar-Hernández & Knight-Jones 2006
* <i>Megalomma cinctum</i> (as <i>Megalomma</i> sp. in Yuan 1992)	Fitzhugh, 2003
<i>Myxicola aesthetica</i> (Claparède 1870)	Knight-Jones & Bowden 1984
<i>Perkinsiana milae</i> Giangrande & Gambi, 1997	Gambi et al. 2000
<i>Perkinsiana rubra</i> (Langerhans 1880)	Knight-Jones & Bowden 1984
<i>Pseudobranchiomma minima</i> Nogueira & Knight-Jones 2002	Nogueira & Knight-Jones 2002
<i>Pseudobranchiomma perkinsi</i> Knight-Jones and Giangrande, 2003	Knight-Jones & Giangrande 2003
<i>Pseudobranchiomma punctata</i> (Treadwell 1906)	Nogueira & Knight-Jones 2002
<i>Pseudobranchiomma schizogenica</i> Tovar-Hernández and Dean, 2014	Tovar-Hernández 2014
* <i>Pseudopotamilla reniformis</i> (Bruguière 1789)	Kolbasova et al. 2013
<i>Sabella discifera</i> Grube, 1874	Rioja 1929; Knight-Jones & Bowden 1984

Tab. 2

Sabellids where asexual reproduction has been reported. Note that species marked with an asterisk reproduces also sexually, see text for details.

In *Sabella discifera* worms regenerating posterior ends may be accompanied by one or two shorter individuals of similar width, that are regarded as offspring budded off by fission from the parent portion. The tubes are separate and unbranched, except for occasional short branches near the proximal end. Presumably the clonal offspring leave the parental tube at one end or the other before they secrete their own tubes (Rioja 1929, Knight-Jones & Bowden 1984). Abdominal constrictions resulted in two to four abdominal fragments positioned in the parental tube of *Pseudopotamilla reniformis* in a chain-like fashion. These fragments are different and some clonal offspring regenerate the crown and the thorax, whereas other restore both the crown and thorax anteriorly and pygidium posteriorly. The clonal offspring make cracks in the posterior part of the parental tube, curve their bodies sidewise and pull their head and posterior abdomen first and then the rest of the body through the opening. The emerging clone builds a transparent tube attached to a neighboring tube in the basal layer of the aggregation (Kolbasova et al. 2013). The same developmental pattern was also documented in *Pseudobranchiomma schizogenica*, where clonal offspring regenerate the crown and the collar, whereas others were found restoring both the crown and the collar anteriorly and the pygidium posteriorly (Tovar-Hernández & Dean 2014). Tubes of *Branchiomma curtum* contained many developing scissiparous offspring posterior to the parents. The posteriormost parts of the abdomen separate into a few multi-segment fragments, and anteriorly each segment chaetae of thoracic type are gradually formed. Such regeneration is usually imperfect, producing individuals with fewer thoracic segments than the usual eight thoracic segments (Tovar-Hernández & Knight-Jones 2006), as seen also in *Branchiomma nigromaculatum* (Berrill 1978), *Branchiomma bairdi* (Tovar-Hernández et al. 2009b, 2011) and some species of *Sabellastarte* (Murray 2010). In contrast, in *Bispira manicata* a higher number of thoracic segments is produced after regeneration (Capa 2008, Fig. 15D).

Within Sabellidae, the replacement of a body part lost through traumatic injury (either natural fission, or autotomy and amputation) is varying (Bely 2006, Licciano et al. 2012, Fig. 15A-H). Species may be capable or incapable of regenerating anterior segments (Fig. 15A, D-F), posterior segments, and/or terminal asegmental structures (Fig. 15B-C, G-H). Specimens of *Branchiomma bairdi* have been found with two pygidia and the bifurcate posterior end (Tovar-Hernández et al. 2009b, Fig. 15B). Regeneration takes place via epimorphosis (replacement of missing parts by cell proliferation and the growth of new tissue), morphallaxis (the remodeling of pre-existing structures without cell proliferation) or a combination of both mechanisms. Recently, however, Agata et al. (2007) proposed the “intercalary model” whereby organisms initially form the most distal part and then reconstitute the intermediate regions by appropriate intercalation of newly generated tissues between the newly formed distal part and the remaining body.

Epimorphosis was described for *Amphiglena mediterranea* (Giangrande et al. 2010), for *Sabellastarte* spp. (Murray 2010) and for *Branchiomma luctuosum* (Licciano et al. 2012). Combining epimorphosis and morphallaxis is a process described by Berrill (1931, 1977, 1978), Berrill & Mees (1936a, b), Murray (2010), Licciano et al. (2012), Murray et al. (2013) and Kolbasova et al. 2013 for *Branchiomma bombyx* (Dalyell 1853), *B. nigromaculatum*, *Bispira melanostigma* (Schmarda 1861), *B. volutacornis*, *Megalomma vesiculosum*, *Potamilla torelli* (Malmgren 1866), *Pseudopotamilla reniformis*, *Sabella pavonina* and *S. spallanzanii*.

According to Kolbasova et al. (2013), morphallaxis is likely to be less energy-consuming than epimorphosis because it involves remodeling of some pre-existing structures, whereas epimorphosis requires ex novo formation of missing segments from blastema. Moreover, morphallaxis provides rapid restoration of a large amount of thoracic segments simultaneously, and supports rapid regeneration and high survival rate. Thus, *Branchiomma luctuosum* survives after induced fragmentation, but shows high mortality of fragments and slow regeneration rate, whereas *Branchiomma nigromaculatum*, *Sabella spallanzanii*, *Sabellastarte* spp., and *Pseudopotamilla reniformis* regenerate easily and have a high survival rate (Berrill 1977 1978, Licciano et al. 2012, Kolbasova et al. 2013, Murray et al. 2013).

The regeneration capabilities can vary greatly even between phylogenetically close species. For instance, *Myxicola infundibulum* cannot regenerate

anterior segments, even if just a single anterior segment is removed (Nicol in Wells 1952). It just can regenerate the crown, and only if a stump of this structure is present. In contrast, its congener *M. aesthetica* can regenerate several anterior segments lost (Berrill 1931, Okada 1934).

In *Fabrisabella*, *Jasmineira* and some species of *Sabella* (as *S. penicillus*), an abscission zone at the base of crown has been documented (Kennedy & Kryvi 1980, Tovar-Hernández 2008). It is a pre-established zone of rupture where, under various circumstances, the radiolar crown becomes detached from the body. In *Fabrisabella* and *Jasmineira*, the abscission zone or breaking plane is a discrete area located immediately above the radiolar bases (Cochrane 2003, Tovar-Hernández 2008, Fig. 15A, E-F), and it is a typical feature of members of these genera. In *Sabella pavonina* and *Myxicola aesthetica*, the abscission zone is located in the cartilaginous matrix, and this allows for a fast regeneration of the missing structure (Berrill 1931, Okada 1934). Abscission involves a rupture of the paramyosin muscle cells which form bridges connecting extensions from the epimysium of the body wall musculature and form the cartilage matrix of the crown (Kennedy & Kryvi 1980). *Sabella pavonina* is able to control the loss of its radiolar crown, so this abscission is a kind of autotomy. The high regenerative ability found in several sabellids is not necessarily linked to the presence of asexual reproduction, as in *Sabella spallanzanii* and *Amphiglena mediterranea* (Giangrande et al. 2010).

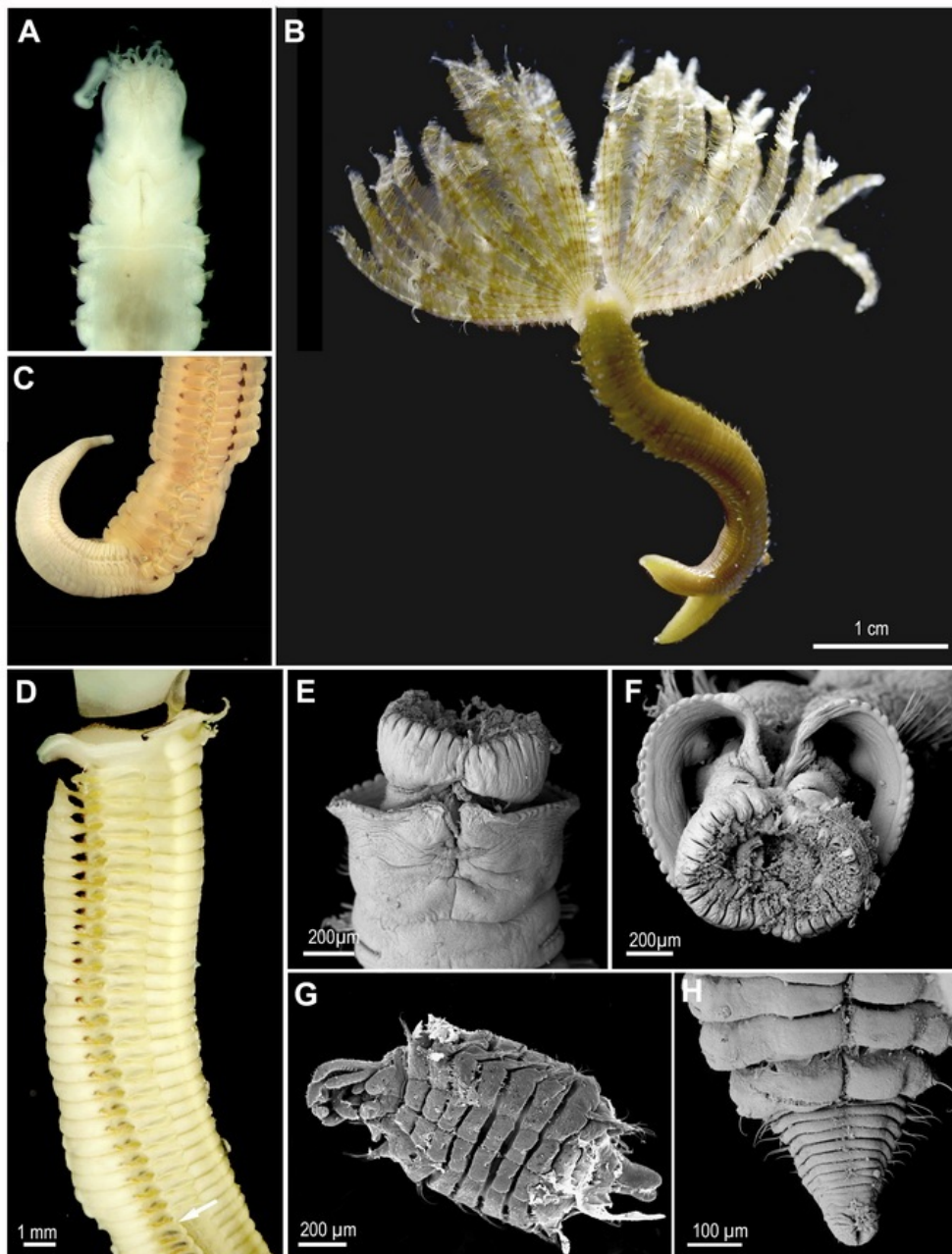


Fig. 15
Breakage and regeneration. A, Radiolar crown broken at abscission zone, *Fabrisabella* sp. from USA; B, *Branchiomma bairdi* from Mexico, with two pygidia after imperfect regeneration; C, *Bispira manicata* from Australia, regenerating posterior abdominal segments and pygidium; D, Thorax of *Bispira manicata* showing a high number of thoracic segments (to the arrow) after imperfect regeneration; E, Radiolar crown broken at abscission zone, ventral view, *Jasmineira* sp. from Australia; F, Same, anterior view; G, *Pseudobranchiomma schizogenica* from Mexico, offspring after scissiparity; H, *Parasabella* sp. from Australia regenerating posterior abdominal segments and pygidium. A-D, Light microscope photographs, E-H, Scanning electron micrographs. Images by: A, C, E-F, H, M. Capa; B, H. Bahena-Basave; D, E. Wong; G, M. A. Tovar-Hernández.

Distribution, Biology and Ecology

Ecology and Distribution

Sabellids live typically in marine environments, although some taxa belonging to the genera *Desdemonia*, *Laonome*, and *Euchone* are able to live in

estuarine conditions, withstanding abrupt changes in salinity and temperature (Hutchings & Murray 1984, Castelli et al. 1988, Capa et al. 2014), and members of *Caobangia* are exclusive of fresh waters (Jones 1974, Glasby et al. 2009).

Many species inhabit littoral hard substrates as epibionts on algae, associated with sponges, molluscs, and ascidians (Fig. 16A, D). Other live in crevices of rocks and corals, and some of them, such as some species of *Sabellastarte* or *Bispira* species, are exploited for ornamental purposes (Capa et al. 2010, Murray et al. 2013, Fig. 16B, C). A number of species are foulers, colonizing artificial substrates of marinas, harbours and other sheltered areas, where they can reach very high densities, as reported for species of the genera *Branchiomma*, *Eudystilia*, *Megalomma*, *Parasabella* and *Sabella* (Licciano et al. 2005, 2007, Stabili et al. 2006, 2009, Tovar-Hernández 2009, Capa et al. 2013a, Fig. 16A, E).

Species belonging to *Jasmineira*, *Chone*, *Euchone*, *Fabrisabella*, *Perkinsiana* and *Potaspina*, have been reported in soft-bottoms, from shallow waters down to 1000 m (e. g., Hartman 1969, 1978, Fauchald 1972, Ruff & Brown 1989, Capa 2007, Méndez 2006, 2013, Tovar-Hernández 2008) but some have been collected down to 300 meters in Antarctica (Tovar Hernández et al. 2012, Capa et al. 2013b).

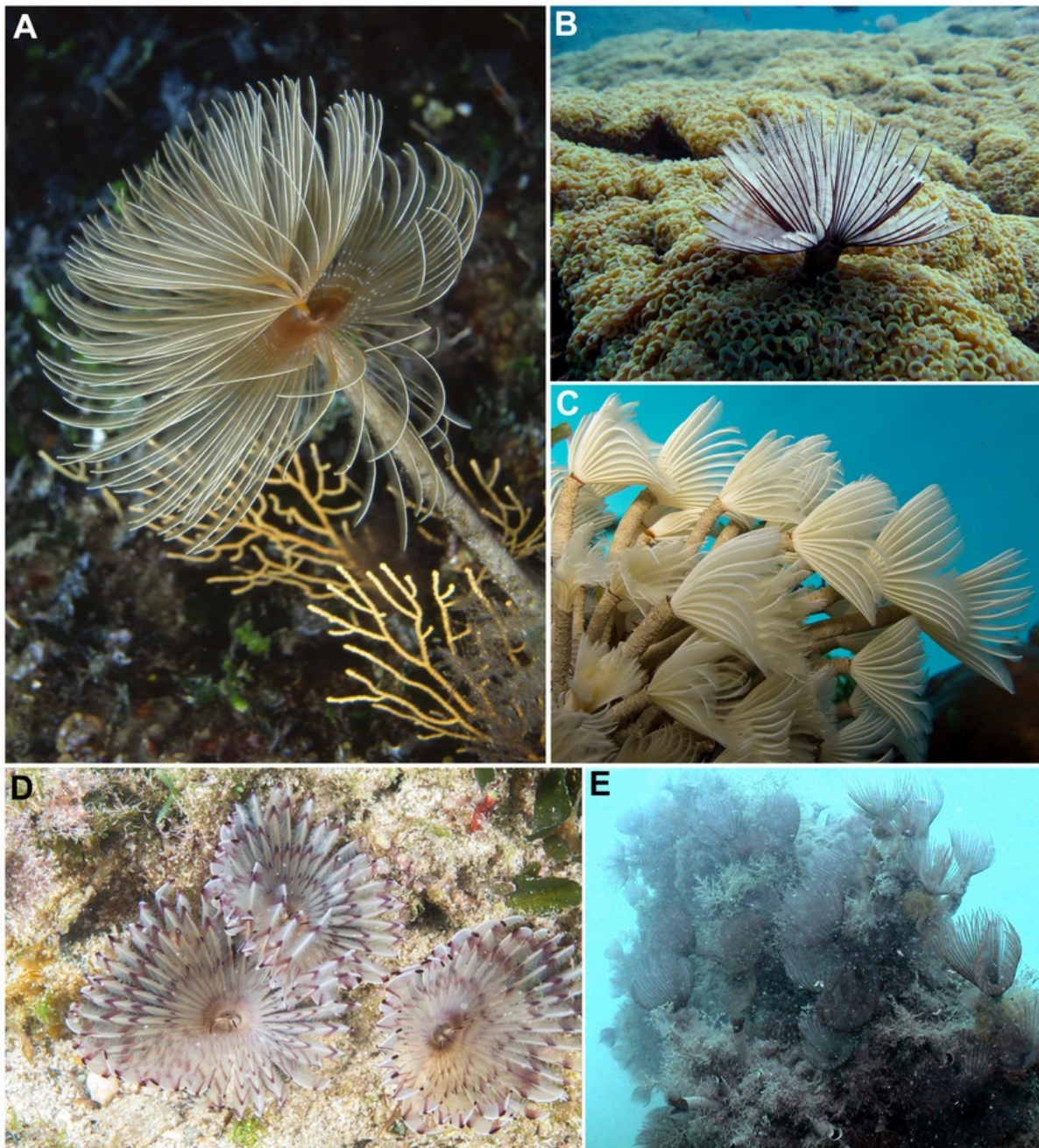


Fig. 16 Sabellids in their environment. A, *Sabella spallanzanii* from Italy; B, *Sabellastarte* sp. from Indonesia; C, *Bispira brunnea* from Mexico; D, *Bispira viola* from Italy; E, *Branchiomma luctuosum* from Italy; Images by: A, R. Pronzato; B, C. Pichon; C, H. Bahena-Basave; D, S. Causio; E, F. Mastrotoaro.

Considering the distribution within continental shelf, a latitudinal pattern can be outlined at generic level. Thirty genera and most of the species are found in tropical areas, mainly in the Indo-Pacific (Giangrande & Licciano 2004, Fig. 17). *Caobangia*, *Amamobaea* Krøyer, 1856 and *Stylomma* are exclusive of the tropics (Jones 1974, Tovar-Hernández & Salazar-Vallejo 2006, Capa 2007), whilst *Megalomma*, *Sabellastarte*, *Sabellonga* Hartman, 1969, *Branchiomma*, *Bispira*, and *Notaulax* seem to have, with few exceptions, a tropical and temperate distribution (Perkins 1984, Knight-Jones & Perkins 1998, Knight-Jones & Mackie 2003, Tovar-Hernández & Knight-Jones 2006, Tovar-Hernández & Carrera-Parra 2011). Most of the genera abundant in the Indo-Pacific region are absent at high latitudes. By contrast, genera well represented in cold areas (such as *Chone*, *Euchone*, *Jasmineira*) are almost absent in the Indo-Pacific. The genus *Eudystilia* is present only in the northern hemisphere, whilst *Amphicorina*, is mainly distributed in the Southern Hemisphere (Giangrande & Licciano

2004). Lastly, *Perkinsiana* has 11 species distributed in southern cool areas and is particularly abundant in the Antarctic Ocean (Tovar-Hernández et al. 2012). The Antarctic region appears richer in number of genera than the Arctic (15 present in the Antarctic against nine in the Arctic) and shows a higher degree of endemism (AG, unpublished data).

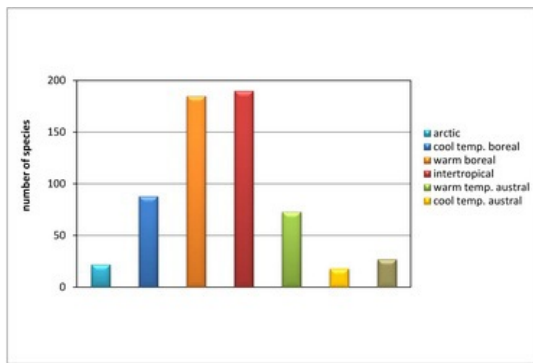


Fig. 17
Distribution of sabellid species richness among domains.

A number of recent revisions, in some cases including molecular data, have clarified and restricted the distribution of some species, as happened to *Chone duner* Malmgren, 1867 (Tovar-Hernández et al. 2007), *Megalomma vesiculosum* (Montagu 1815) (Giangrande & Licciano 2008), several species of *Branchiomm* (Capa et al. 2013a), *Sabella* (Knight-Jones & Perkins 1998), and *Sabellastarte* (Capa et al. 2011a). In this context, some species such as *Myxicola infundibulum*, formerly considered cosmopolitan, are at present object of investigation evidencing the existence of cryptic forms (Greaves et al. 2010).

The distribution range of some species was recently expanded following unintentional translocation out of their natural expected distribution range (e. g., Kuris & Culver 1999, Çinar et al. 2006, El Haddad et al. 2008, Çinar 2009, Tovar-Hernández et al. 2009 a, b, 2011, Gravili et al. 2010, Zenetos et al., 2011, 2012, Capa et al. 2014). In some cases, none or very little genetic variation between long distance and disjunct populations has been quantified, assessing the status as introduced of these species (Patti & Gambi 2001, Read et al. 2011, Capa et al. 2013a). A well-known case is the Atlantic-Mediterranean species *Sabella spallanzanii* (Fig. 16A) that about 20 years ago was introduced in Australia and subsequently in New Zealand. In these countries, *Sabella spallanzanii* became a pest, heavily impacting on marine ecosystems and causing serious coastal economic consequences (Lemmens et al. 1996). Other examples of invasive species are *Branchiomm* *lucuosum* (Grube 1870) originally described from the Red Sea, introduced in the Mediterranean basin at least 20 years ago and currently reaching densities of up to 900 ind m² (Bianchi 1983, Licciano et al. 2002, Çinar et al. 2006, El Haddad et al. 2008, Zenetos et al. 2011) and also reported from Brazil (Nogueira et al. 2006); and *Branchiomm* *bairdi* (McIntosh 1885) originally described from the Caribbean and recently reported in the Gulf of California, the Mediterranean, the Canary Islands and Australia (Çinar 2009, Tovar-Hernández et al. 2009a, b, 2011, Zenetos et al. 2011, Giangrande et al. 2012, Arias et al. 2013, Capa et al. 2013a), reaching densities of 16 ind m² in the Mediterranean (Arias et al. 2013) and 18000 ind m² in the Gulf of California (Tovar-Hernández et al. 2014).

Biology and Behavior

Sabellids are epibenthic suspension feeders exposing their radiolar crown out of their tube for collecting particles from the water column (Figs. 1A, 116A-E). The radiolar crown can be protected from hostile environment or predation by quickly and completely retracting inside the tube (Higuchi et al. 1986, Giangrande 1991, Licciano et al. 2012). Moreover, autotomy of the radiolar crown can occur in some taxa as an escape mechanism (to distract predators whilst the worm retracts inside tube), as a selective mechanism (rejecting a crown that has been mutilated or suffers malformation), or as a response to stress (Kennedy & Kryvi 1980) like for example in *Sabella spallanzanii* (Giangrande et al. 2014).

Radiolar crown has a role also in gas exchange. It accounts for 80% of the total respiration in species having a strongly attached crown (Giangrande 1991), but worms losing the crown (explained below) can compensate their gas exchange needs with body wall respiration. This is made possible by rhythmic movements of the body that generate currents of the water contained in the tube in both directions (i. e., irrigation) (Giangrande 1991, Nash & Keegan 2003). The involved respiratory surfaces seem to be the ventral shields and the parapodial areas, both greatly vascularized (Giangrande 1991). Some species open apart the two halves of the crown almost forming one plane (Figs. 1B, C, 2A-D), while others keep them close forming a shallow funnel around their mouth (Figs. 1D, 4A). The expanded radioles and the arrangement of each of the two rows of pinnules (forming an angle of over 90°) generate an intricate grid for capturing particles from the water column (Nicol 1931). Water currents are created by the cilia on the pinnules and the ventral radiolar appendages if present (Bonar 1972). When particles are collected by the cilia they are directed into the ciliated groove located at the inner side of the radioles, where they are taken down to the mouth area with the help of mucus secreted by epithelial cells (Nicol 1931, Bonar 1972).

In most sabellids, a sorting of particles according to their size takes place, a process in which radiolar structures such as the dorsal lips and radiolar appendages play a main role (Bonar 1972, Perkins 1984). The small-sized particles are swept into the mouth as food, the medium-sized ones enter the ventral sacs to be used for tube building (when present Fig. 3E-G), and the large-sized ones are rejected off the dorsal lips and radiolar appendages. Medium size particles are cemented together with mucus, molded into strings at the edges of the anterior end of the tube, so that the anterior portion of the tube. Small species with no such radiolar appendages use the dorsal lips for rough material sorting in two categories (Bonar 1972).

Most of the species feed on phytoplankton, but they also can utilize both particulate and dissolved organic matter, as well as bacterioplankton (Licciano et al. 2005, 2007). Gut content of *Bispira volutacornis* (Montagu 1804) included rests of benthic diatoms, peridinians, silicoflagellates, foraminiferans, tintinnids, annelid/crustaceans bristles and detritus (Nash & Keegan 2003).

The ventral shields present in most sabellids secrete a semi-transparent material consisting of a mucopolysaccharide-protein complex secreted by the ventral shield glands or other epithelial glands. This mucus is used to cement different particles in tube building, which is a constant process accompanying animal growth. The ventral sacs and some of the anterior appendages, when present, are involved in the growth and reconstruction of the anterior end of the tube, while the pygidial structures and epithelium that secretes mucus, are responsible of the tube building at the posterior end (Nicol 1931). The ventral sacs and the collar folds, when present, are the two most essential parts of the sediment-tube building apparatus. *Myxicola* lacks both of these

structures, reason why its tube is entirely built with the mucus secreted by the glands occurring dorsally as well as ventrally, and no sediment is attached (Nicol 1931). In *Chone*, and probably other small sabellids, the sorting mechanism is only rudimentary and no is collected for tube building. Worms out of a tube immediately start boring into the sediment with its pygidium, initially laying on its ventral surface but soon rolling from side to side gaining traction on the substratum with its parapodial setae and pushing deeper into the sediment. Glands in the epidermis secrete mucus so around its surface sticking sand, shell fragments, fecal material, and assorted debris forming a thin sand-covered tube (Bonar 1972). The mucus outer layer hardens but its production is continuous, lubricating the inside of the tube and making it also thicker (Bonar 1972). The resulting tube is oriented vertically in the sediment, is two or three times the length of the animal. However, *Chone* is not as sedentary as most tube-worms and can leave and build several tubes within a week (Bonar 1972). Tube building in *Glomerula pilosetosa* has not been studied but it is possible that members of this species have secretory glands in the collar similar to those present in serpulids.

The role of mucous secretions has been investigated not only in tube building process but also in absorbing metabolites (Bonar 1972). Sabellids, as other invertebrates, can release defensive molecules against microorganisms and/or epibionts mixed with their mucus (Bonar 1972, Stabili et al. 2009). A defensive haemolytic activity of the mucus in *Sabella spallanzanii* (Canicatti et al. 1992) may be related with their association to eutrophic environments that require efficient mucosal defense mechanisms since they are under constant threat from a rich mixture of microorganisms in the surrounding water (Stabili et al. 2006, 2009, 2011).

Unlike serpulids that left a significant fossil record, sabellid fossils are uncommon. A reported case is that of *Glomerula lombricus* (Defrance 1827) as encrusters on scleractinian corals from the Agrio Formation (Early Cretaceous; 132-126 Million years ago) in Neuquén Basin, Argentina (Garberoglio & Lazo 2011). Subsequently, several fossil species of *Glomerula* have been recorded for the Netherlands, Campan, Maastricht, Belgium and northern Germany (Jäger 2004, 2012, Kočí 2012). Not long ago *Calcisabella piloseta* Perkins, 1991 was described as the first sabellid with calcareous tube. This monotypic genus is currently considered synonymous of *Glomerula* (Jäger 2004) and the species *Glomerula pilosetosa* represents the unique extant species of the genus, endemic from the Great Barrier Reef, Australia. The ultrastructure of the tubes of *Glomerula* is clearly different from that of serpulids suggesting that the acquisition of calcareous tubes is an evolutionary convergence with serpulids (Vinn et al. 2008).

Symbiosis

Sabellids can act both as host and symbiont. In their large revision of symbiotic polychaetes, Martin and Britayev (1988) mentioned Sabellidae as boring parasites. Some interactions between these boring worms and their hosts seem to be negative, making the species to be labelled as “parasitic” borers. Among them, *Caobangia* (Fig. 1H) exclusively inhabits shells of several fresh-water genera of snails (Jones 1974) and *Terebrasabella heterouncinata* Fitzhugh & Rouse, 1999 (Ruck & Cook 1998, Fitzhugh & Rouse 1999) burrows in the shells of various marine gastropods. Infestation by *Terebrasabella heterouncinata* has been shown to cause deformation and weakening of the shell, a reduction in the growth rate, or the death of the abalone and marketability of cultured abalone in South Africa and California, where it was recently introduced (Fitzhugh 1996, Oakes & Fields 1996, Culver et al. 1997). Members of *Megalomma*, *Notaulax*, *Perkinsiana*, *Pseudopotamilla* can bore into of dead coral and limestone (Chugthai & Knight-Jones 1988, Nishi & Nishimira 1999, Fonseca et al. 2006).

Copepods belonging to the families Gastrodelphyidae List, 1889 and Sabelliphilidae Gurney, 1927 are typically external symbionts of Sabellidae (Boxshall & Halsey 2004; Fig. 18A-C), and only one species of Rhynchomolgidae Humes & Stock, 1972 was recorded as parasite of sabellids, associated to *Myxicola infundibulum* (Bocquet & Stock 1958).

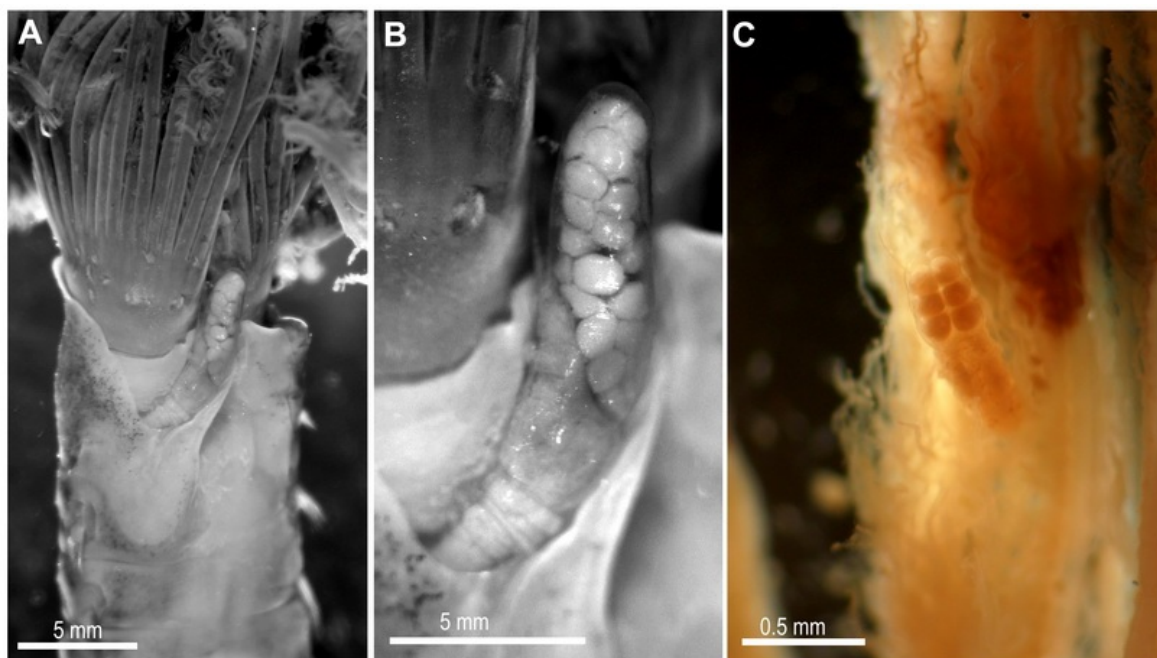


Fig. 18
Symbiont copepods. A, The copepod *Gastrodelphys dalesi* attached to the dorsal pockets of collar in *Megalomma circumspectum* from Mexico; B, Detail of *Gastrodelphys dalesi*; C, *Sabellacheres antarcticus* attached to radioles of *Perkinsiana antarctica*. A-C, Light photographs. Images by: A-B, M. A. Tovar-Hernández; C, B. Yáñez-Rivera.

Some copepods, such as *Gastrodelphys dalesi* (Green 1961), can utilize different sabellid species as hosts (Dudley 1964, Boxshall & Halsey 2004, Gómez & Tovar-Hernández 2008). By contrast *Gastrodelphys clausii* Graeffe, 1883 is only known from *Bispira volutacornis* (Nash & Keegan 2006). Species of *Sabellacheres* Sars, 1862, are known to establish species-specific relationships with sabellid hosts: *Sabellacheres gracilis* Sars, 1862 with *Myxicola*

infundibulum, *Sabellacheres aenigmatopygus* Carlton, 1971 with *Pseudopotamilla reniformis*, *Sabellacheres drachi* Laubier, 1968 with *Potamilla torelli* (Malmgren 1866), and *Sabellacheres antarcticus* Suárez-Morales & Boxshall, 2012 with *Perkinsiana brigittae* Tovar-Hernández et al., 2012 (Dudley 1964, Laubier 1968, Carton 1971, Boxshall & Halsey 2004, Suárez-Morales & Boxshall 2012). Moreover, *Sabelliphilus elongatus* Sars, 1862 has only been found on the radioles of *Sabella pavonina*, and *Sabelliphilus sabelliphilus sarsi* Claparède 1870 on *Sabella spallanzanii* (Gotto 1960, Carton 1966). It has been reported that *Sabelliphilus elongatus* extracts oil or fat by slight erosion of the pigmented epithelium, and may also utilize its mucus. Nevertheless, although these copepods are reported to be ectoparasites there are no specific studies concerning the infestation, and much of the nature of the association between copepods and their sabellid hosts remains largely unknown (Nash & Keegan 2006).

The life cycle of *Ceratomyxa auerbachii* Kabata, 1962, a myxosporean parasite of the Atlantic herring *Clupea harengus* Linnaeus, 1761, requires *Chone infundibuliformis* Krøyer, 1856 as an alternate invertebrate host. During the life cycle of this parasite the actinospore is released from the coelom of the sabellid host, infests the fish and develops in the kidney to form a parvicapsula myxospore which is the stage infective to the polychaete worm (Køie et al. 2008). Recently, an unidentified parasite gregarine apicomplexan, has been found within the coelomic cavity of *Branchiommma bairdi* (Arias et al. 2013).

Phylogeny

The first sabellid described was *Sabella penicillus* Linnaeus, 1767, and the family Sabellidae was erected by Latreille in 1825. A close relationship between Sabellidae (including Fabriciinae) and Serpulidae has always been assumed, being the group classified under names such as Serpulacea (Grube 1850), Sabelliformia (Benham 1896) or Serpulimorpha (Uschakov 1955). The current name for the order Sabellida was established by Dales in 1962, but the order has suffered changes in its composition along time (Fauchald 1977, Fitzhugh 1989, Rouse & Pleijel 2001, among others). It is now mostly accepted the restricted use of Sabellida to accommodate three families: Sabellidae, Serpulidae and Fabriciidae (Kupriyanova & Rouse 2008, Capa et al. 2011a).

The change on the concept of Sabellida through time has also impacted on the diagnosis of Sabellidae. Fitzhugh (1989) performed the first phylogenetic analysis of the group, synonymized with Sabellidae some taxa previously considered as separate families (i.e. Sabellongidae Hartman 1969 and Caobangiidae Jones 1974), and subdivided the family into two subfamilies, Sabellinae and Fabriciinae, emending the diagnoses of both. Rather than the presence of avicular or acicular uncini, which were thought by that time to separate Sabellinae from Fabriciinae (Rioja 1923, Fauchald 1977), or the presence or absence of thoracic uncinal companion chaetae (Fauchald 1972), the author showed that what separates these two groups are the presence of at least two rows of vacuolated skeletal cells within the radioles, with the exception of *Caobangia*, and the dorsal fusion of radiolar lobes, both characters occurring in Sabellinae and not in Fabriciinae (Fitzhugh 1989, 1991).

This view of Sabellidae changed recently, when Serpulidae was found nested within Sabellidae and sister to Fabriciinae (Kupriyanova & Rouse 2008, Capa et al. 2011b, Fig. 19A). Kupriyanova and Rouse (2008) raised the fabriciid clade to family level, while Capa et al. (2011b) added the presence of dorsal and ventral lips as diagnostic for Sabellidae, together with several synapomorphies for Fabriciidae. As currently conceived, Sabellidae counts on 40 genera. The most comprehensive phylogeny to date, including both morphological and molecular data included representatives of 20 of these genera, among a broad range of outgroups (Capa et al. 2011a, Fig. 19A). Sabellidae was found to gather two major clades, none of them with robust support. These clades are somehow consistent with other recent phylogenetic hypothesis based in morphological features, with the exception of the position of the *Amphicorina-Myxicola-Chone-Dialychone-Jasmineira-Fabrisabella* group and related taxa (e. g., Nogueira et al. 2010, Fig. 19B), basal in analyses that only consider morphological features but not in combined molecular and morphological analyses. Nevertheless, further studies need to be undertaken before formulating conclusions about the evolution of features within the sabellid radiation.

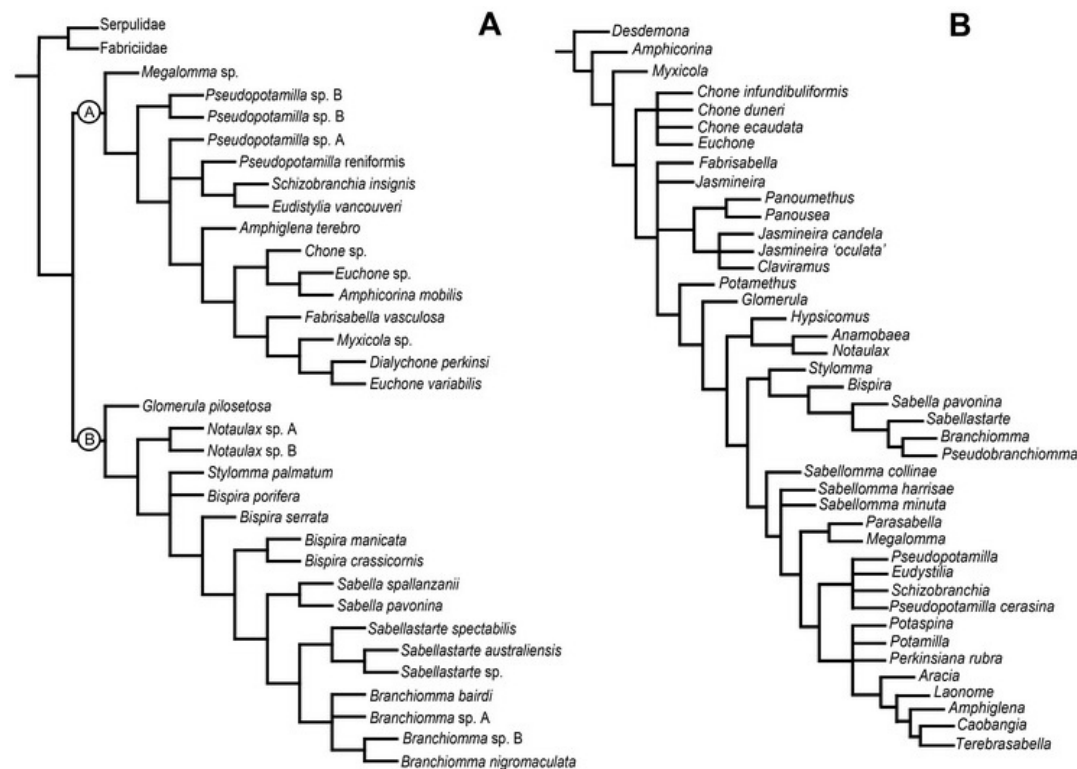


Fig. 19 Phylogenetic hypotheses within Sabellidae based on: A, morphological and molecular data (fragments of the nuclear ribosomal RNA genes 18S and 28S, and the mitochondrial gene 16S); B, morphological data. A modified from Capa et al. 2011a, B modified from Nogueira et al. 2010.

Classification

The diagnoses for Sabellidae and each of its genera are given below. Numbers of currently accepted nominal species are also given, but some genera need a deep taxonomic revision. When numbers are tentative, it has been indicated with an asterisk. A relative measure of the size of the specimens is given in the diagnoses: forms less than 1 cm long were considered short bodied, medium-sized taxa are between 1–5 cm long, and those longer than 5 cm are considered herein as long-bodied.

Family Sabellidae Latreille, 1825

Type genus: *Sabella* Linnaeus, 1767.

Diagnosis: Tube dwelling annelids inhabiting mucous tubes, frequently with particles of sediment embedded (*Glomerula* represents the exception, with calcified tubes). Radiolar crown with two basal lobes fused dorsally, supported by an internal structure of vacuolated cells arranged in at least two rows along radiolar axes (except for *Caobangia*, which has a single row). Radiolar crown with dorsal and ventral lips, vacuolated cells frequently also supporting dorsal lips. Radiolar flanges, basal membrane, basal flanges, and dorsal and ventral radiolar appendages present or not. Peristomium subdivided in two rings; posterior peristomial ring usually forming a collar around base of radiolar crown. Notopodia from segment 1, neuropodia from segment 2. Thoracic notopodia with chaetae arranged in superior and inferior groups. Thoracic neuropodia with acicular or avicular uncini, sometimes with companion chaetae. Abdominal notopodia with avicular uncini, or as rasp-shaped plates. Abdominal neuropodia with neurochaetae arranged in anterior and posterior groups. Compound eyes or eyespots frequently present on radioles, peristomium, body segments (interramal eyespots) and pygidium. Pygidial cirrus absent or present.

***Amphicorina* Claparède 1864**

Type species: *Fabricia (Amphicorina) armandi* Claparède 1864, by subsequent monotypy (Rouse 1994).

40 species.

Diagnosis: Short bodied sabellids, with 2–5 pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent. Radiolar eyes absent. Dorsal radiolar and pinnular appendages both absent; 1–2 pairs of ventral radiolar appendages. Ventral lips present; parallel lamellae and ventral sacs absent. Anterior peristomial ring with ventral lobe entire or bifurcated. Posterior peristomial ring collar with mid-dorsal gap and straight, crenulated, or with small ventral notch on anterior margin. Peristomial vascular loops absent. Peristomial eyespots present. Thorax with eight chaetigers, abdomen with 4–15. Glandular ridge on chaetiger 2 present, not always conspicuous. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior thoracic notochaetae of following chaetigers elongate, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae. Thoracic uncini acicular, with teeth above main fang arranged on transverse rows, progressively shorter, or with at least one distinctly larger tooth on proximal row; neuropodial companion chaetae absent. Abdominal uncini with rasp-shaped dentition, main fang present, handle absent and poorly developed, squared to rectangular breast. Abdominal neurochaetae as needle-like chaetae, on anterior group, and modified, elongate, narrowly hooded chaetae, on posterior one. Pygidium with eyespots. Pygidial cirrus absent. Main references: Fitzhugh 1989, Rouse 1994 (as *Oriopsis* Caullery & Mesnil, 1896), Giangrande et al. 1999, Yoshihara et al. 2012.

***Amphiglana* Claparède 1864**

Type species: *Amphicora mediterranea* Leydig, 1851, designated by Bush (1905).

12 species.

Diagnosis: Short bodied sabellids (Fig. 1E), with 4–8 pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present; dorsal basal flanges absent, ventral basal flanges present. Radiolar eyes absent. Dorsal lips with radiolar appendages, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips, parallel lamellae and ventral sacs absent. Anterior peristomial ring low, of even height. Posterior peristomial collar absent (Fig. 1E). Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with 7–9 segments; abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, broadly hooded; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and medium to long-sized handle; neuropodial companion chaetae with distally elongated tear-drop shaped hood. Abdominal uncini avicular, with several rows of progressively shorter teeth, developed breast and short to medium-sized handle. Abdominal neurochaetae of anterior group as elongate, broadly hooded chaetae, posterior group of abdominal neurochaetae absent. Pygidium with eyespots. Pygidial cirrus absent. Main references: Fitzhugh 1989, Rouse & Gambi 1997, Capa & Rouse 2007.

***Anamobaea* Krøyer, 1856**

Type species: *Anamobaea orstedii* Krøyer, 1856, by monotypy.

2 species.

Diagnosis: Medium sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Radiolar crown with elongate basal lobes; basal membrane present, radiolar flanges absent, dorsal and ventral basal flanges present. Radiolar eyes as numerous eyespots arranged in longitudinal rows in restricted area of radioles. Dorsal lips with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips and parallel lamellae present; ventral sacs inside the radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar present, with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and short ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax and abdomen with numerous chaetigers, each over 30 (such long thorax is unique among sabellids). Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae as superior notochaetae of following chaetigers, spine-like; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with similar in size teeth arranged transverser rows above main fang, developed breast and medium sized handle; neuropodial companion chaetae with roughly symmetrical hood and gently tapering distal end. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae paleate on anterior group, and modified, elongate, narrowly hooded chaetae on posterior one. Pygidial eyespots unknown. Pygidial cirrus absent. Main references: Fitzhugh 1989, Tovar-Hernández & Salazar-Vallejo 2006.

***Aracia* Nogueira, Fitzhugh and Rossi, 2010**

Type species: *Kirkia heterobranchiata* Nogueira, López and Rossi, 2004, by original designation.

3 species.

Diagnosis: Short bodied sabellids, with 4–6 pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal lips low and rounded, dorsal radiolar and pinnular appendages absent; ventral radiolar appendages present. Ventral lips present; parallel lamellae and ventral sacs absent. Anterior peristomial ring low, of even height. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots present. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with short handle, developed breast and several rows of progressively shorter teeth above main fang; neuropodial companion chaetae with denticulate head and long, gently tapering roughly symmetrical tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of anterior group as elongate, broadly hooded chaetae, posterior group with modified, elongate, narrowly hooded chaetae. Pygidial eyespots present in juveniles. Pygidial cirrus absent. Main references: Nogueira et al. 2004, Tovar-Hernández 2014.

***Bispira* Krøyer, 1856**

Type species: *Amphitrite volutacornis* Montagu, 1804, designated by Bush (1905).

22 species.

Diagnosis: Mediu

m to large sized sabellids, with numerous pairs of radioles in semicircular (Fig. 16D) to spiral radiolar lobes; each with at least four rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent. Paired compound eyes usually present along radioles (Fig. 3C). Dorsal lips with radiolar and pinnular appendages (Fig. 2C); ventral radiolar appendages absent. Ventral lips and parallel lamellae present; ventral sacs outside radiolar crown (Fig. 3E). Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with at least eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae similar to superior notochaetae of following chaetigers elongate, narrowly hooded; inferior thoracic notochaetae spine-like (Fig. 6B). Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with assymetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of anterior group in C-shaped to spiral arrangement, chaetae of posterior group enclosed in the arc; spine-like chaetae on anterior group and modified, elongate, narrowly hooded chaetae, on posterior one. Pygidium with eyespots. Pygidial cirrus absent. Main references: Fitzhugh 1989, Knight-Jones & Perkins 1998, Capa 2008.

***Branchiomma* Kölliker, 1858**

Type species: *Amphitrite bombyx* Dalyell, 1853, by monotypy (Fitzhugh 1989).

30 species.

Diagnosis: Short to large sized sabellids (Figs. 12A; 16E), with variable number of pairs of radioles in semicircular to one-whorled radiolar lobes, each radiole with at least four rows of vacuolated cells. Basal membrane present, radiolar flanges and basal flanges absent. Paired stylodes present on outer radiolar surface (feature unique among sabellids), variable in shape. Paired compound radiolar eyes present along radioles (Figs. 3D, 9B-C). Dorsal lips with radiolar appendages (Figs. 2B, 3H), pinnular appendages present or absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present; ventral sacs outside radiolar crown (Fig. 3G). Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar with mid-dorsal gap, fused or not to faecal groove laterally, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots may be present in juveniles and smaller species. Thorax usually with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae spine-like. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae absent. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of anterior group spine-like chaetae in C-shaped arrangement, chaetae of posterior group enclosed in the arc, elongate or modified, elongate, narrowly hooded chaetae, on anterior and posterior abdominal chaetigers, respectively. Pygidium frequently with eyespots. Pygidial cirrus absent. Main references: Fitzhugh 1989, Knight-Jones et al. 1991, Knight-Jones 1994, Nogueira et al. 2006, Tovar-Hernández & Knight-Jones 2006.

***Caobangia* Giard, 1893**

Type species: *Caobangia billeti* Giard, 1893, by monotypy.

7 species.

Diagnosis: Short sized sabellids (Fig. 1H), a few millimeters long, with three pairs of radioles in semicircular radiolar lobes; each with single row of vacuolated cells (unique feature among sabellids). Basal membrane, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal lips, ventral lips, ventral sacs and parallel lamellae all absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar absent. Peristomial vascular loops absent. Peristomial eyespots unknown. Thorax with seven chaetigers, abdomen with numerous segments. Glandular ridge on chaetiger 2 absent. Ventral shields inconspicuous. Interramal eyespots absent. Collar chaetae unknown, superior thoracic notochaetae of following chaetigers elongate, narrowly hooded, inferior thoracic notochaetae from chaetiger 3, narrowly hooded. Neuropodial uncini only present on chaetiger 2 as palmate hooks (Fig. 8E). Abdominal uncini avicular, with rasp-shaped crest, developed tapered breast and short handle; posterior uncini with elongate neck between breast and main fang. Abdominal neurochaetae as elongate, narrowly hooded chaetae to short, broadly hooded, in single group, probably the anterior one. Pygidial eyespots absent. Pygidial cirrus absent. Main references: Jones 1974, Fitzhugh 1989.

***Chone* Krøyer, 1856**

Type species: *Chone infundibuliformis* Krøyer, 1856, by original designation.

12 species.

Diagnosis: Large bodied sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent. Radiolar eyes absent. Dorsal lips rounded, radiolar appendages absent, dorsal pinnular appendages present; 2–8 pairs of ventral radiolar appendages. Ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with

narrow ventral lobe. Posterior peristomial ring collar present, usually with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with eight chaetigers, abdomen with variable number. Narrow glandular ridge on chaetiger 2. Ventral shields absent. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae and paleate. Thoracic uncini acicular, with teeth above main fang of different sizes arranged on transverse rows, medial tooth of basal row larger, hood present, handle long; neuropodial companion chaetae absent. Abdominal uncini with squared to rectangular breast, handle absent, few rows of teeth above main fang; uncini progressively larger from dorsal to ventral edges of tori. Abdominal neurochaetae of anterior group as elongate, narrowly hooded chaetae, on anterior abdominal chaetigers, and modified, elongate, narrowly hooded chaetae on posterior group of anterior abdominal chaetigers, and both groups of posterior segments. Pygidium with eyespots. Pygidial cirrus absent. Main references: Tovar-Hernández & Sosa-Rodríguez 2006, Tovar-Hernández 2008.

***Claviramus* Fitzhugh, 2002**

Type species: *Sabella candela* Grube, 1863, by original designation.

3 species.

Diagnosis: Short-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane absent, radiolar flanges only present at radiolar tips, expanded and cup-shaped (feature unique among sabellids), basal flanges absent; radiolar eyes absent. Dorsal lips with radiolar appendages, pinnular appendages apparently absent; ventral radiolar appendages present, few to several pairs. Ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with broad, triangular, ventral lobe. Posterior peristomial ring collar with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots may be present. Thorax with eight chaetigers, abdomen with 9–12. Glandular ridge on chaetiger 2 present or not. Ventral shields present on thorax, absent on abdomen. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae broadly hooded, or narrowly and broadly hooded. Thoracic uncini acicular, with short teeth above main fang arranged on transverse rows, hood present, handle long; neuropodial companion chaetae absent. Abdominal uncini avicular, with distinctly short handle, developed squared to rectangular breast and several transverse rows of short teeth above main fang. Abdominal neurochaetae in single group of narrowly hooded chaetae. Pygidium with eyespots present in at least some species. Pygidial cirrus absent. Main reference: Fitzhugh 2002.

***Desdemona* Banse, 1957**

Type species: *Desdemona ornata* Banse, 1957, by original designation.

3 species.

Diagnosis: Short bodied sabellids, with three pairs of radioles (Fig. 1F-G) in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane present, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal radiolar and pinnular appendages absent; one pair of ventral radiolar appendages. Ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with wide ventral lobe. Posterior peristomial ring collar absent. Peristomial vascular loops absent. Peristomial eyespots present. Thorax and abdomen each with eight chaetigers. Glandular ridge on chaetiger 2 present, not always conspicuous. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae. Thoracic uncini acicular, with similarly sized teeth above main fang arranged in transverse rows, hood absent, handle long; neuropodial companion chaetae absent. Abdominal uncini rasp-shaped, main fang present, handle absent and poorly developed breast. Abdominal neurochaetae as single group of modified, elongate, narrowly hooded chaetae. Pygidium with eyespots. Pygidial cirrus absent (Fig. 1F-G). Main references: Banse 1957, Hutchings & Murray 1984, Fitzhugh 1989.

***Dialychone* Claparède 1870**

Type species: *Dialychone acustica* Claparède 1870, by original designation.

18 species.

Diagnosis: Mid- to large sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent. Radiolar eyes absent. Dorsal lips elongate, radiolar and pinnular appendages both absent; ventral radiolar appendages present. Ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with triangular or bilobed ventral lobe. Posterior peristomial ring collar present, low, with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent or present. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge present on chaetiger 2, in some species also on other posterior thoracic and anterior abdominal segments. Ventral shields absent. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae and paleate. Thoracic uncini acicular with teeth progressively shorter, arranged on transverse rows above main fang, hood present, handle long; neuropodial companion chaetae absent. Abdominal uncini with breast squared to rectangular, handle absent, main fang with several rows of similarly sized teeth on top; uncini progressively larger from dorsal to ventral edges of tori. Abdominal neurochaetae as elongate, narrowly hooded chaetae. Posterior body with simple pre-pygidial depression. Pygidium with eyespots. Pygidial cirrus sometimes present. Main reference: Tovar-Hernández 2008.

***Euchone* Malmgren, 1866**

Type species: *Sabella analis* Krøyer, 1856, designated by Bush (1905).

34 species.

Diagnosis: Short to large bodied sabellids, with several pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges usually present, basal flanges absent. Radiolar eyes absent. Dorsal lips with radiolar appendages, dorsal pinnular appendages absent or present; 2–6 pairs of ventral radiolar appendages. Ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops present in *E. analis*. Peristomial eyespots absent. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 present. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae and paleate. Thoracic uncini acicular (Fig.

7F), with similarly sized teeth above main fang arranged on transverse rows, hood present, handle long; neuropodial companion chaetae absent. Anterior abdominal uncini with roughly triangular breast, or squared to rectangular (Fig. 7I), handle absent, main fang with several rows of similarly sized teeth on top; posterior abdominal uncini, especially on pre-pygidial depression, with rasp-shaped dentition (covering the entire length of main fang) or transitional between few rows of teeth (covering partially main fang) and rasp-shaped. Abdominal neurochaetae of anterior group as elongate, narrowly hooded chaetae on anterior abdominal chaetigers; modified, elongate, narrowly hooded chaetae on posterior group of anterior abdominal chaetigers and both groups of posterior segments. Posterior body with pre-pygidial depression (Fig. 5F-G) occupying at least three chaetigers, usually with lateral wings. Pygidial eyespots absent. Pygidial cirrus absent (Fig. 5F-G). Main references: Banse 1970, 1972, Fitzhugh 1989, Cochrane 2003, Bick & Randel 2005, Giangrande & Licciano 2006.

***Euchoneira* Licciano, Giangrande and Gambi, 2009**

Type species: *Euchoneira knoxi* Licciano, Giangrande and Gambi, 2009 by original designation.

Monotypic.

Diagnosis: Large species, with several pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal lips without radiolar and pinnular appendages; ventral radiolar appendages present. Ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar with wide mid-dorsal gap, dorsal margins entire (dorsal gap absent), with short mid-ventral incision, ventral lappets absent. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with eight chaetigers, large number of chaetigers in abdominal region. Glandular ridge on chaetiger 2 present. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae and broadly hooded. Thoracic uncini acicular with teeth progressively shorter, arranged on transverse rows above main fang, hood present, handle long; neuropodial companion chaetae absent. Abdominal notopodia with avicular uncini with well-developed handle, squared to rectangular breast, rows of teeth over the main fang similarly sized. Abdominal neuropodial fascicles with transverse rows of narrowly hooded chaetae on both groups. Pre-pygidial depression present, well developed, with lateral wings. Pygidial eyespots absent. Pygidial cirrus absent. Main reference: Licciano et al. 2009.

***Eudistylia* Bush, 1905**

Type species: *Sabella vancoveri* Kinberg, 1866, senior synonym of *Eudistylia gigantea* Bush, 1905, by original designation.

6 species*.

Diagnosis: Medium to large sized sabellids, with numerous pairs of radioles in spiraled radiolar lobes, each radiole with at least four rows of vacuolated cells; larger specimens sometimes with dichotomously branching radioles (feature unique among sabellids). Basal membrane, radiolar flanges and basal flanges absent. Unpaired compound radiolar eyes present on all radioles except for ventralmost pair. Dorsal lips with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips, parallel lamellae present, ventral sacs inside the radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax usually with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with roughly symmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of both groups elongate, broadly hooded chaetae. Pygidial eyespots may be present. Pygidial cirrus absent.

Main references: Bush 1905, Fitzhugh 1989.

***Euratella* Chamberlin, 1919**

Type species: *Laonome salmacidis* Claparède 1870, by monotypy.

1 species*.

Diagnosis: Radioles in semicircular radiolar lobes. Basal membrane present. Radiolar eyes present. Other radiolar structures unknown. Posterior peristomial collar reduced or absent. Thorax with eight chaetigers, abdomen with variable number. Superior notochaetae narrowly hooded, inferior thoracic notochaetae broadly hooded (probably paleate). Thoracic uncini avicular with short handle; neuropodial companion chaetae absent. Abdominal uncini similar to the thoracic ones. Other features not mentioned herein unknown.

Main references: Claparède 1870, Fauchald 1977.

***Fabrisabella* Hartman, 1969**

Type species: *Fabrisabella vasculosa* Hartman, 1969, by monotypy.

2 species.

Diagnosis: Medium-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent. Radiolar eyes absent. Radiolar crown often found incomplete, sectioned from abscission zone located above the radiolar bases (feature only shared with *Jasmineira*). Dorsal lips without radiolar appendages or pinnular appendages; ventral radiolar appendages present. Ventral lips present, parallel lamellae and ventral sacs absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar with narrow mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops present. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 present (Fig. 15A). Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini acicular, with teeth similar in size arranged on transverse rows above main fang, hood present, handle long; neuropodial companion chaetae absent. Abdominal uncini avicular, with long handle, breast reduced to narrow swelling and distinctly elongate neck between breast and main fang. Abdominal neurochaetae of anterior group as elongate, narrowly hooded chaetae, on anterior abdominal chaetigers, and modified, elongate, narrowly hooded chaetae on posterior group of anterior abdominal chaetigers, and both groups of posterior segments. Pygidial eyespots absent. Pygidial cirrus absent. Main references: Hartman 1969, Fauchald 1972, Fitzhugh 1989, 2002.

Glomerula Nielsen, 1931

Type species: *Serpulites gordialis* von Schlotheim, 1820.

7 species, of which one extant (previously known as *Calcisabella pilosetosa* Perkins, 1991) and six extinct.

Diagnosis: Short-sized sabellids, with five pairs of radioles in semicircular radiolar lobes, each radiole with four rows of vacuolated cells. Basal membrane and radiolar flanges both present, basal flanges most likely absent; radiolar eyes absent. Dorsal lips without radiolar or pinnular appendages; ventral radiolar appendages present, ventral lips and parallel lamellae present, ventral sacs unknown. Peristomial collar with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots present. Thorax with 11–15 chaetigers, abdomen with 9–12. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, narrowly hooded; inferior thoracic notochaetae broadly hooded. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and handle absent; neuropodial companion chaetae distally hooked. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae as elongate and modified, elongate, narrowly hooded chaetae, on both groups. Pygidial eyes unknown. Pygidial cirrus absent. Main reference: Perkins 1991.

Hypsicomus Grube, 1870

Type species: *Sabella stichophthalmos* Grube, 1863, subsequent designation by Bush (1905).

monotypic.

Diagnosis: Medium sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Radiolar crown with elongate basal lobes, basal membrane and radiolar flanges present, basal flanges absent. Numerous radiolar eyespots arranged in longitudinal groups on lateral sides of radioles. Dorsal lips with radiolar appendages, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Posterior peristomial ring with two pairs of accessory lamellae, between the dorsal collar margins (feature unique among sabellids). Peristomial vascular loops absent. Peristomial eyespots absent. Thorax and abdomen with numerous chaetigers. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, spine-like; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of minute teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with roughly symmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of anterior group paleate; posterior group with elongate, narrowly hooded and modified, elongate, narrowly hooded chaetae, on anterior and posterior abdominal segments, respectively. Pygidial eyespots may be present. Pygidial cirrus absent. Main references: Perkins 1984, Fitzhugh 1989.

Jasmineira Langerhans, 1880

Type species: *Jasmineira caudata* Langerhans, 1880, by monotypy.

16 species*.

Diagnosis: Short to medium-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each with two rows of vacuolated cells. Basal membrane, radiolar flanges and basal flanges absent. Radiolar eyes absent. Radiolar crown often found incomplete, sectioned from abscission zone located above the radiolar bases (feature only shared with *Fabrisabella*). Dorsal lips with or without radiolar appendages, pinnular appendages absent; ventral radiolar appendages present; ventral lips present, ventral sacs and parallel lamellae absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar present with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops present in some species. Peristomial eyespots absent. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 present. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae as bayonet-chaetae and paleate (Fig. 6C). Thoracic uncini avicular, teeth similar in size arranged on transverse rows above main fang (Fig. 8A), hood present; neuropodial companion chaetae absent. Abdominal uncini avicular, with long handle, breast reduced to narrow swelling and distinctly elongate neck between breast and main fang. Abdominal neurochaetae of anterior group as elongate, narrowly hooded chaetae on anterior abdominal chaetigers, and modified, elongate, narrowly hooded chaetae on posterior group of anterior abdominal chaetigers, and both groups of posterior segments. Pygidium without eyespots. Pygidial cirrus absent or present (Fig. 5H). Main references: Knight-Jones 1983, Fitzhugh 1989, 2002.

Laonome Malmgren, 1866

Type species: *Laonome kroyeri* Malmgren, 1866, by monotypy.

9 species.

Diagnosis: Medium sized sabellids with numerous pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane reduced or absent, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal lips with or without radiolar appendages, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips present, parallel lamellae absent or fused together, ventral sacs absent. Peristomial collar present, usually with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thin, white transverse ridge at border between posterior peristomial ring and chaetiger 1 (feature unique among sabellids). Thorax usually with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded, inferior thoracic notochaetae paleate (Fig. 7A). Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast, handle absent (Fig. 7H); neuropodial companion chaetae usually absent. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae broadly hooded on both groups. Pygidial eyespots absent. Pygidial cirrus absent. Main references: Fitzhugh 2002, Capa 2007.

Megalomma Johansson, 1925

Type species: *Branchiomma köllikeri* Claparède 1870, a junior synonym of *Sabella lanigera* Grube, 1846.

34 species.

Diagnosis: Medium to large sized sabellids, with variable number of pairs of radioles in semicircular to circular radiolar lobes, each radiole with numerous rows of vacuolated cells (up to 30 cells). Basal membrane, radiolar flanges and basal flanges absent. One to several radioles with a single, sessile, compound radiolar eye, situated subdistally on inner margin of radiole (feature unique among sabellids, Figs. 1A, 2E-F, 12E-F). Dorsal lips with radiolar appendages, pinnular appendages absent or present; ventral radiolar appendages absent, ventral lips and parallel lamellae present, ventral sacs usually present, inside radiolar crown; keel and caruncle present in some species (Fig. 4G-H). Anterior peristomial ring low, of even height. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with at least eight chaetigers, abdomen with variable number. Glandular ridge on chaetigers 2-3 sometimes present. Ventral shields present. Interramal eyespots usually present. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae broadly hooded, classified into three types: type A (distal end narrowing abruptly), type B (progressively tapering distal tip), type C (emergent shaft thick, short and with rounded distal margin). Thoracic uncini avicular, with several rows similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with asymmetrical hood, teardrop shaped, with elongate tip (Fig. 8G). Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae as broadly or narrowly hooded chaetae on both groups, depending on the species. Pygidial eyespots absent. Pygidial cirrus absent. Main references: Fitzhugh 1989, 2003, Tovar-Hernández & Salazar-Vallejo 2008, Capa & Murray 2009, Tovar-Hernández & Carrera-Parra 2011.

***Myxicola* Renier in Meneghini, 1847**

Type species: *Terebella infundibulum* Renier, 1804, designated by Bush (1905).

7 species*.

Diagnosis: Medium to large sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent; radiolar eyes absent. Dorsal lips with radiolar appendages, pinnular appendages absent; 3-6 pairs of ventral radiolar appendages, ventral lips developed, extending dorso-ventrally along inner surface of base of radiolar lobes; parallel lamellae and ventral sacs absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar absent (Fig. 3I). Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with up to eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 present. Ventral shields absent. Interramal eyespots may be present. Thoracic notochaetae and abdominal neurochaetae in irregular bundles, arranged in low, circular tori, groups within fascicles not differentiated. Thoracic uncini acicular, with similarly sized teeth above main fang on transverse rows, hood absent, long handle; neuropodial companion chaetae absent. Abdominal uncini avicular, handle absent, breast developed and several rows of shorter teeth above main fang. Abdominal notopodial tori forming almost complete cinctures around body (feature unique among sabellids) with elongate, narrowly hooded chaetae. Pygidial eyespots absent. Pygidial cirrus absent.

Main references: Fitzhugh 1989, 2003, Capa et al. 2011.

***Notaulax* Tauber, 1879**

Type species: *Notaulax rectangulata* Levinsen, 1883, by monotypy.

20 species.

Diagnosis: Medium to large sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Radiolar crown with elongate basal lobes (Fig. 4A-B); basal membrane (Fig. 4A), radiolar flanges, and dorsal and ventral basal flanges present (Fig. 4B). Numerous eyespots arranged in longitudinal rows on lateral sides of radioles (Figs 1D, 9A). Dorsal lips with radiolar appendages, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, ventrally entire or with mid-ventral incision and short ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with at least eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae spine-like, arranged in distally oblique longitudinal rows (feature unique among sabellids); superior thoracic notochaetae spine-like, inferior thoracic notochaetae paleate (Fig. 6F). Thoracic uncini avicular, with several rows of minute and similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with strongly asymmetrical hood stouter on one margin (Fig. 8F) and thin, elongate tip. Abdominal uncini similar to the thoracic ones (Fig. 8C). Abdominal neurochaetae as paleate and needle-like chaetae, on anterior and posterior groups, respectively. Pygidial eyespots may be present. Pygidial cirrus absent. Main references: Perkins 1984, Fitzhugh 1989.

***Panoumethus* Fitzhugh, 2002**

Type species: *Panoumethus dubius* Fitzhugh, 2002, by monotypy.

Monotypic.

Diagnosis: Medium-sized sabellids, with eight pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal lips with radiolar appendages, pinnular appendages absent; 2-3 pairs of ventral radiolar appendages. Ventral lips and parallel lamellae both present, ventral sacs absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and short ventral lappets. Peristomial vascular loops absent. Peristomial eyespots unknown. Thorax with eight chaetigers, abdomen with numerous segments. Glandular ridge on chaetiger 2 present. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior thoracic notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini acicular, with similarly sized teeth above main fang on transverse rows, hood absent, long handle; neuropodial companion chaetae with asymmetrical hood and elongate tip. Abdominal uncini avicular, with several rows of short teeth above main fang, developed breast and handle reduced to short knob, Abdominal neurochaetae of both groups as narrowly hooded chaetae. Pygidial eyespots absent. Pygidial cirrus absent. Main reference: Fitzhugh 2002.

***Panousea* Rullier & Amoureux, 1969**

Type species: *Panousea africana* Rullier & Amoureux, 1969, by monotypy.

Monotypic.

Diagnosis: Medium-sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane, radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal lips with radiolar and pinnular appendages; several pairs of ventral radiolar appendages. Ventral lips and parallel lamellae present, ventral sacs inside the crown. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots unknown. Thorax with eight chaetigers, abdomen with numerous segments. Glandular ridge on chaetiger 2 present. Ventral shields present. Interramal eyespots absent. Collar chaetae in longitudinal, distally oblique rows of narrowly hooded chaetae; superior thoracic notochaetae elongate, narrowly hooded; inferior thoracic notochaetae as bayonet and paleate chaetae Thoracic uncini acicular, with similarly sized teeth above main fang arranged on transverse rows, hood present, handle long; neuropodial companion chaetae with roughly symmetrical hood and elongate tip. Abdominal uncini avicular, with several rows of short teeth above main fang, developed breast and handle reduced to short knob. Abdominal neurochaetae as elongate and modified, elongate, narrowly hooded chaetae. Pygidial eyespots absent. Pygidial cirrus absent. Main references: Rullier & Amoureux 1969, Fitzhugh 1989.

***Paradialychone* Tovar-Hernández, 2008**

Type species: *Chone americana* Day, 1973, designated by Tovar-Hernández (2008).

15 species.

Diagnosis: Medium to large sized sabellids, with 3–13 pairs of radioles in semicircular radiolar lobes, each radiole with two rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent; radiolar eyes absent. Dorsal lips with radiolar and pinnular appendages; 1–6 pairs of ventral radiolar appendages. Ventral lips present, parallel lamellae and ventral sacs absent. Anterior peristomial ring with triangular or bilobed ventral lobe. Posterior peristomial ring collar low, with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent or present. Thorax with eight chaetigers, abdomen with variable number. Ventral shields absent. Glandular ridge on chaetiger 2 present, narrow or laterally broader (Fig. 10B). Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae as bayonet and paleate chaetae. Thoracic uncini acicular, with transverse rows of progressively shorter teeth above main fang, larger tooth offset from midline on basal row, hood present, handle long; neuropodial companion chaetae absent. Anterior abdominal uncini, with roughly rectangular breast, handle absent, and large tooth at midline main fang on proximal row, followed by a series of smaller teeth; uncini progressively larger from dorsal to ventral edges of tori. Posterior abdominal uncini with hooked breast, handle absent. Abdominal neurochaetae as elongate and modified, elongate, narrowly hooded chaetae. Posterior body segments with pre-pygidial depression. Pygidium with eyespots. Pygidial cirrus may be present in some species. Main references: Tovar-Hernández 2008.

***Parasabella* Bush, 1905**

Type species: *Parasabella media* Bush, 1905 by original designation.

25 species.

Diagnosis: Medium to large sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Basal membrane and radiolar flanges present, basal flanges absent. Radiolar eyes usually absent. Dorsal lips with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Peristomial collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots may be present in juveniles. Thorax with up to nine chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae broadly hooded (Fig. 6A). Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with bulbous hood and elongated tip (feature unique among sabellids, Fig. 8H). Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae elongate and modified, elongate, narrowly hooded chaetae, the latter group only present on posterior group of posterior abdominal segments. Pygidial eyespots may be present in juveniles. Pygidial cirrus absent. Main references: Perkins 1984, Fitzhugh 1989.

***Perkinsiana* Knight-Jones, 1983**

Type species: *Sabella rubra* Langerhans, 1880, by original designation.

19 species.

Diagnosis: Short to medium-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with at least two rows of vacuolated cells, frequently four or more rows. Basal membrane and radiolar flanges present or absent, basal flanges absent. Radiolar eyes absent. Dorsal lips usually with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs absent. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots may be present in juveniles. First segment enlarged (about twice length of following ones). Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded, inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and handle variable in length; neuropodial companion chaetae with roughly symmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae fascicles with transverse rows of broadly hooded chaetae on anterior group; posterior group either with elongate, broadly hooded chaetae, on anterior abdominal segments, or elongate, narrowly hooded chaetae, on posterior abdominal chaetigers. Pygidial eyespots may be present. Pygidial cirrus absent. Main references: Knight-Jones 1983, Fitzhugh 1989, Capa 2007, Tovar-Hernández et al. 2012.

***Potamethus* Chamberlin, 1919**

Type species: *Potamis spathiferus* Ehlers, 1887, by monotypy.

9 species*.

Diagnosis: Medium-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells (one species with a single row). Basal membrane present, radiolar flanges and basal flanges absent; radiolar eyes absent. Dorsal lips with radiolar appendages, pinnular appendages absent; ventral radiolar appendages absent, ventral lips, parallel lamellae and ventral sacs all present, the latter inside

radiolar crown. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar present, of variable morphology. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 present. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, breast developed or not and medium-sized handle; neuropodial companion chaetae present, with long handle and distal asymmetrical tip. Abdominal uncini avicular, with several rows of short teeth above main fang, reduced breast, distinctly elongate neck between breast and main fang, and elongate handle. Abdominal neurochaetae as elongate, narrowly hooded chaetae, on anterior group, and modified, elongate, narrowly hooded chaetae, on posterior group. Pygidial eyespots absent. Pygidial cirrus absent. Main references: Knight-Jones 1983, Fitzhugh 1989.

***Potamilla* Malmgren, 1866**

Type species: *Sabella neglecta* Sars, 1850, designated by Bush (1905).

18 species*.

Diagnosis: Medium sized sabellids with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Basal membrane present, radiolar flanges and basal flanges absent; radiolar eyes absent. Dorsal lips without radiolar appendages, pinnular appendages present; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins fused laterally to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax usually with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae broadly hooded. Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with roughly symmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae as elongate, broadly hooded chaetae, on both groups. Pygidial eyespots probably present in juveniles. Pygidial cirrus absent. Main references: Knight-Jones 1983, Fitzhugh 1989.

***Potaspina* Hartman, 1969**

Type species: *Potaspina pacifica* Hartman, 1969, by monotypy.

2 species.

Diagnosis: Short to medium-sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Basal membrane present or absent, radiolar flanges absent, dorsal basal flanges absent, ventral flanges present or absent. Radiolar eyes absent. Dorsal lips with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs probably absent. Anterior peristomial ring low, of even height. Posterior peristomial ring collar with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots unknown. Thorax with 8–9 chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent (with doubts). Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Anterior Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with denticulate head and elongate, gently tapering symmetrical or asymmetrical tip; neurochaetae of last three thoracic chaetigers as subdistally bent, distally tapering spines replacing uncini (feature unique among sabellids); companion chaetae absent. Abdominal uncini avicular, with short to medium-sized handle, poorly developed breast and elongate neck between breast and main fang, with transverse rows of similarly sized teeth above main fang. Abdominal neurochaetae of both groups elongate, broadly hooded chaetae. Pygidial eyespots unknown. Pygidial cirrus absent. Main references: Fitzhugh 1989, Capa 2007.

***Pseudobranchiomma* Jones, 1962**

Type species: *Pseudobranchiomma emersoni* Jones, 1962, by monotypy.

17 species.

Diagnosis: Short to medium-sized sabellids, with variable number of pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Basal membrane and radiolar flanges present, the later usually with lateral serrations along some extension; basal flanges absent. Dorsal lips with radiolar appendages, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs outside radiolar crown. Peristomial collar with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots may be present in juveniles. Thorax with 4–14 chaetigers, usually less than eight, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae spine-like Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and short-sized handle; neuropodial companion chaetae absent. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of anterior group spine-like chaetae, in arc or spiral arrangement, and modified, elongate, narrowly hooded chaetae, enclosed in the arc, on posterior group. Pygidium with eyespots. Pygidial cirrus absent. Main references: Jones 1962, Fitzhugh 1989, Nogueira & Knight-Jones 2002, Knight-Jones & Giangrande 2003, Nogueira et al. 2006, Tovar-Hernández & Dean 2014.

***Pseudopotamilla* Bush, 1905**

Type species: *Amphitrite reniformis* Bruguère, 1789, by original designation.

16 species*.

Diagnosis: Medium sized sabellids with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells. Basal membrane, radiolar flanges and basal flanges absent. One to several unpaired compound radiolar eyes bulging along outer radiolar margins, on at least some dorsal radioles, except for dorsal-most pair (Fig. 9D). Dorsal lips with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar present, with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, with a mid-ventral incision and short ventral lappets, and usually also with dorso-lateral incisions. Peristomial vascular loops absent. Peristomial eyespots may be present. Thorax and abdomen with variable number of chaetigers. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of

following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with asymmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of both groups as elongate, broadly hooded chaetae. Pygidial eyespots may be present. Pygidial cirrus absent. Main references: Knight-Jones 1983, Fitzhugh 1989, Capa 2007.

***Sabella* Linnaeus, 1767**

Type species: *Sabella pavonina* Savigny, 1822, designated by Bush, 1905.

3 species.

Diagnosis: Medium to large sized sabellids, with numerous pairs of radioles with radiolar lobes in semicircles to spiraled arrangement (Figs. 3A, 16A), each with at least four rows of vacuolated cells. Basal membrane present (Fig. 3B), radiolar flanges and basal flanges absent. Radiolar eyes absent. Dorsal radiolar appendages present, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs outside radiolar crown (Fig. 3F). Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with at least eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded, inferior thoracic notochaetae spine-like. Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae present, with gently tapering asymmetrical tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of anterior group as spine-like chaetae, in spiraled arrangement, posterior group absent on anterior abdominal segments, as modified, elongate, narrowly hooded chaetae on posterior segments. Pygidial eyespots present. Pygidial cirrus absent. Main references: Fitzhugh 1989, Knight-Jones & Perkins 1998.

***Sabellastarte* Krøyer, 1856**

Type species: *Sabellastarte indica* Savigny, 1822, designated by Bush (1905).

8 species.

Diagnosis: Large sized sabellids, with numerous pairs of radioles in semicircular to spiraled arrangement (Fig. 16B), each radiole with at least four rows of vacuolated cells. Basal membrane present, radiolar flanges absent, dorsal basal flanges present, ventral flanges absent. Radiolar eyes absent. Dorsal radiolar appendages present, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring with narrow ventral lobe. Posterior peristomial ring collar present, with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with 7–9 chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded (Fig. 7E); inferior thoracic notochaetae spine-like (Fig. 7D). Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle (Fig. 8B); neuropodial companion chaetae absent. Abdominal uncini similar to the thoracic ones (Fig. 7G). Abdominal neurochaetae of anterior group spine-like, in a C-shaped or spiraled arrangement, posterior group with modified, elongate, narrowly hooded, and needle-like chaetae chaetae, on anterior and posterior abdominal segments, respectively. Pygidial eyepots present. Pygidial cirrus absent. Main references: Fitzhugh 1989, Knight-Jones & Mackie 2003.

***Sabellomma* Nogueira, Fitzhugh & Rossi, 2010**

Type species: *Parasabella minuta* Treadwel, 1941, by original designation.

3 species.

Diagnosis: Short to medium-sized sabellids with 4–9 pairs of radioles in semicircular radiolar lobes, each radiole with four rows of vacuolated cells. Basal membrane present, radiolar flanges and basal flanges absent. Radiolar eyes irregularly distributed along radioles. Dorsal radiolar appendages present, pinnular appendages absent or present; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs outside radiolar crown. Peristomial collar present, with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax usually with four to five chaetigers, abdomen with variable number. Glandular girdle on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded, inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of progressively shorter teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with slightly asymmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones; abdominal neurochaetae of both groups as elongate, narrowly hooded chaetae. Pygidium with eyespots. Pygidial cirrus absent.

Main reference: Nogueira et al. 2010.

***Sabellonga* Hartman, 1969**

Type species: *Sabellonga disjuncta* Hartman, 1969, by monotypy.

Monotypic.

Diagnosis: Medium sized sabellids known from a single complete specimen missing crown (Fitzhugh 1989). Ventral lips, parallel lamellae and ventral sacs all apparently present. Anterior peristomial ring not visible. Peristomial collar present, with wide mid-dorsal gap, mid ventral incision and ventral lappets. Peristomial vascular loops absent. Thorax with 13 chaetigers, abdomen with large numbers. Glandular girdle on chaetiger 2 absent. Ventral shields present. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with roughly symmetrical hood and gently tapering tip. Most Abdominal uncini similar to the thoracic ones, last five notopodia with falcate acicular spines replacing uncini (feature unique among sabellids); abdominal neurochaetae of both groups as elongate, broadly hooded chaetae. Pygidial eyespots probably present. Pygidial cirrus absent. Main reference: Fitzhugh 1989.

Genus *Schizobranhia* Bush, 1905

Type species: *Schizobranhia insignis* Bush, 1905, by original designation.

3 species.

Diagnosis: Medium to large sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with at least four rows of vacuolated cells; some radioles branched (feature unique among sabellids). Basal membrane and radiolar flanges absent, dorsal basal flanges present, ventral flanges absent. Unpaired compound eyes along radioles on all except for ventralmost pair. Dorsal lips with radiolar and pinnular appendages; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and short ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax usually with eight chaetigers, abdomen with variable number. Ventral shields present. Glandular ridge on chaetiger 2 absent. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded, inferior thoracic notochaetae paleate. Thoracic uncini avicular, with several rows of similar in size teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with roughly symmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Abdominal neurochaetae of both groups as elongate, broadly hooded chaetae. Pygidial eyespots may be present. Pygidial cirrus absent.

Main references: Bush 1905, Fitzhugh 1989.

***Stylomma* Knight-Jones, 1997**

Type species: *Sabella palmata* Quatrefages, 1866, by monotypy.

2 species.

Diagnosis: Medium-sized sabellids, with numerous pairs of radioles in semicircular radiolar lobes, each radiole with more than four rows of vacuolated cells. Basal membrane and radiolar flanges both present, dorsal basal flanges with anterior joint (feature unique among sabellids), ventral flanges absent; large unpaired compound radiolar eyes on inner surface of tip of radioles or close to it (unique among sabellids) or paired eyes along lateral sides of radioles. Dorsal radiolar appendages present, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips and parallel lamellae present, ventral sacs inside radiolar crown. Anterior peristomial ring low, of even height. Posterior peristomial ring collar with wide mid-dorsal gap, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with eight chaetigers, abdomen with variable number. Glandular ridge on chaetiger 2 absent. Ventral shields present. Interramal eyespots present. Collar chaetae like following chaetigers with superior elongate, narrowly hooded chaetae, and inferior spine-like chaetae. Thoracic uncini avicular, with several rows of minute feature unique teeth above main fang, developed breast and medium-sized handle; neuropodial companion chaetae with asymmetrical hood and gently tapering tip. Abdominal uncini similar to the thoracic ones. Anterior group of abdominal neurochaetae absent, posterior group with spine-like chaetae, in C-shaped arrangement. Pygidial eyespots may be present. Pygidial cirrus absent.

Main references: Knight-Jones & Perkins 1998, Capa 2007.

***Terebrasabella* Fitzhugh and Rouse, 1999**

Type species: *Terebrasabella heterouncinata* Fitzhugh and Rouse, 1999, by monotypy.

3 species.

Diagnosis: Short sized sabellids, a few millimeters long, with two pairs of radioles, each with two rows of vacuolated cells. Basal membrane and radiolar flanges both absent, dorsal basal flanges absent, ventral flanges present. Radiolar eyes absent. Dorsal radiolar appendages present, pinnular appendages absent; ventral radiolar appendages absent. Ventral lips, parallel lamellae and ventral sacs absent. Anterior peristomial ring indistinct. Posterior peristomial ring collar present, with narrow mid-dorsal gap, dorsal margins laterally fused to faecal groove, mid-ventral incision and ventral lappets. Peristomial vascular loops absent. Peristomial eyespots absent. Thorax with eight chaetigers, abdomen with three. Glandular ridge on chaetiger 2 absent. Ventral shields poorly marked. Interramal eyespots absent. Collar chaetae similar to superior notochaetae of following chaetigers, elongate, narrowly hooded; inferior thoracic notochaetae broadly hooded. Thoracic uncini of 2-3 types, anterior chaetigers with acicular uncini, with several rows of teeth above main fang, or palmate; posterior thoracic uncini avicular, with medium-sized handle, developed breast and similarly sized teeth above main fang; neuropodial companion chaetae present on chaetigers 2-6, with roughly symmetrical teardrop shaped hood and gently tapering tip, absent on chaetigers 7-8. Abdominal uncini acicular, breast poorly to well developed, several rows of teeth above main fang, or palmate. Abdominal chaetae of both groups narrowly hooded. Pygidial eyespots absent. Pygidial cirrus absent.

Main references: Fitzhugh & Rouse 1999, Murray & Rouse 2007.

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