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Sabellariidae Johnston, 1865

María Capa, Pat Hutchings

Introduction

Sabellariidae Johnston, 1865 is a well-defined, and highly specialized group of marine annelids commonly known as honeycomb or sandcastle worms. They live in characteristic tubes of cemented sand grains, other mineral or biogenic particles such as foraminifera (Kirtley 1994), sometimes attached to one another forming large reefs that can extend over several kilometers. They cannot survive out of their tubes and are unable to build new ones if removed from them. Sabellariids have a well-developed operculum with rows of golden paleae that can seal the entrance of the tube when the animal withdraws into it (Figs. 1A, B, Fig. 2A, C). Both structures, tube and operculum, provide protection from desiccation, silt deposition, and predators.

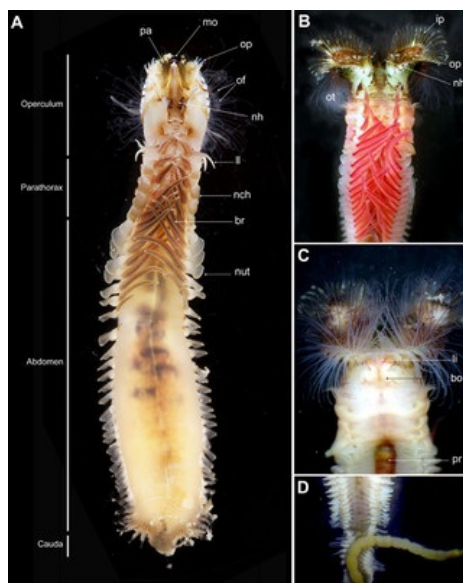


Fig. 1

Photographs of live specimens. A, *Lygdamis giardi* (McIntosh, 1885), dorsal view, from Lizard Island, Australia, showing the four specialized regions; B-D,

Idanthyrsus australiensis (Haswell, 1883), from Sydney, Australia; B, anterior end, dorsal view, C, anterior end, ventral view, D, posterior end, ventral view. (Photos A, A. Semenov; B-D, modified from Capa et al. 2012); br branchiae, ip inner paleae, ll lateral lobes (notopodial lobes chaetiger 2), mo median organ, nch notochoatae, nh nuchal hooks, nut notopodial uncinial tori, of oral filaments, op opercular papillae, op outer paleae, pa paleae.

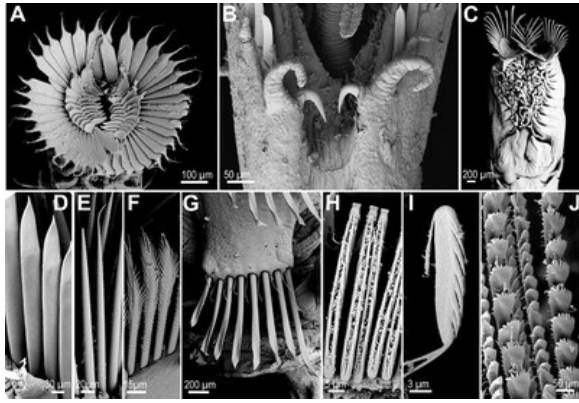


Fig. 2

A, Operculum, top view, *Sabellaria lungalla* Hutchings et al., 2012; B, Nuchal spines (hooks) and palps of *Lygdamis augeneri* Kirtley, 1994; C, Anterior end, ventral view of *Idanthyrsus australiensis* (Haswell, 1883); D-F, Outer paleae; D, *Lygdamis giardi* (McIntosh, 1885); E, *Phalacrostemma maloga* Hutchings et al., 2012; F, *Idanthyrsus nesos* Hutchings et al., 2012; G, Parathoracic notopodia of *I. australiensis*; H, Abdominal uncini of *I. australiensis*, frontal view; I, Abdominal uncini of *L. giardi*, lateral view; J, Detail of abdominal neurochaetae of *I. australiensis*.

The monophyly of Sabellariidae has been assessed (Capa et al. 2012, Hutchings et al. 2012), and relies on synapomorphies such as the presence of an operculum formed by the head and two anterior segments, a pair of peristomial palps, nuchal organs located at the base of palps, a building organ, oral filaments originating from segment 1 (not the peristomium), paleae on the anterior segments, uncini without a rostrum or main fang and without a handle or manubrium, segmental branchiae inserted dorsally on the parapodia and an expansion of the gut in the abdomen called the 'proventriculus'.

There are currently 130 nominal species (Hutchings et al. 2012) belonging to 12 genera, considered monophyletic in most but not in all cases (Capa et al. 2012, Hutchings et al. 2012). *Sabellaria* Lamarck, 1812, *Idanthyrsus* Kinberg, 1867, and *Lygdamis* Kinberg, 1867 represent more than half of all the species described in the family. In contrast, *Gunnarea* Johansson, 1927, *Paraidanthyrsus* Kirtley, 1994, and *Bathysabellaria* Lechapt & Gruet, 1993 have only one or two known species. Members of this family have been reported from all major oceans, and seas. Most described sabellariids live in intertidal or shallow depths but there are some genera, and species, restricted to the continental shelf or the deep sea. Although most genera seem to be broadly distributed or cosmopolitan, the species distribution and ecological niche appears to be geographically restricted and with bathymetric limitations, driven by abiotic factors required for settlement and tube-building (e.g. water temperature, water movement, availability of consolidated substrate and types and abundance of sediment) (Kirtley 1994, Bastida-Zavala & Becerril-Tinoco 2009). The best studied species are mainly gregarious and intertidal, and they are characterized by a long life span, very high fecundity, high dispersal capability and planktotrophic larvae which remain in the plankton for long periods (Giangrande 1997, McCarthy et al. 2003). In gregarious species, larval settlement is induced by the presence of conspecific reefs (Pawlik 1988a,b).

Some fossils tubes from Mexico, Chile and the USA, from the Cambrian (more than 550 million years old), have been attributed to members of this family (Caline et al. 1988, Pohler 2004). Recognizable sabellariid fossil tubes have been reported from the Pleistocene rocks in Chile (Philippi 1887, Kirtley & Tanner 1967).

Morphology

Sabellariids are medium sized annelids, with adults measuring 2-5 cm long. They have compact and wide bodies. Live animals are often pigmented brown or green with conspicuous red, brown or green branchiae due to blood pigments (Fig. 1A, B). Their segmented body is divided up into four specialized regions: the operculum, parathorax, abdomen, and caudal region. A review of the diverse terminology used to describe the various morphological features of the family has recently been undertaken (Capa et al. 2012), and the names proposed have been followed herein.

The operculum is the most characteristic feature of this group of annelids, and it is a complex, and specialized structure formed by the fusion of the head (prostomium and peristomium), and the first two chaetigers (thorax) (Figs. 1A, B, 2A, C). Two head outgrowths as fleshy lobes distally bear rows of simple chaetae, the paleae, and are surrounded by appendages called opercular papillae (Figs. 1A, B, 2A, C). The opercular lobes range from completely fused (*Bathysabellaria*, *Neosabellaria* Kirtley, 1994 and *Phragmatopoma* Mörch, 1863) to completely separated (*Gesaia* Kirtley, 1994, *Idanthyrsus*, *Lygdamis*, *Mariansabellaria* Kirtley, 1994, *Paraidanthyrsus*, *Phalacrostemma* Marenzeller, 1895, and *Sabellaria*), with the intermediate condition with a deep ventral groove on the ventral margin (*Gunnarea* and *Tetereus* Caullery, 1913). The distal end of the operculum, or the disc, is oriented perpendicular or obliquely to the longitudinal axis of the body (Fig. 2A). On the ventral and inner side of each opercular lobe, other simple (unbranched) or compound (branched) appendages, the tentacular or oral filaments may be inserted (Figs. 1C, 2C). Tentacular (oral) filaments are ciliated and often grooved proximally, and are involved in the transport of food particles to the mouth sediment particles for tube construction (Dales 1952, Orrhage 1978, Dubois et al. 2005, Riisgård & Nielsen 2006). In species of *Phalacrostemma*, the oral filaments are replaced by elongate buccal flaps or oral plates or by apophyseal ridges along the margins of the buccal cavity (Kirtley 1994, Capa et al. 2012). A pair of grooved, ciliated, and contractile (Treadwell 1926, Faroni-Perez pers. comm.) palps is present (Orrhage 1978, Orrhage & Eiby-Jacobsen 1998, Orrhage & Müller 2005).

The prostomium has been defined as a narrow ridge fused laterally to the first chaetiger (Dales 1952, Fauchald 1977) in species with completely separated opercular lobes and it is represented externally by a triangular area on the anterior ventrum between fused opercular stalks, between the mouth opening and the beginning of the oral filaments (Lechapt & Kirtley 1996). An unpaired appendage, referred to as the median organ, is present at the dorsal junction of the opercular lobes, when these are not completely fused (Kirtley 1994) or at the base of the operculum, in the anterior midline of prostomium, in *Bathysabellaria spinifera* Lechapt and Kirtley, 1996 with fused lobes, and is considered a prostomial structure (Lechapt & Kirtley 1996).

The opercular paleae are simple chaetae (often referred to as capillaries or spines) with a proximal shaft, attached to the muscular tissue (Ebling 1945, Kirtley 1994), and a distal exposed, and generally ornamented blade. Paleae consist of an inner core, striated longitudinally, and a clear, and homogeneous outer layer referred to as thecae with more or less packed fibers or microtubules (Ebling 1945, Kirtley 1994), thicker in the shaft than on the blade. In some paleae an alveolar structure can be observed, consisting of gas-filled cavities arranged in longitudinal and transverse rows. The chaetogenesis of paleae occur in two separate chaetigerous sacs on each lobe (Ebling 1945, Dales 1952, Orrhage 1978), forming each two distinct series of paleae; the outer and inner rows (Wilson 1929, Hartman 1944), corresponding to the chaetae from the first two anterior highly modified segments. Larval paleae are all similar in shape but intermediate forms are produced in juvenile stages until metamorphosis (Wilson 1929, Eckelbarger 1976, Eckelbarger & Chia 1976). During settlement the chaetal sacs rotate and the paleae that located on the innermost side become the outer paleae and vice versa, the chaetae sacs enlarge to form the opercular stalks continuing as separated lobes or else fusing together partially or completely (Fauchald 1977, Lechapt & Kirtley 1996).

Even though adults possess two rows of paleae, the orientation of their distal blades sometimes gives animals the appearance of presenting three concentric rows of paleae, the inner, and the median rows formed in the inner chaetigerous sac (Kirtley 1994). In those cases (*Neosabellaria*, *Phragmatopoma* and *Sabellaria* species), the blades of the median and inner row can be both directed inwards or the median paleae can be directed outwards. The outer paleae are generally arranged in facing semicircles on each side, but in species of *Phalacrostemma* they display a bi-spiral arrangement (Kirtley 1994). Opercular paleae are replaced during metamorphosis and subsequent adult growth changing their shape during ontogeny (Dales 1952, Gruet 1991). In larval stages (features retained in some adults), they have been classified as choanothecae, hemithecae, and platythecae depending on the shape of the section of the blade (for a description of different types see Kirtley 1994). Adults show a great diversity in number, shape, and size of paleae, and the terminology used for describing the different morphologies in the literature is highly variable (Fig. 2A, D-F). They display variation in the angle of the longitudinal axis of blades, and shafts (from straight to geniculate), the shape of the blade (flat, concave, or cylindrical), the shape of the lateral, and distal margins (smooth or denticulate), and most of the possible combination of these conditions can be found in some sabellariids, with up to four different paleae morphologies being present within a species (when two types of 'middle' paleae can be found in addition to the outer and inner paleae). Most sabellariids bear stout and cylindrical chaetae on the dorsal edge of the opercular lobes, called nuchal spines, with straight or bent distal pointed tips (also known as nuchal hooks, Fig. 1A, B), and with a more or less developed limbation on the inner or outer margin of the hooks (Fig. 2B). They are formed in the sacs of the opercular paleae, and are therefore considered as derived from chaetiger 1 (Orrhage 1978). Ventrally, on both sides of the building organ, the neuropodia of chaetiger 1 is provided with conical cirri, and capillary neurochaetae. The neuropodia of the second thoracic segment bears cirri, and bundles of capillary neurochaetae with thecae that make them appear as bipinnate (as referred to by Kirtley 1994). Dorsal cirri (one to three), referred herein as lateral lobes may be present in this segment, between the noto- and neuropodia (Fig. 1A, B). Branchiae can be present or absent on segment 2. Three or four parathoracic segments follow the thorax. They are provided with notopodia as enlarged lobes, and conical neuropodia. Although chaetae in neuropodia are smaller in size, notopodia bear retractile stout chaetae with lanceolate tips and cylindrical capillary chaetae alternating in one row (e. g. Kieselbach & Hausen 2008) (Fig. 2G). In some genera, the lanceolate chaetae are frayed or have denticulate tips. Neuropodia show higher variation between taxa and some species have both lanceolate chaetae and capillaries while others only bear capillaries or lanceolate chaetae. All segments have paired conical branchiae (Fig. 1A, B), provided with transverse rows of cilia. Glandular areas are present on the ventrum of this parathoracic region, and they produce adhesive substances for tube building (Vovelle 1965, Wang et al. 2010).

An abdominal region follows the parathoracic segments. This region can be easily separated by the presence of uncini in the notopodia. Some authors indicate an absence of lanceolate neurochaetae, and only the presence of capillaries in this region, although a gradual change has been observed in some species (Kieselbach & Hausen 2008). Abdominal segments are biramous, with notopodia as transverse tori, with a single row of pectinate uncini with two rows of similar-sized denticles pointing anteriorly, diminishing in width posteriorly (Fig. 2H, I), and neuropodia bearing conical ventral cirri, and fascicles of capillary chaetae arranged in one or two rows with two separated formation sites (Kieselbach & Hausen 2008) (Fig. 2J). Dorsal parapodial branchiae are present on abdominal segments, in some species they are restricted only to anterior abdominal segments while in others they are present to the pygidium, and decrease in size posteriorly (Fig. 1A, B).

The cauda is an apparently unsegmented body region (see Wilson 1929 for a different view point). It is a smooth and cylindrical tube that is curved along the ventral surface of the abdomen where faeces are evacuated through its distal anus (Fig. 1D).

Few studies have been undertaken on the internal morphology of Sabellariidae and available information is scant and patchy. The cuticle of *Sabellaria vulgaris* Verrill, 1873 lacks any collagenous orthogonal grid of thick fibrils (Storch 1988) as found in many other polychaetes. Myogenesis has been studied in *Sabellaria alveolata* (Brinkmann & Wanninger 2010). In the early trochophore stage the first muscles appear in close proximity to the chaetal sacs. Then pharyngeal musculature starts to form and the muscles of the chaetal sacs develop and later two longitudinal muscles start to differentiate on the dorsal side and two on the ventral side, with the onset of elongation in the hyposphere. In the metatrochophore additional pharyngeal and chaetal sac muscles develop followed by formation of transversal thorax muscles on the ventral side. Pre-metamorphic larval stages already have a complex musculature consisting of prominent chaetal sac muscles that are interconnected by muscular bands. Two dorsal and two ventral longitudinal strands run along the body and, in addition, the parathoracic segments bear transverse and oblique muscles and the pygidium is provided with circular musculature.

The gut is a straight tube running from mouth to anus, including cauda, with a broadened structure referred as to 'proventriculus' (Kirtley 1994) in anterior abdominal segments. Adults lack buccal organ (Dales 1962), although it is not known if it is present during development (Rouse 2001). The axial proboscis is non-muscular, and lack dorsolateral folds (Purschke & Tzvetlin 1996). The gut is provided with absorptive and serous gland cells which are thought to secrete proteolytic enzymes into the lumen of the gut (Michel 1988). Circular muscles surround the pharynx (Brinkmann & Wanninger 2010). The circulatory system has been described as closed and without a heart body (Eisig 1887, Fauchald & Rouse 1997, but see Eckelbarger 1979 for a different opinion). Some confusion has taken place in this regard, probably due to the interpretation of the intravasal chlorogogen gland (Eisig 1887) as a string heart body inside the dorsal blood vessel in the thoracic region situated above a large nephridium (Meyer 1887, 1888, Rouse & Fauchald 1997, Rouse 2001).

Neosabellaria cementarium (Moore, 1906) has, like most polychaetes, two well-developed fluid transport systems, the blood vascular system and the segmented coelomic cavities. Sabellariids have only a simple peritoneal layer of highly interdigitating cells, which separates the blood and coelomic fluid (Smith 1986, as *Sabellaria cementarum*). The blood in *N. cementarium* arises as a fluid during the larval stage, and the haemoglobins are produced later (Smith 1986) and are dissolved in the blood without distinct blood corpuscles. While the branchiae of sabellariids presumably function as sites for oxygen exchange this actually needs to be confirmed (Hutchings 2000).

Larvae of *Neosabellaria cementarum* are provided with protonephridia with podocytes (Smith 1986, Smith & Ruppert 1988, as *Sabellaria cementarum*). The excretory system of adults consists of a single pair of metanephridia and terminal monocoelated cells provided with a long duct that extends caudally for

a few segments, U-turns frontally, and leads to the exterior of the animal on the dorsal side of the first segment (Dehorne 1952, Meyer 1887, Smith 1986, Smith & Ruppert 1988, Bartolomaeus & Quast 2005). Posterior segmental organs act as gonoducts (Meyer 1887). The ovaries are distinct, retroperitoneal, paired structures located on the genital blood vessels which extend from the caudal face of the intersegmental septa of abdominal segments (Eckelbarger 1979).

The brain is surrounded by ganglion cells except on the ventral side and has four commissures, as most annelids (Orrhage 1978), situated in the same plane (Orrhage & Müller 2005). The first two communicate with the ventral roots of the oesophageal connective and the other two merge laterally into the dorsal roots of this connective (Orrhage & Müller 2005). A detailed description of the cephalic nervous system, placement of ganglia and innervation of some anterior structures on some *Sabellaria* and *Idanthyrsus* species can be found in Orrhage (1978). He concludes that the paired anterior structures, referred herein as palps, are homologous to the palps of polychaete families (also corroborated later by Orrhage & Eibye-Jacobsen 1998 and Orrhage & Müller 2005), that the oral filaments are extended lateral parts of the upper lip of the mouth (suggested previously by Johansson 1927), and that the opercular lobes with their paleae and dorsal hooks or chaetae (if present) represent the notopodia of the first two segments (as indicated also by Dales 1952).

Studies on the neurogenesis show that sabellariid larvae express both larval and adult features. For instance, late larval stages of *Sabellaria alveolata* start forming the cerebral ganglion and the two circumoesophageal connectives, considered as adult features, before metamorphosis. Moreover and contrary to previous studies (Lacalli 1984), it seems like sabellariid larvae are not provided with two separate nervous systems but only have one (Voronezhskaya et al. 2003, McDougall et al. 2006, Brinkmann & Wänninger 2008). Another distinct attribute with respect to generation of the neural system in other annelids is that, at least in *S. alveolata*, three pairs of segmental neurons are formed synchronously and simultaneously to the formation of the first three larval segments while all commissures of the ventral central nervous system develop sequentially in a strict anterior to posterior progression, even though the two thoracic segments form anterior to the first three larval segments in Sabellariidae (Wilson 1929, Cazaux 1964, Eckelbarger 1975, Brinkmann & Wänninger 2008).

Several sensory organs have been reported in a number of sabellariids. In the median line of the fused part of the opercular lobes, cup-shaped spots of brown pigments are present, containing innervated and therefore probably light sensitive cells (Eckelbarger 1975, 1977, Orrhage 1978, Kirtley 1994). The median organ (Fig. 1A) has also been attributed with a sensory function (Kirtley 1994) but no detailed studies have investigated this to date. Both eyespots and median organ are considered as prostomial structures (Dales 1952, Lechapt & Kirtley 1996, respectively). The specialized epithelium at the base of each palp is innervated from the dorsal and ventral commissure of the dorsal root of the circumoesophageal connective. There is evidence that they represent the nuchal organs (Orrhage 1978, Kirtley 1994, Purschke 1997). Lateral organs are absent. The ciliated tentacles present in larval stages, have also been suggested as potential sensory organs in several species (Amieva & Reed 1987).

Reproduction and Development

The reproductive strategies and the development in Sabellariidae have been studied in several species, mainly gregarious and with intertidal distribution, including *Sabellaria alveolata* (Linnaeus, 1767) (Wilson 1929, 1970a, Cazaux 1964, Brinkmann & Wänninger 2008), *S. spinulosa* (Leuckart, 1849) (Wilson 1929, 1970b), *S. vulgaris* Verrill, 1873 (Curtis 1975, Eckelbarger 1975), *S. floridensis* Hartman, 1944 (Eckelbarger 1977), *Lygdamis muratus* (Allen, 1904) (Bhaud 1975, Wilson 1977), *Phragmatopoma lapidosa* (see Eckelbarger 1976, Mauro 1975, Eckelbarger & Chia 1976), *Phragmatopoma californica* (see Eckelbarger 1977, Pernet & Strathmann 2011), *Idanthyrsus* sp. (see Bhaud & Fernández-Álamo 2001) and *Neosabellaria cementarium* (see Pernet & Strathmann 2011). These larvae share the external morphology until the late planktonic stage when they develop some of the characteristic generic features such as the number of parathoracic segments, the absence or presence of opercular spines or hooks with or without limbation (Bhaud & Fernández-Álamo 2001) or some of the opercular paleae (Mauro 1975). Larvae of *Neosabellaria* and *Phragmatopoma* species are provided with a prototroch and also a recently identified metatroch and food groove ciliary bands, required for opposed-band feeding (Pernet & Strathmann 2011) (Fig. 3).

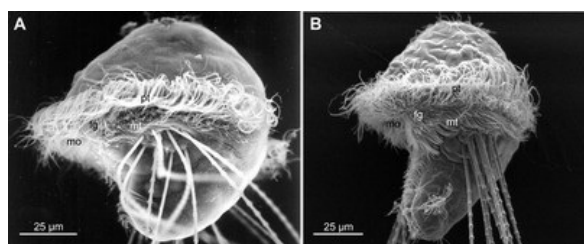


Fig. 3

Scanning electron micrographs of trochophore larvae showing the ciliary bands and provisional chaetae. A, Nine-day-old larva of *Neosabellaria cementarium*, lateral view; B, Five-day old larva of *Phragmatopoma californica*, lateral view; fg food groove, mo mouth, mt metatroch, pt = prototroch. Originals from Pernet & Strathmann 2011.

Larvae of *Phragmatopoma californica* possess simple rhabdomeric ocelli as light-sensitive organs on either side of the dorsal hump. The most likely function of the sensory tufts is either mechanoreception or chemoreception (Amieva et al. 1987). Late larval stages are equipped with tentacles with specific motile and immotile cells for perception of settlement cues and discrimination of appropriate adult environments (Amieva & Reed 1987, Amieva et al. 1987). These tentacles are also involved in feeding, construction of the mucous tube in the juvenile, locomotion, attachment, and become the palps of the adults (Amieva & Reed 1987). Since they arise from behind the prototroch (Dales 1962), on the anterior margin of the upper transverse lip, in front of, and dorsal to the mouth (Johansson 1927, Orrhage 1978), they are considered as peristomial palps (for other points of view see Amieva et al. 1987). In late larval development the cauda arises posteriorly (Eckelbarger 1975) but further abdominal segments are added ahead of it with growth after its appearance, indicating that pygidium is not terminal.

In *Phragmatopoma*, metamorphosis involves an elongation of the body, and dramatic changes in the head region. The tentacles rotate anteriorly until they project forward, the chaetae are replaced by 6-10 pairs of primary paleae, the entire head shrinks in relative size, the building organ appears ventral to the mouth, and various appendages develop on a number of segments (Eckelbarger 1976). After settlement, development continues rapidly; within one month, juveniles closely resemble the adult worm (Eckelbarger 1976).

Distribution, Biology, and Ecology

Most species of Sabelliariidae live in the surf zone or shallow depths (less than 10 m deep) but members of *Bathysabellaria*, *Gesaia* and *Phalacrostemma*, and other sabelliariids species are restricted to particular oceanic provinces, such as continental shelf or the deep sea. Whilst most genera of this family occur in several oceans, only *Gesaia* is regarded as being cosmopolitan (Kirtley 1994). Sabelliariid species appear to be geographically restricted even though they have planktotrophic larvae of long duration with the potential to be dispersed (Scheltema 1986, Pawlik & Mense 1994, Giangrande 1997). This suggests that other factors are responsible for their limited distributions such as habitat, depth and ecological requirements, which are required for settlement and construction of their tubes (Kirtley 1994, Bastida-Zavala & Becerril-Tinoco 2009). Larval behaviour in the water column (i.e. vertical migration) is not well understood. Considering the statistical modelling of larvae dispersion/retention (Ayata et al. 2009) it is possible that in stable environmental conditions, sabelliariids reproduce by recruitment from nearby populations, which maintains the well-known reefs or aggregates over the time, but the connections between long distances are mainly due to extreme events, evidenced by the release of gametes during storms (Barry 1989, Faroni-Perez pers. com.).

At depths below the wave action (2 m deep) there is not enough current for the animals to feed and capture sand grains for tube building (Kirtley 1966) and probably the colonies reported below 100 m are located where strong submarine currents occur (Kirtley & Tanner 1968), although there is no actual experimental data to support this concept.

Shallow water sabelliariids show some zonation pattern in the intertidal and subtidal (Achari 1974, Pohler 2004, Bailey-Brock et al. 2007) and intertidal species can withstand several hours of exposure to air during low tide (Pohler 2004). Sabelliariids are generally found in or near soft bottoms, since they rely on availability of sand grains to build their tubes. However they do need to firmly cement their tube onto a stable substrate. *Phragmatopoma lapidosa* has shown some tolerance to burial experiments for short periods and low depth burial, but colonies mostly died after over one week of burial below 10 cm of sand (Sloan & Irlandi 2008).

A study dedicated to determining the species delimitation between morphologically similar species of *Phragmatopoma* in the Atlantic, and Pacific coasts of America (*P. californica*, *P. caudata* Krøyer in Mörch, 1863, and *P. virgini* Kinberg, 1867, two of which have been shown to be able to interbreed in the laboratory, found molecular evidence to support the validity of each of these species (Pawlik 1988b, Drake et al. 2007).

Sabelliariidae has been regarded as a homogenous group of polychaetes in regards to their reproductive strategies based mainly on shallow water species, and, at least those that have been studied, seem to be gonochoric, broadcast spawners, and with external fertilization (Wilson 1991, Giangrande 1997). Populations are composed of equal proportions of males and females (Dales 1952, Eckelbarger 1976) with no sexual dimorphism except for the colour of the gamete-containing abdominal segments in mature individuals, with creamy-white sperm, and steel-blue eggs (Kirtley 1966, 1968, DeJorge et al. 1969, Eckelbarger 1976).

In *Phragmatopoma lapidosa* gametes first develop in both sexes about six to eight weeks after larval settlement, and the worms are fully mature after four months (Eckelbarger 1976). Females have discrete ovaries in abdominal segments where oogenesis takes place until near the end of vitellogenesis (Eckelbarger 2005). Detailed studies on the early stages of oogenesis of *Phragmatopoma* showed that both Golgi and rough endoplasmic reticulum are involved in yolk synthesis and distinctive yolk bodies are found, but disappear in the mature eggs (Eckelbarger 1979, 1988). The developing oocytes have egg membranes in *Sabellaria* Lamarck, 1812 (Pasteels 1965a,b, Franklin 1966) and *Phragmatopoma* (see Eckelbarger 1979, 2005) which have well developed microvilli and they are assumed to be involved in nutrient absorption during oogenesis and are also involved in fertilization (Franzén & Rice 1988). In *Phragmatopoma lapidosa* oogenesis takes 48 hours and the oocytes have extensive contact with the lumen of the genital blood vessels and show high endocytotic activity (Eckelbarger 1979, 1988, 2005).

Mature sperm of *Sabellaria alveolata* (Linnaeus, 1767) and *Idanthyrsus australiensis* (Haswell, 1883) (as *I. pennatus*) have distinctive long, tapering, and striated acrosomes, and laterally displaced flagella (Pasteels 1965a, Eckelbarger 1984, Jamieson & Rouse 1989). Within the acrosome, three regions may be distinguished: a long tapering anterior region with evenly spaced transverse striations, a central region made up of an electron dense collar with concentric rings, and a posterior region separated from the nucleus which is bulbous and surrounds a central subacrosomal space that contains loosely packed filaments (Franzén & Rice 1988).

Males and females release the gametes into their tubes through a series of gonoducts in the abdominal segments that are later expelled into the water column in short bursts by the rapid withdrawal of the head region into the tube (Eckelbarger 1984). The presence of sperm in the water generally stimulates spawning of other adjacent males, and also induces the eggs release by females (Eckelbarger 1984). *Phragmatopoma californica* is sexually mature all year long (Barry 1989). Spawning has been reported as continuous, semi-continuous or seasonal depending on the species studied (Eckelbarger 1976, Smith & Chia 1985). The eggs of *Phragmatopoma caudata* (as *P. lapidosa*) are sticky, and adhere to sand grains upon expulsion, which could be an adaptation to restrict dispersal in the turbulent surf zone (Eckelbarger 1984). *Phragmatopoma californica* exhibits a spawning response to damage from intense storms allowing to maximize reproductive effort when the likelihood of recruitment success and the probability of adult mortality are high (Barry 1989). Experimental studies on the changes occurring inside the fertilized egg and meiotic and meiosis related events are critical in polarizing the egg cell (Dorresteijn & Fischer 1988) and setting up the animal and vegetal poles. Parallel to this ooplasmic segregation (Costello 1948) localization of developmental potential is occurring, giving cells the capacity to form the mesoderm and the apical tuft in future larvae as shown for *Sabellaria vulgaris* and *Neosabellaria cementarium* (see Hatt 1932, Render 1983). Subsequent cleavages produce blastomeres with quantitative differences of the egg plasm (Speksnijder & Dohmen 1983). For more details of the early cleavages and the development of the early embryo including species of *Sabellaria* (see Dorresteijn & Fischer 1988, and references therein).

In *Phragmatopoma*, metamorphosis, and settlement occur after 14-30 days, in laboratory conditions (Mauro 1975, Eckelbarger 1975, 1976, 1977, Amieva & Reed 1987). Field study estimated longer planktonic lifetime being between 2 to 5 months for *Phragmatopoma californica* (Fewkes, 1889) (Barry 1989) and between 4 and 10 weeks for *Sabellaria alveolata* (see Dubois et al. 2007), although this species has also reported as remaining competent in the plankton for up to 11 months (Wilson 1971). Upon settling, the larva actively moves over the substrate, presumably evaluating possible attachment sites, and when this is selected the metamorphosing larva secretes, and attaches a cylindrical, muco-proteinaceous tube on which it begins cementing small fragments that generally increase in size with growth (Kirtley 1966, Multer & Milliman 1967).

Sabelliariids may live between three and ten years (Wilson 1971, Gruet 1986). They actively build tubes made of sand, shell fragments or other suitable particles attached by glue to the dark layer of mucoprotein secretions (Vovelle 1965, Gaill & Hunt 1986, Wang et al. 2010). The tubes are attached to a variety of substrata, including rocks, seaweeds or invertebrates or other sabelliariid tubes (Uebelacker 1984, Hutchings 2000, Morgado & Tanaka 2001,

Pérez et al. 2005). In sabellariid reefs, the tubes are arranged in parallel as a honey-comb, with the tube opening facing major currents, growing as a three-dimensional structure.

Sabellariids are suspension-feeders that collect particles from the water column using their extended oral filaments that can reach about 1.5 cm above the aperture of its tube (Dubois et al. 2005, 2009). The body and tentacle movements are able to create a current, in the opposite direction to the surrounding water circulation near the animals that allows them to collect and sort particles efficiently before their collection in food grooves (Dubois et al. 2005). Oral filaments, palps, mouth, and lips are ciliated structures also accompanied by mucocytes that secrete mucopolysaccharides helping in the transport of the particles into the mouth, and which prevents particles being removed by local currents (Dales 1952, Dubois et al. 2005). There are several mechanisms preceding the particle ingestion including the above mentioned bi-directional particle transport on the oral tentacles, acting as a preliminary sorting mechanism, pseudofaeces production allowing individuals to reject excess particles before ingestion, and the contribution of the palps to cleaning the oral tentacles when overloaded (Dubois et al. 2005, 2009).

Several species, mainly of *Phragmatopoma*, *Sabellaria*, *Gunnarea*, and *Idanthyrsus*, build small aggregates to large reefs in the intertidal, and shallow waters on temperate, and tropical coasts in many parts of the world (Achari 1974, Kirtley 1974, Caline et al. 1988, Caline et al. 1992, McCarth et al. 2008, Barrios et al. 2009). *Sabellaria* and *Idanthyrsus* are present in Australia 'but massive reefs have not been observed (Hutchings et al. 2012). Larvae in swarms have been observed to settle almost synchronously with densities of up to 4 million per square meter (Kirtley 1994, although Dubois et al. 2007 provide other figures). However, aggregations of adult colonies are seldom more densely spaced than 15,000 to 60,000 individuals per square meter in temperate areas (Caline et al. 1988, Kirtley 1994) and higher in tropical latitudes (Faroni-Perez, pers. com), indicating massive larval death after settlement. Reefs off the coast of Florida can cover areas of nearly 1 km wide and 9.8 km long. These reefs can occupy wide areas along the coast, and dominate the marine habitat and are considered important in the sorting, deposition, and stabilization of beaches and, protecting the shore from heavy surf (Kirtley 1967, Multer & Milliman 1967, Gram 1968, Kirtley & Tanner 1968, Achari 1974, Caline et al. 1988, Pawlik 1988a,b), and in some places enhancing its distribution has been considered as a protective measure to reduce beach erosion (Pohler 2004). Sabellariid reefs are protected under the international network of protected sites Natura 2000 network (www.natura.org).

Reef-building sabellariids have been the focus of several taxonomic, biological, and ecological studies since they have been considered as one of the most important building organisms after corals in coastal environments (Fournier et al. 2010). In such colonies the number of crevices which could provide shelter for other organisms is reduced but as the reef breaks up with time, it provides habitats for various organisms (Gruet 1982). Large and old reefs are considered hotspots of diversity, providing refuge, and food for many invertebrate species (e.g. Wilson 1971, Caline et al. 1988, Pawlik 1988a,b, Dubois et al. 2002, Sepúlveda et al. 2003, McCarth et al. 2008, Fournier et al. 2010, Desroy et al. 2011), and fish (Gilmore 1977, Lindeman & Snyder 1999).

Larvae of gregarious sabellariids are induced to settle by the presence of conspecific cemented sand tubes or mucous tubes of juveniles (Eckelbarger 1978a,b, Pawlik 1986, 1988a,b, 1992) and few species (i.e. *Phragmatopoma californica*) have been shown to be able to delay metamorphosis while searching for conspecific aggregations (Pawlik 1988b). Chemical signals which control the settlement are species-specific. Specific free fatty acids used in the mucoproteins 'cement' secreted by the worms to stick the sand particles in tube formation were isolated as the inducers for metamorphosis in two species of *Phragmatopoma* (Pawlik 1986, 1988a,b). But these compounds did not trigger settlement in some gregarious *Sabellaria* species, suggesting they are species specific (Pawlik 1988a,b, 1992). Larvae can also colonize a new substratum if unsuccessful in locating conspecifics (Toonen & Pawlik 1994), if the food supply is low and also in cases of currents transporting larvae that find suitable and available substrate (Bremec et al. 2013). Solitary species do not show this preference for conspecifics already in the settlement area. In laboratory experiments, *Neosabellaria cementarium* (as *Sabellaria cementarium*) show no settlement preferences for conspecific tube sand (Pawlik & Chia 1991), but a large reef has been reported (Posey et al. 1984). Similarly, *Sabellaria nanella* Chamberlin, 1919 reported as solitary (Bremec & Lana 1994) was recently observed in dense aggregates (Bremec et al. 2013). These formations by species previously reported as solitary are likely the result of larval entrainment and concentration at the time of settlement (Pawlik & Manse 1984).

Sabellariids reefs are entirely dependent on the recruitment of planktonic larvae for reef maintenance, and growth (Pawlik & Faulkner 1988). The main biological factors that affect the structural development of reefs seem to be the reproduction, and recruitment mechanism of the pelagic larvae, which are modelled by physical factors associated with the local hydrodynamics (Gruet 1986, La Porta & Nicoletti 2009, Culloty et al. 2010, Bremec et al. 2013).

The proteinaceous adhesive produced to glue tube particles by sandcastle worms is secreted from the building organ onto suitable particles as they are pressed onto the end of the tube. The major protein components of the adhesive are a group of polyacidic and polybasic heterogeneous proteins, referred to as P3cX (Zhao et al. 2005, Wang et al. 2010). The glue is secreted a fluid that penetrates into the holes between the particles but seconds after becomes a foam with porous granules, completely solidified after some hours (Vovelle 1965, Wang et al. 2010). The physicochemical properties of this adhesive makes it an ideal water-borne underwater bioadhesive (Shao et al. 2009, Wang et al. 2010). This cement has also been shown to have practical applications in medicine, and is used as a degradable adhesive for broken bone reconstruction (Shao et al. 2009, Shao & Stewart 2010, Winslow et al. 2010).

Phylogeny and Taxonomy

Like in many other annelid families, the taxonomic history of the Sabellariidae has been convoluted. The first species of Sabellariidae to be mentioned in the scientific literature was by Réaumur in 1711, described fifty years later as *Tubularia arenosa anglica* (Ellis, 1755). Linnaeus (1758) used these illustrations in *Systema Naturae* 10th Edition and published it as *Tubipora arenosa*. In the 12th Edition it was synonymized with *Sabella alveolata* (Linnaeus 1758) and later to *Sabellaria alveolata* (Lamarck, 1812). Johnston (1865) erected the family name Sabellariidae although many subsequent workers used the younger name *Hermellidae* which was erected by Malmgren (1867) based on the name *Hermella*, a synonym of *Sabellaria* (Kirtley, 1994). Subsequent studies by Kinberg (1867), Marenzeller (1895), Ehlers (1901), Moore (1906), Caullery (1913), Fauvel (1914) Annenkova (1925), Treadwell (1926) Johansson (1927) Hartman (1944) and Kirtley (1994) described additional species and their morphology.

Even before the recent assessment of the monophyly of the family (Capa et al. 2012), the cohesion of the group relied upon morphological features such as the presence of the operculum bearing rows of paleae derived from the first two segments, the presence of the oral filaments on the operculum, the division of the body into four regions, and the arrangement of chaetae. One of the main taxonomic contributions to this group is the worldwide taxonomic revision of the family undertaken by Kirtley in 1994. He rearranged species within genera and erected new ones, increasing the number of genera to 12. Kirtley (1994) also classified genera into two subfamilies, Sabellariinae, and Lygdamiinae, based merely on the number of parathoracic segments, a condition that is established very early in the course of development (Bhaud & Fernández-Álamo 2001). But his revision and classification was not performed in a phylogenetic framework and recent phylogenetic analyses of the family found no support of these two subfamilies (Capa et al. 2012,

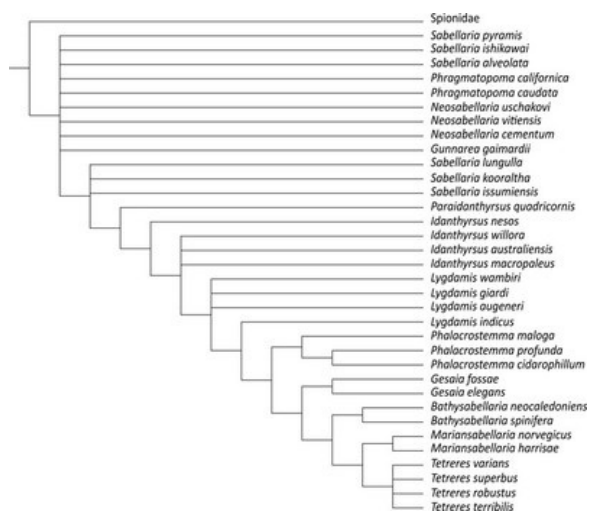


Fig. 4

Proposed phylogenetic hypothesis of members of Sabellariidae, based on morphological data (modified from Hutchings et al. 2012)

Subsequent studies have dealt mainly with new species descriptions or partial taxonomic revisions of certain genera (e.g. Lechapt & Kirtley 1998, Nishi & Kirtley 1999, Nishi & Núñez 1999, Nishi et al. 2004, Bailey-Brock et al. 2007, Nishi et al. 2010, Hutchings et al. 2012), increasing the total number of nominal species in the family to 130.

The phylogenetic affinities of the Sabellariidae are still not well understood (e.g. Capa et al. 2012) and close relationships with members of Sabellida (Levinsen 1883, Meyer 1888, Hatschek 1893, Benham 1896, Knight-Jones 1981, Fitzhugh 1989, Rouse & Fauchald 1997), Spionida (Meyer 1888, Caullery 1914, Dales 1962), or Terebellida (Savigny 1822, Fauchald 1977) have been suggested based on morphological features. More recent phylogenetic hypotheses combining morphological and molecular data have indicated that Sabellariidae is closely related to spionids although with low support (Rousset et al. 2004, Capa et al. 2011, 2012) and other studies including behavioral, and ecophysical information (Amieva & Reed 1987, Dubois et al. 2005) backing up earlier larval development and palp innervation studies (Dales 1962).

The two phylogenetic studies of the family to date (Capa et al. 2012, Hutchings et al. 2012), based on morphological features, were unable to resolve the relationships between members of Sabellariidae unless implied weighting was applied (see Capa et al. 2012, for details on methodology), due to the high amount of homoplasy accumulated in the group. The subfamilies erected by Kirtley (1994) were in both cases recovered as paraphyletic (Fig. 4).

Key characters with phylogenetic signal are those from the operculum and anterior end (Capa et al. 2012). They show a broader morphological variation between members of Sabellariidae and a combination of short opercula, and geniculate outer paleae and inner concave paleae arranged in semicircles were considered the synapomorphies for a well-supported clade including *Phalacrostemma*, *Bathysabellaria*, *Gunnarea*, *Paraidanthyrus*, *Sabellaria*, *Phragmatopoma*, and *Neosabellaria* (Capa et al. 2012). This clade was also recovered monophyletic later on but excluding *Neosabellaria* and *Gunnarea*, with an uncertain position in the tree (Hutchings et al. 2012). In contrast, the number of parathoracic segments was showed to be homoplastic with four segments being the plesiomorphic condition reducing to three twice during the radiation of the sabellariids (Capa et al. 2012, Hutchings et al. 2012). Gregarious and reef-building sabellariids were found scattered on the tree indicating that this behaviour, together with the physiological and ecological adaptations found in members of the colonial species seem not to have any phylogenetic constraint (Capa et al. 2012).

The monophyly of *Bathysabellaria*, *Idanthyrus*, *Mariansabellaria*, *Phalacrostemma*, *Phragmatopoma* and *Tetreres*, has been assessed but *Gesaia*, *Lygdamis*, *Sabellaria*, and *Neosabellaria* could be paraphyletic (Capa et al. 2012, Hutchings et al. 2012).

Classification and Genera Diagnoses

Family Sabellariidae Johnston, 1865

Diagnosis: Tubicolous annelid with compact body divided in four regions: operculum (head and thorax), parathorax, abdomen, and cauda. Operculum formed by prostomium, peristomium and first two segments. It bears two peristomial palps, a median organ, a building organ adjacent to the mouth, tentacular filaments originating from segment 1 and characteristic chaetae called paleae. Nuchal organs located at base of palps. Parathorax with unique parapodial rami and lanceolate chaetae in noto- and neuropodia. Abdomen with unequal parapodial rami and with uncini in notopodia, with two longitudinal rows of 6-9 teeth each, a subrostrum and subrostral process present, without a handle or manubrium; and simple capillaries or lanceolate chaetae in neuropodia. Cauda is a smooth cylindrical tube, apparently unsegmented, that is curved along the ventral surface of the abdomen. Parapodial branchiae present on most segments along body. Tube made out of mucus and sediment particles.

* Synapomorphies or unique combinations of features are underlined in those genera for which monophyly has not been assessed (*Gesaia*, *Lygdamis*, *Neosabellaria* and *Sabellaria*).

Bathysabellaria Lechapt & Gruet, 1993

Type species: *Bathysabellaria neocaledoniensis* Lechapt & Gruet, 1993

Two gregarious species found in deep water (450-700 m) off New Caledonia (Lechapt & Kirtley 1998).

Diagnosis: Opercular lobes completely fused along its length. Opercular disc perpendicular to longitudinal axis. Numerous opercular papillae varying in size depending on the species. Outer paleae numerous, arranged in semicircles; shaft and blade slightly geniculate (forming an angle), blades faintly excavated, with smooth margins, except when distal tips frayed or broken. Inner opercular paleae arranged in semicircles, giving the appearance of one

row, straight, slightly excavated, with smooth margins. One pair of nuchal spines, only slightly curved distally. Three or four simple (unbranched) tentacular filaments present; buccal flaps absent. Palps similar in length to operculum. Conspicuous median organ present (Kirtley 1994 corrigenda). Neuropodia of segment 1 with one cirrus on each side of building organ and capillary chaetae. Segment 2 with one pair of triangular-shaped lateral lobes. Thoracic branchiae absent. Four parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae only capillaries. Abdominal branchiae present, reduced or absent in posterior segments.

***Gesaia* Kirtley, 1994**

Type species: *Phalacrostemma elegans* Hartman & Fauchald, 1971: 152 (not Fauvel 1911)

Eight species reported from deep water of all major oceans, between 770 and 5790 m (Kirtley 1994).

Diagnosis: Operculum longer than wide, completely divided into two free lobes and distal disc perpendicular to operculum; few (4–8 pairs) long and conical opercular papillae. Three to five simple (unbranched) tentacular filaments along margins of buccal cavity. Buccal flaps absent. Palps shorter or similar in length to operculum with obvious groove. Conspicuous median organ (cirrus) at dorsal junction of lobes present. Outer paleae arranged in semicircles with straight, cylindrical, smooth blades (with frayed thecae but no proper denticles). Inner opercular paleae arranged in a single row, like a short line, on the dorsal half of the inner margin of lobes, with straight cylindrical and smooth blades. One pair of nuchal hooks, without limbation. Neuropodia of segment 1 with two or three pairs of cirri on both sides of building organ and without neurochaetae. Two lateral lobes in segment 2 (only described in type species). Thoracic branchiae present (according to Kirtley 1994). Four pairs of parathoracic segments. Parathoracic neurochaetae only capillaries.

***Gunnarea* Johansson, 1927**

Type species: *Hermella gaimardi* (Quatrefages, 1848)

One species from Cape Town, South Africa (Quatrefages 1848), forming reefs from intertidal to 47 m (Kirtley 1994).

Diagnosis: Operculum length similar to maximum width, with lobes partially fused (with deep indentation on ventral margin) and distal disc perpendicular to longitudinal axis. Numerous small and rounded opercular papillae on its perimeter. Outer paleae arranged in semicircles; geniculate, with flat blades, smooth lateral margins, and distal margin with asymmetrical tooth. Inner paleae arranged in semicircles, as a single row, strongly geniculate, with flattened, but excavated, blades. Nuchal spines absent. Palps shorter than half of the operculum. Tentacular filaments compound. Buccal flaps absent. Conspicuous median organ absent. Neuropodia of segment 1 with one cirrus on each side of building organ and capillary neurochaetae. Two triangular lobes between noto- and neuropodia of segment 2, ventral one, broad and subdivided or with crenulated margins. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar but smaller. Abdominal branchiae present on most abdominal segments.

***Idanthysus* Kinberg, 1867**

Type species: *Idanthysus macropaleus* Schmarda, 1861

Twenty species, generally found in shallow water in the tropics or temperate waters as isolated individuals but some species also inhabit boreal and deep water domains and aggregations of individuals have also been found (Hutchings et al. 2012).

Diagnosis: Operculum longer than wide with lobes completely divided and distal end sloping posteriorly (oblique to longitudinal axis) and operculum papillae varying in number and size depending on species. Outer paleae arranged in semicircles with straight and flat blades and lateral and distal margins appearing sharply denticulated. Inner opercular chaetae arranged in one row along the inner margin of opercular lobes, with straight and cylindrical blades. One or two pairs of nuchal spines with bent tips (hooks) with or without limbations on the concave margin. Palps similar in length to the operculum. Conspicuous median organ with eyespots on its sides (on specimens examined). Tentacular filaments compound (branching); buccal flaps absent. Neuropodia of segment 1 with capillary chaetae, with conical cirri (only one pair of cirri in all species examined). Segment 2 with one to four triangular lateral lobes. Three parathoracic segments with notochaetae consisting of lanceolate and capillary chaetae and only thin lanceolate neurochaetae (on species examined). Branchiae from segment 2 diminishing in size on posterior abdominal segments.

***Lygdamis* Kinberg, 1867**

Type species: *Lygdamis indicus* Kinberg, 1867

Nineteen species (Hutchings et al. 2012). Species are known from the shallow subtidal areas, shallow shelf areas and on continental slopes to depths of 515 m, most records are from tropical and subtropical latitudes with a few from boreal waters.

Diagnosis: Operculum longer than wide with lobes completely separated and distal end sloped posteriorly (oblique to longitudinal axis). Numerous opercular papillae varying in size depending on the species. Outer paleae arranged in semicircles, straight, with flat blades, lateral and distal margins smooth. Inner opercular chaetae arranged in one row along the inner margin of opercular lobes with straight and cylindrical or slightly flattened blades. One pair of nuchal spines with bent tips (hooks) and without limbations. Palps similar in size to the operculum. Median organ elongate at the dorsal junction of the opercular lobes. Tentacular filaments compound (branching); buccal flaps absent. Neuropodia of segment 1 with a conical cirrus, with or without capillary chaetae. Segment 2 with three triangular-shaped lobes between noto- and neuropodia, in some species rounded and small. Four parathoracic segments with notochaetae consisting of lanceolate and capillary chaetae and neurochaetae similar in shape but smaller. Branchiae from segment 2 to mid abdominal segments.

***Mariansabellaria* Kirtley, 1994**

Type species: *Phalacrostemma norvegicum* Strømgen, 1971

Four species reported from 180 to 2000 m of the west coast of North and South America and Norway (Kirtley 1994).

Diagnosis: Operculum longer than wide with lobes completely divided into two symmetrical halves and distal disc perpendicular to longitudinal axis; long conical papillae around its perimeter. Outer paleae, arranged in semicircles, straight and cylindrical or slightly flattened with smooth margins. Inner paleae, few in number, arranged in a short single row near the dorsal junction of margin of lobes, straight and cylindrical. One or more pairs of straight nuchal spines without limbation. Palps grooved and (considerably) longer than operculum. Tentacular filaments arranged in single rows. Buccal flaps absent. Conspicuous median organ absent. Neuropodia of segment 1 with one cirrus on each side of building organ; capillary neurochaetae absent. One or two

triangular lateral lobes on segment 2. Thoracic branchiae absent. Four parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae only capillaries. Members of the genus have a conspicuous ventral glandular area on the parathoracic segments (Kirtley 1994), a potential autapomorphy for the group. Branchiae present on anterior abdominal segments but not on posterior ones.

***Neosabellaria* Kirtley, 1994**

Type species: *Sabellaria cementarium* Moore, 1906

Seven species restricted to the Indo-Pacific (Bailey-Brock et al. 2007).

Diagnosis: Operculum length similar to maximum width, with lobes completely fused, although shallow mid ventral indentation sometimes present at proximal end; distal end flat and perpendicular to longitudinal axis. Conical and small opercular papillae. Outer paleae numerous, arranged in semicircles, geniculate, with excavated blades, smooth lateral margins and denticulated distal margin with a midline plume. Inner opercular paleae giving the appearance of two rows. Middle paleae geniculate with excavated, smooth blades and pointed tips directed outwards, some species with rounded-tipped blades also present. Innermost paleae strongly geniculated, with short and concave ones directed inwards. Nuchal spines absent. Compound tentacular filaments arranged in series of rows; buccal flaps absent. Palps shorter than half length of operculum (often half of the operculum length). Median organ at dorsal junction of lobes of opercular stalk present in some specimens, but small. Neuropodia of segment 1 with one pair of cirri and capillary chaetae. Segment 2 with two pairs of triangular-shaped lobes between noto- and neuropodia. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar in shape but smaller. Abdominal branchiae absent in posterior segments.

***Paraidanthysus* Kirtley, 1994**

Type species: *Hermella quadricornis* Schmarda, 1861

Monotypic, species known from only from New Zealand nearshore shallow water.

Diagnosis: Operculum with length similar to width, lobes completely divided into two free lobes and distal disc perpendicular to longitudinal axis and numerous short papillae around its perimeter. Outer paleae arranged in semicircles, geniculate, with flat blades, lateral margins with long and pointed denticles, distal margin without a distal plume. Inner paleae in a single row, arranged in semicircles, strongly geniculate, with flat blades and tips directed inwards. Two or three pairs of nuchal hooks with bent tips (hooks) and limbation of the convex side. Tentacular filaments compound (branching) arranged in more than eight rows; buccal flaps absent. Palps similar in length to operculum. Conspicuous median organ absent. Segment 1 with a small and rounded cirrus on both sides of building organ and with capillary chaetae on the neuropodia. Segment 2 with two triangular-shaped lateral lobes. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries, similar in shape but smaller in neuropodia. Abdominal branchiae absent in posterior abdominal segments.

***Phalacrostemma* Marenzeller, 1895**

Type species: *Phalacrostemma cidariophilum* Marenzeller, 1895

Thirteen species that live solitary or in aggregations; reported from deep water in different localities of the Atlantic and Indo-Pacific (Lechapt & Kirtley 1998, Hutchings et al. 2012).

Diagnosis: Opercular width similar to length, operculum completely divided into two free lobes and distal disc perpendicular to operculum; eight to ten pairs of long and conical opercular papillae around lobes. Few simple (unbranched) tentacular filaments along margins of buccal cavity, absent in some species. Buccal flaps present (or secondarily absent). Palps similar in length to operculum. Small median organ at dorsal junction of lobes. Outer paleae arranged in a spiral with straight, cylindrical, smooth blades (with ornamented thecae but no denticles). Few (2-8) pairs of inner opercular paleae present, arranged in a short line on the dorsal half of the inner margin of lobes, straight, cylindrical or slightly flattened blades and smooth margins. Two to five pairs of nuchal spines with bent tips (hooks) present and limbation on the concave margin. Neuropodia of segment 1 with one to three cirri on both sides of building organ and capillary neurochaetae. Segment 2 with two digitiform lateral lobes between noto- and neuropodia. Thoracic branchiae present. Four pairs of parathoracic segments. Parathoracic notopodia with lanceolate and capillaries alternating, neuropodia with capillaries and fine lanceolate chaetae. Abdominal dorsal branchiae absent in posterior segments.

***Phragmatopoma* Mörch, 1863**

Type species: *Phragmatopoma caudata* Krøyer in Mörch, 1863

Four species, all forming large reefs in the intertidal and shallow water areas (with the exception of *P. californica* found to depths of 200 m) with an ampho-American distribution (Kirtley 1994, Drake et al. 2007).

Diagnosis: Operculum longer than wide, with lobes completely fused to each other, although shallow mid ventral indentation sometimes present in proximal end. Distal disc flat and perpendicular to longitudinal axis. Numerous digitiform and short opercular papillae around perimeter of distal disc. Outer paleae numerous, arranged in semicircles; geniculate, with flat blades, smooth lateral margins, distal denticles, and a midline plume. Inner opercular paleae giving the appearance of two concentric rows, with paleae strongly geniculate with convex blades and pointed tips directed inwards, middle paleae almost covering innermost paleae. Nuchal spines absent. Compound (branching) tentacular filaments arranged in series of rows; buccal flaps absent. Palps similar in length to operculum. Conspicuous median organ absent. Neuropodia of segment 1 with one pair of conical cirri on both sides of building organ and capillary chaetae. Segment 2 with two pairs of triangular-shaped lateral lobes. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar in shape but smaller. Abdominal branchiae continue to posterior segments.

***Sabellaria* Lamarck, 1812**

Type species: *Sabella alveolata* Linnaeus, 1767

Thirty-nine species; solitary and/or gregarious, found mainly in the Atlantic and Indo-Pacific Oceans.

Diagnosis: Operculum length similar to maximum width, completely divided into two symmetrical lobes; distal disc flat and perpendicular to longitudinal axis. Numerous short and conical opercular papillae around operculum. Outer paleae numerous, arranged in semicircles; geniculate, with flat blades,

smooth lateral edges, and smooth or denticulated distal margin and, sometimes, a midline plume. Inner opercular paleae of various shapes, giving the appearance of two rows arranged in two concentric rows. Middle paleae strongly geniculate with excavated blades and smooth margins, pointing outwards; innermost paleae strongly geniculate, with short concave blades and smooth margins, directed inwards. Nuchal spines, when present, as 3–6 pairs of straight spines. Compound (branching) tentacular filaments arranged in series of rows; buccal flaps absent. Palps similar or shorter than operculum. Conspicuous median organ at the dorsal junction of the opercular lobes in some species and small or absent in others, with eyespots on its lateral margins (in the species examined). Neuropodia of segment 1 with one pair of conical cirri and capillary chaetae. One triangular shaped lobe ventrally, on both sides of building organ. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar in shape but smaller. Abdominal branchiae present on most abdominal segments, missing from posterior-most in some species.

Tetreses Caullery, 1913

Type species: *Hermella varians* Treadwell, 1901

Twelve species from Atlantic, Pacific and Southern Oceans (Kirtley 1994, Hutchings et al. 2012). Some species inhabit a broad bathymetric range (Kirkegaard 1996) but also found at 9–45 m in the Java Sea.

Diagnosis: Operculum longer than wide with lobes partially fused to each other (with deep indentation on ventral margin) and distal disc perpendicular to longitudinal axis, with large conical papillae around its perimeter. Outer paleae arranged in semicircles, straight, with flat blades and smooth lateral and distal margins. Inner paleae few in number, arranged in a single short row on ventral side of operculum, with straight, flattened blades. One pair of large nuchal hooks with broadened shafts; without limbations or enlarged shaft. Palps deeply grooved, longer than operculum. Tentacular filaments arranged in single rows. Buccal flaps absent. Small median organ at the dorsal junction of the lobes present. Neuropodia of segment 1 with one cirrus on each side of building organ; capillary neurochaetae present. Four long, tapering lateral lobes on segment 2. Thoracic branchiae absent. Four parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating, similar in shape but smaller in neuropodia. Abdominal branchiae present, diminishing in size posteriorly.

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Taxonomic Categories

Phylum: Annelida

Subphylum: Pleistoannelida

Class: Sedentaria

Order: Sabellida

Family: Sabelliidae

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