

Review

Fanworms: Yesterday, Today and Tomorrow

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Abstract: Sabellida Levinsen, 1883 is a large morphologically uniform group of sedentary annelids commonly known as fanworms. These annelids live in tubes made either of calcareous carbonate or mucus with agglutinated sediment. They share the presence of an anterior crown consisting of radioles and the division of the body into thorax and abdomen marked by a chaetal and fecal groove inversion. This study synthesises the current state of knowledge about the diversity of fanworms in the broad sense (morphological, ecological, species richness), the species occurrences in the different biogeographic regions, highlights latest surveys, provides guidelines for identification of members of each group, and describe novel methodologies for species delimitation. As some members of this group are well-known introduced pests, we address information about these species and their current invasive status. In addition, an overview of the current evolutionary hypothesis and history of the classification of members of Sabellida is presented. The main aim of this review is to highlight the knowledge gaps to stimulate research in those directions.

Keywords: Sabellida; Sabellidae; Serpulidae; Fabriciidae; Annelida; polychaetes; biodiversity assessment; systematics; methods; gaps of knowledge



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1. Introduction

Sabellida Levinsen, 1883 is a morphologically uniform clade of sedentary annelids historically given a rank of Order. Sabellida currently includes members of Fabriciidae Rioja, 1923, Sabellidae Latreille, 1825, and Serpulidae Rafinesque, 1815 [1–3]. They are commonly known as fanworms, feather-duster worms, or flowers of the sea, because their radioles are arranged in a crown, protruding from the tube made of calcium carbonate or mucus with agglutinated sediment (Figure 1). In addition to the presence of protective tube and the prostomial crown made of radioles with secondary ramifications (generally referred as pinnules, but see [4] for Fabriciidae), which are mainly used for feeding and respiration, all members of Sabellida share the presence of chaetal inversion [thoracic chaetigers with simple chaetae on notopodia and uncini (hooks) on neuropodia, and abdominal chaetigers with opposite arrangement]. Sabellida includes about 1200 species distributed world-wide, from tropical to polar waters and found in all habitats, from freshwater to fully marine conditions, and intertidal to deepest ocean trenches.

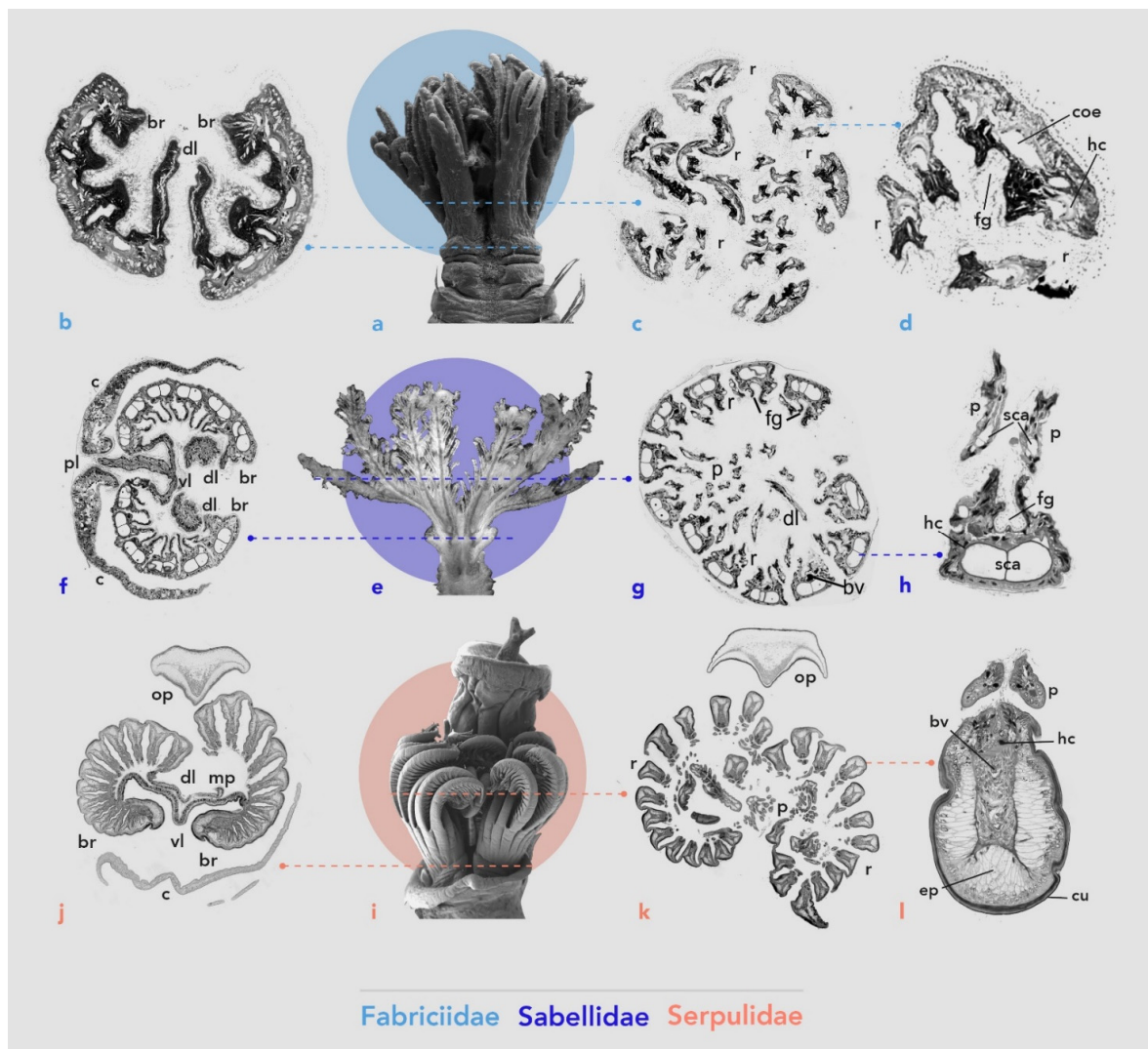


Figure 1. Comparison of the radiolar crown structure among the three families of Sabellida. (a) Anterior end of *Fabricia stellaris*, dorsal view; (b) Histological section of crown of *F. stellaris* at base; (c) Histological section of crown of *F. stellaris* at mid-length; (d) Histological section of one radiole and presumed pinnules of *F. stellaris*; (e) Anterior end of *Laonome xeprovala*, dorsal view; (f) Histological section of crown of *Laonome xeprovala* at base; (g) Histological section of crown of *L. xeprovala* at mid-length; (h) Histological section of one radiole and pinnules of *L. xeprovala*; (i) Anterior end of *Spirobranchus lamarki*, ventral view; (j) Histological section of crown of *S. lamarki* at base; (k) Histological section of crown of *S. lamarki* at mid-length; (l) Histological section of one radiole and pinnules of *S. lamarki*. Abbreviations: br: base of radioles; bv: blood vessel; c: collar; coe: coelom; cu: cuticle; dl: dorsal lips; ep: epithelium; fg: faecal groove; hc: hyaline cartilage; mp: mouth palp; op: opercular peduncle; p: pinnules; pl: parallel lamellae; r: radioles; sca: supporting cellular axis; vl: ventral lips.

The Sabellida concept and even the group name has changed over time. Since their erection in the early 19th century, sabellids (including fabriciids), building soft sediment tubes, and serpulids, building calcareous tubes, have always been considered related, based on their general morphology and grouped into the section *Amphitrites sabelliennes* [5], the family Serpulacei [6], family Serpulacea [7–9], Serpulidae [10], and finally Sabellida [11,12].

With the advent of cladistic analyses, close relationships of sabellids and serpulids with Sabellariidae Johnston, 1865, Siboglinidae Caullery, 1914 and Oweniidae Rioja, 1917 have been suggested, and consequently the composition of Sabellida expanded to incorporate these three taxa (e.g., [13]) (Figure 2). However, subsequent molecular analyses using increasing number of taxa and DNA markers revealed that the three late incorporated taxa were neither closely related to fanworms, nor to each other [14–16].

Morphological lines of evidence related to the ontogeny, internal anatomy, position of the ciliated groove, as well as chaetal morphology and arrangement also supported this lack of close relationship [17–26]. Consequently, Sabellida now again includes only fanworms (Figure 2), but the former sabellid subfamily Fabriciinae has been elevated to Fabriciidae based on DNA evidence [1–3,24,27]. The sister group of Sabellida, according to the latest phylogenomic studies, is a clade including Spionidae Grube, 1850 and Sabellariidae [14,28,29].

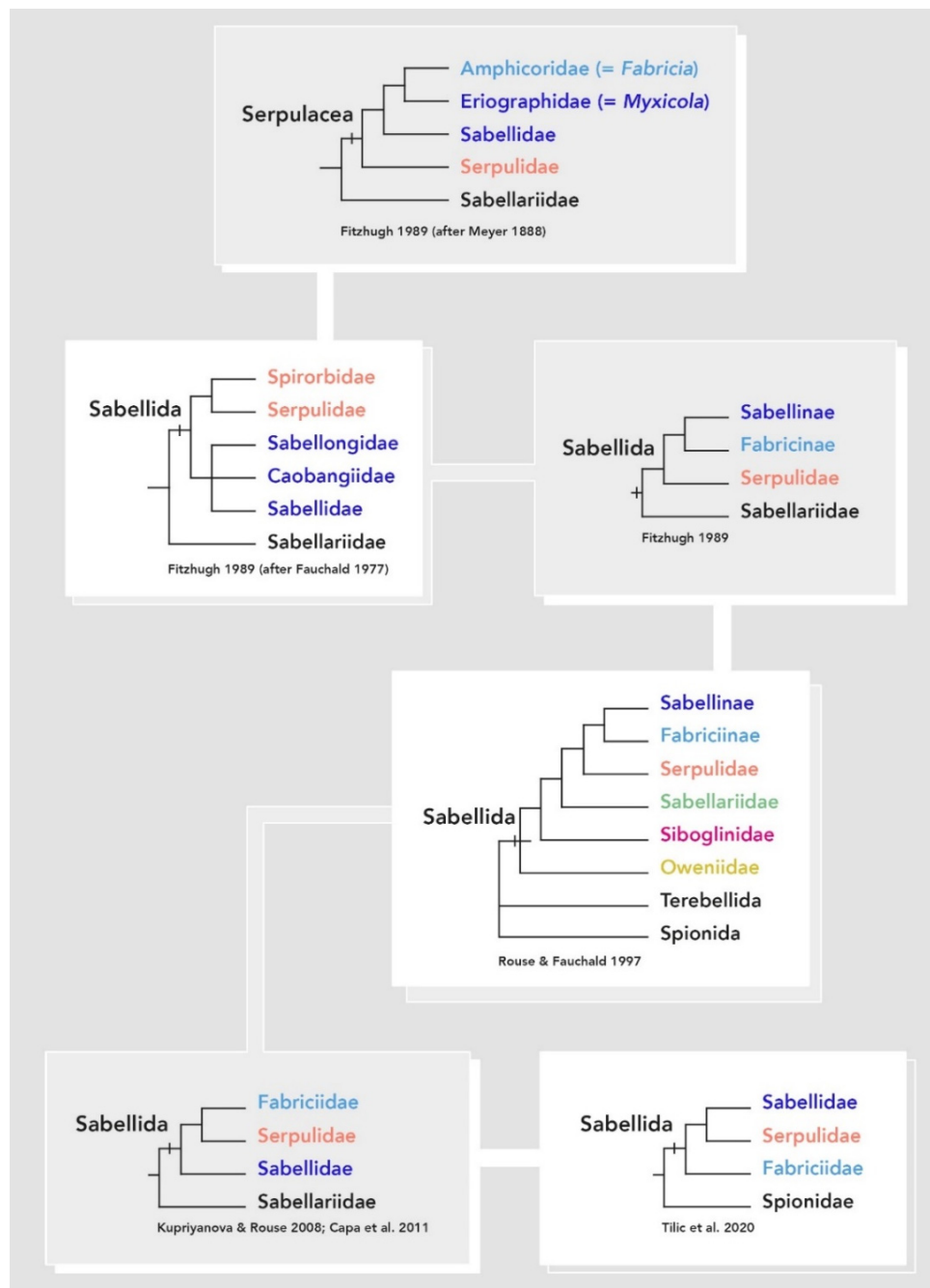


Figure 2. History of the evolutionary hypotheses within Sabellida. The coloured taxa indicate the groups that had been considered as members of Sabellida (or Serpulacea) according to the represented phylogenetic hypotheses. In light blue are members of the currently accepted Fabriciidae, in dark blue are Sabellidae and Serpulidae are in orange. In green, pink and yellow are other taxa previously considered as Sabellida.

Most of the taxonomic work in the Sabellida has aimed to document the regional species diversity, rather than to provide comprehensive world-wide generic revisions. These regional studies have been geographically unevenly distributed because of their strong association to political, economic, historical and traditional context. Moreover, available georeferenced databases (i.e., in Global Biodiversity Information Facility, GBIF, <https://www.gbif.org> (accessed on 3 March 2021)) are also biased, as not all biodiversity information from museum collections and research institutions is shared with this service. The information available in GBIF database not necessarily adequately reflects true species richness and abundance in natural habitats, as more conspicuous, well-known or easier to identify species are predominant in such datasets.

The main aim of this study is to synthesise in a single, easily accessible publication the current knowledge of evolutionary relationships, classification, species diversity and distribution of Sabellida, paying special attention to the latest surveys and novel methodologies used for species delimitation. As some members of Sabellida are easily translocated by anthropogenic means and establish outside of their native ranges, updated information about their invasive status is provided. Another important goal was to highlight the knowledge gaps in order to stimulate research in those directions.

2. Materials and Methods

The present study is a literature review of the information on the Sabellida species diversity, distribution and ecology, highlighting the geographic areas that need further scientific effort and the taxonomic groups that need revisions. The characters and methods used for species delineation have been revised. We summarise the phylogenetic position of Sabellida and the relationships within the group from a historic perspective.

The World Register of Marine Species (WoRMS) [30] database has been key for accounting the number of current valid taxa and analyses of species richness. However, this list has been further revised, including synonymies, new combinations, corrections of names for gender agreement, years of publication, specification of habitats, type localities, and assigning statuses such as *inquirenda* or *indeterminable* to taxa (Appendix A).

Scientific names for all taxa are followed by the authority the first time a taxon is mentioned in the text and in the supplementary material tables (Tables S1–S3). However, due to the high number of taxa dealt with in this review, the citations of authorships have not been included in the reference list. Since many species are still reported as having suspiciously wide distributions, generalised type localities (not details of precise collection locations) are included in Tables S1–S3). Original descriptions, details of type localities and synonymies can be found in WoRMS [30].

Biodiversity information (occurrence data) is referred to the geographic regions (realms) proposed by Spalding et al. [31] for the marine and Udvardy [32] for limnic environments with terminological changes by Olson et al. [33]. Type localities instead of currently reported distributions were used to assign each species to a biogeographic realm. Available biodiversity records have been downloaded as global maps with georeferenced occurrences for Fabriciidae, Sabellidae and Serpulidae separately from the Global Biodiversity Information Facility (GBIF platform, [34]). Distribution of the most common taxa at global scale and species richness in each of the marine realms have been analysed and discussed. In order to delimit these realms in the GBIF maps, polygons following the boundaries of these realms have been drawn with the tools given at the GBIF platform.

DNA sequences available at the National Center for Biotechnology Information (NCBI, [35]) and Barcode of Life Data System (BOLDSystems [36]) have been used to assess the state of the genetic information available for each of the three groups of fan-worms. Moreover, current trends, including phylogenomic data are discussed.

3. Results

3.1. Systematics

The history of the Sabellida as Fabriciidae + Sabellidae + Serpulidae) has been convoluted. Rafinesque [37] grouped the worms with calcareous tubes as Serpularia, now Serpulidae. The subfamily Spirorbinae was established for small-bodied serpulids with spirally coiled tubes [38] and the subfamily Filograninae for the taxa with pinnulated operculum-bearing radioles or lacking opercula [39]. Thus, Serpulidae was subdivided into Filograninae, Serpulinae, and Spirorbinae until Pillai [40] elevated the Spirorbinae to the family status. However, even first morphology-based phylogenetic analyses suggested that Spirorbinae are more closely related to Serpulinae than to Filograninae [19,41,42] and that Filograninae is paraphyletic [41,43,44]. Moreover, further analyses integrating molecular data [45–49] unequivocally found both traditional Serpulinae and Filograninae paraphyletic, and Spirorbinae nested within Serpulidae. Thus, consensus that recognition of Spirorbidae would make Serpulidae a paraphyletic group has prevailed and the rank of the spirorbids was lowered back to Spirorbinae [50].

Initially, Sabellidae included the large-bodied species of fanworms. Rioja, in 1923 [39], divided Sabellidae in three subfamilies: Fabriciinae Rioja (1923), gathering species with acicular uncini; Myxicolinae (only *Myxicola* Koch in Renier, 1847), having radioles joined by a membrane for most of their length, abdominal uncinal tori forming almost complete cinctures and tubes made of thick gelatinous mucus; and Sabellinae, characterised by avicular thoracic uncini, often with companion chaetae, distinct faecal groove and ventral shields. Johansson [51] included *Myxicola* in Fabriciinae. Fauchald [12] followed Rioja's arrangement and recognized Sabellongidae Harman, 1969 (with *Sabellonga* Hartman, 1969) and Caobangiidae Chamberlin, 1919 (with *Caobangia* Giard, 1893) as valid taxa.

As a result of the first morphology-based phylogenetic analysis of Sabellidae (as perceived at the time), using Serpulidae as the outgroup [42], only subfamilies Fabriciinae and Sabellinae were recognised and their composition changed dramatically (Figure 2). *Caobangia*, 1893 was included in Fabriciinae, while *Myxicola*, *Sabellonga* and some genera previously considered as fabriciins (*Chone* Krøyer, 1856, *Desdemona* Banse, 1957, *Euchone* Malmgren, 1866, *Fabrisabella* Hartman, 1969 and *Jasmineira* Langerhans, 1880) were recovered in Sabellinae. The Sabellinae was defined by the presence of the “radiolar skeleton” composed of at least two rows of vacuolated cells and dorsally fused radiolar lobes [42]. The subfamily Fabriciinae was characterised by the presence of rasp-shaped (having several rows of teeth) abdominal uncini, absence of ventral lips, separated radiolar lobes (except in *Caobangia*) and the absence of “radiolar skeleton” (except in *Caobangia*, with one longitudinal row of vacuolated cells). Later *Caobangia* was transferred to Sabellinae, simplifying the definition for Fabriciinae [52].

Analyses of molecular data have changed the understanding of the relationships within Sabellida. Molecular data provided evidence of Serpulidae being sister to Fabriciinae, and Sabellinae the sister group of this clade [1]. Consequently, Fabriciinae was raised to the family rank (Fabriciidae, Figure 2). Further studies supported the validity of the three families, although relationships among them were not consistently supported [2,24,27]. The latest study using transcriptomes for a broad range of sabellids recovered Fabriciidae as sister to a clade of Sabellidae and Serpulidae [3] (Figure 2). Now it is generally accepted that Sabellidae does not include Fabriciidae [1,2,24,27] and is more closely related to Serpulidae than to Fabriciidae [3].

3.1.1. Fabriciidae

Monophyly of Fabriciidae is supported by the branching patterns of the radiolar crown, the absence of ventral lips, abdominal uncini with elongate handle referred to as manubrium, and presence of radiolar hearts [4] (Table 1, Figure 3), as well as by reproductive characters [27]. Relationships among fabriciids were first explored using morphological data [42,53–60]. Although the phylogenies were not fully resolved, these studies recovered two main groups: one paraphyletic, branching off at the base of the tree and including

Fabriciola Friedrich, 1939, *Manayunkia* Leidy, 1859, *Monroika* Hartman, 1951, and a clade with the remaining nine genera considered valid at the time. The position of *Pseudofabriciola* Fitzhugh, 1990b varied with the different analyses [57].

Table 1. Morphological diagnostic features of the three taxa of Sabellida.

Feature	Fabriciidae	Sabellidae	Serpulidae
Tube material	mucus and sediment/none	mucus and sediment *	calcium carbonate
Radiolar lobes	separated	fused	separated
Vacuolated cells supporting radioles	absent	present	absent
Operculum	absent	absent	absent or present
Thoracic membrane	absent	absent	present
Thoracic uncini	acicular	avicular **	avicular
Number of abdominal chaetigers	usually three (exceptionally two or four)	more than three	more than three
Abdominal uncini	with elongate and wide handle (manubrium)	with short handle or lacking handles	lacking handles
Branchial hearts	present	absent	absent

* *Glomerula* is an exception with a calcareous tube; ** *Terebrasabella* is an exception with three types of thoracic uncini: acicular, avicular and palmate.

A recent comprehensive study assessing phylogenetic relationships within Fabriciidae incorporated DNA sequence and reproductive data into a morphological dataset [27]. The results corroborated the apomorphies proposed earlier: the absence of ventral lips, modified abdominal uncini with elongate manubrium and presence of radiolar hearts, together with six apomorphic reproductive traits: (1) spermatogenesis occurring only in the thorax, (2) spermatids developed in large clusters with a central cytophore, (3) presence of a single dorsal sperm duct, (4) presence of a sperm nuclear projection, (5) sperm nuclear membrane thickening, and (6) sperm extra-axonemal sheath. The study recovered the two main groups already revealed by Fitzhugh [42,56,57,61,62]. One clade contained *Manayunkia* and *Echinofabricia* Huang, Fitzhugh and Rouse, 2011 (Genus A in [57]), and branched off basally, sister to all the other Fabriciidae. The second larger clade showed *Rubifabriciola* Huang, Fitzhugh and Rouse, 2011 (the red-eyed '*Fabriciola*'), branching off at the base, sister to six other genera. Some taxa need further study to assess their monophyly since *Novafabricia labrus* Fitzhugh, 1998 was not found nested within other species in the genus (as in [57]), *Monroika africana* (Monro, 1939) formed a polytomy with the *Manayunkia* species, and there were not enough characters to support *Augeneriella* Banse, 1957 and *Pseudoaugeneriella* Fitzhugh, 1988 as distinct genera [27].

With one exception, genera of Fabriciidae have been revised and most of the revisions were accompanied by phylogenies (Table 2). *Brandtika* Jones, 1974 was not included in phylogenetic analyses [27,59] due to poorly preserved types and incomplete descriptions [63].



Figure 3. Some fabriciid representatives showing a range of the diversity of forms found in the group. (a) cf. *Fabriciola* sp., deep-sea basin of the southwest Atlantic; (b,c,h) *Fabricia stellaris*, Baltic Sea; (d,f) *Manayunkia athalassia*, South Australia; (e) *Fabriciola* sp., Brazil (g) *Monroika* sp., Argentina ((c) by A. Dietrich, (d) by G. Rouse, (g) by L. Armendariz).

Table 2. Fabriciid currently accepted genera that have undergone major or partial revisions and phylogenetic analyses (based on morphological features, molecular data or both).

Genera	Number of Species *	Taxonomic Revision	Phylogenetic Studies
<i>Augeneriella</i> Banse, 1957	5	Banse 1957, Fitzhugh 1983, 1990a, 1993	Fitzhugh 1991a-b, 1992, 1993, 2010
<i>Bansella</i> Fitzhugh, 2010	1	Fitzhugh 2010	Fitzhugh 2010
<i>Brandtika</i> Jones, 1974	1	Fitzhugh 2001	NO
<i>Brifacia</i> Fitzhugh, 1998	2	Fitzhugh 1998; Giangrande et al. 2014	Fitzhugh 2010
<i>Echinofabricia</i> Huang, Fitzhugh and Rouse, 2011	4	Huang et al. 2011	Fitzhugh 1991a, 1992, 1993, 1998, 2010 (as genus A)
<i>Fabricia</i> de Blainville, 1828	1	Fitzhugh 1991b, 2010	Fitzhugh 1991a, 1992, 1993, 1998, 2010
<i>Fabricinuda</i> Fitzhugh, 1990b	7	Fitzhugh 1983, 1990b, 2002a; López and Rodríguez 2008	Fitzhugh 1991a, 1992, 1993, 1998, 2002a, 2010; López and Rodríguez 2008
<i>Fabriciola</i> Friedrich, 1939	6	Fitzhugh 1991b, 1992, 1999; Bick 2005	Fitzhugh 1991a, 1992, 1993, 1998, 1999, 2010
<i>Manayunkia</i> Leidy, 1859	10	Sitnikova et al. 2014, Atkinson et al. 2020	Fitzhugh 1991a, 1992, 1993, 1998, 2010; Sitnikova et al. 2014; Pudovkina et al. 2016
<i>Monroika</i> Hartman, 1951	1	Fitzhugh 1992	Fitzhugh 1992, 1998, 2010
<i>Novafabricia</i> Fitzhugh, 1990c	11	Fitzhugh 1983, 1990c, 1998; Bick 2005	Fitzhugh 1991a, 1992, 1993, 1998, 2010
<i>Parafabricia</i> Fitzhugh, 1992	2	Fitzhugh 1992	Fitzhugh 1992, 1993, 1998, 2010
<i>Pseudoaugeneriella</i> Fitzhugh, 1998	5	Fitzhugh 1998	Fitzhugh 1998, 2010
<i>Pseudofabricia</i> Cantone, 1972	1	Fitzhugh 1995	Fitzhugh 1992, 1998, 2010
<i>Pseudofabriciola</i> Fitzhugh, 1990b	13	Fitzhugh 1990c, 1991b, 1993, 1996, 2002a; Fitzhugh et al. 1994, Fitzhugh and Simboursa 1995	Fitzhugh 1991a-b, 1993, 1994, 1996, 1998, 2002a, 2010; Fitzhugh et al. 1994, Fitzhugh and Simboursa 1995
<i>Raficiba</i> Fitzhugh, 2001	1	Fitzhugh 2001	Fitzhugh 2010
<i>Rubifabriciola</i> Huang, Fitzhugh and Rouse, 2011	10	Huang et al. 2011	Huang et al. 2011

* Excluding subspecies.

3.1.2. Sabellidae

Monophyly of Sabellidae is supported by the presence of dorsal and ventral lips, the presence of vacuolated cells supporting radioles and pinnules, and the dorsal fusion of the radiolar lobes (Table 1, Figure 4) [2,3,24,42,52]. Currently, monophyletic clades Sabellinae and Myxicolinae are recognized within Sabellidae, the latter is composed of Amphiglenini and Myxicolini [3]. The current composition of the Sabellinae (now Sabellidae) has not changed significantly since the early cladistic analyses [42,52], although nine genera have been erected since (Table 3), and *Megalomma* Johansson, 1925 was replaced by *Acromegalomma* Gil and Nishi, 2017 because the name was preoccupied by a group of carabid beetles. Fitzhugh [42] provided diagnoses of all genera accepted at the time, with their potential apomorphies. The most recent review of morphology and diagnostic features of genera and species identification is found in [24].



Figure 4. Some sabellid representatives showing a range of the diversity of forms found in the group. (a) *Stylomma palmatum*, Lizard Island, Australia; (b) *Acromegalomma* spp., Lizard Island, Australia; (c) *Paradialychone ambigua*, Lizard Island, Australia; (d) *Pseudobranchiomma paraemersoni*, São Paulo, Brazil; (e) *Laonome xeprovala*, Sea of Azov; (f) *Branchiomma* sp., Mexico; (g) *Bispira brunnea*, Caribbean; (h) *Notaulax* sp., Lizard Island, Australia; (i) *Anamobaea orstedii*, Mexico; (j) *Sabellastarte magnifica*, Mexico. ((a,b,g), by M. Bok; (e) by V. Syomin, (i,j) by H. Bahena).

Table 3. Sabellid currently accepted genera that have gone through major or partial revisions and phylogenetic analyses (either considering morphological features, molecular data or both).

Genera	Number of Species *	Revision	Phylogenetic Analyses
<i>Acromegalomma</i> Gil and Nishi, 2017	38	Perkins 1984, Tovar-Hernández and Salazar-Vallejo 2008; Capa and Murray 2009; Tovar-Hernández and Carrera-Parra 2011, Gil and Nishi 2017	Capa and Murray 2009, Tovar-Hernández and Carrera-Parra 2011
<i>Amphicorina</i> Claparède, 1864	46	Rouse 1990 (as <i>Oriopsis</i>), Cochrane 2003	Cochrane 2003
<i>Amphiglena</i> Claparède, 1864	14	Capa and Rouse 2007; Tilic et al. 2019	Capa and Rouse 2007, Tilic et al. 2019
<i>Anamobaea</i> Krøyer, 1856	2	Tovar-Hernández et al. 2020	NO
<i>Aracia</i> Nogueira, Fitzhugh and Rossi, 2004	3	Nogueira et al. 2004; Tovar-Hernández 2014	Nogueira et al. 2010
<i>Bispira</i> Krøyer, 1856	24	Knight-Jones and Perkins 1998; Capa 2008	Capa 2008
<i>Branchiomma</i> Kölliker, 1859	30	Tovar-Hernández and Knight-Jones 2006	Capa et al. 2013; del Pasqua et al. 2018
<i>Caobangia</i> Giard, 1893	7	Jones 1974	NO
<i>Chone</i> Krøyer, 1856	20	Cochrane 2003, Tovar-Hernández 2005, 2006, 2007a, b, c, 2008	Tovar-Hernández 2008
<i>Claviramus</i> Fitzhugh, 2002	5	Fitzhugh 2002; Nishi et al. 2019	NO
<i>Dialychone</i> Claparède, 1869	19	Tovar-Hernández 2008	Tovar-Hernández 2008
<i>Euchone</i> Malmgren, 1866	35	Cochrane 2003, Giangrande and Licciano 2006, Giangrande et al. 2017	Cochrane 2003
<i>Euchoneira</i> Licciano, Giangrande and Gambi, 2009	1	Licciano et al. 2009	Licciano et al. 2009
<i>Eudistylia</i> Bush, 1905	5	Hartman 1938, Banse 1979	NO
<i>Hypsicomus</i> Grube, 1870	1	Perkins 1984	NO
<i>Jasmineira</i> Langerhans, 1880	19	Cochrane 2003, Capa and Murray 2015	Cochrane 2003
<i>Laonome</i> Malmgren, 1866	10	Fitzhugh 2002, Capa 2007, Bick et al. 2018	Capa 2007
<i>Notaulax</i> Tauber, 1879	26	Perkins 1984	NO
<i>Paradialychone</i> Tovar-Hernández, 2008	16	Tovar-Hernández 2008	Tovar-Hernández 2008
<i>Parasabella</i> Bush, 1905	29	Perkins 1984, Giangrande 1994, Tovar-Hernández and Harris 2010, Capa and Murray 2015b, Keppel et al. 2020	Capa and Murray 2015b
<i>Perkinsiana</i> Knight-Jones, 1983	16	Knight-Jones 1983, Giangrande and Gambi 1997, Tovar-Hernández et al. 2012	NO
<i>Potamethus</i> Chamberlin, 1919	11	Knight-Jones 1983	NO
<i>Potamilla</i> Malmgren, 1866	10	Knight-Jones 1983	NO
<i>Potaspina</i> Hartman, 1969	2	Capa 2007	Capa 2007
<i>Pseudobranchiomma</i> Jones, 1962	19	Knight-Jones 1994, Knight-Jones and Giangrande 2003	Capa and Murray 2016
<i>Pseudopotamilla</i> Bush, 1904	23	Knight-Jones et al. 2017	Capa 2007
<i>Sabella</i> Linnaeus, 1767	39	Knight-Jones and Perkins 1998	NO
<i>Sabellastarte</i> Krøyer, 1856	8	Knight-Jones and Mackie 2003	Capa et al. 2010
<i>Sabellomma</i> Nogueira, Fitzhugh and Rossi, 2010	4	Nogueira et al. 2010, Capa and Murray 2015	Nogueira et al. 2010
<i>Stylomma</i> Knight-Jones, 1997	2	Knight-Jones and Perkins 1998, Capa 2007	Capa 2007
<i>Terebrasabella</i> Fitzhugh and Rouse, 1999	3	Murray and Rouse 2007	Murray and Rouse 2007

* Excluding subspecies.

Phylogeny of Sabellidae has been largely assessed [2,64–70]. Monophyly of *Acromegalomma*, *Amphiglena* Claparède, 1864, *Branchiomma* Kölliker, 1859, *Chone*, *Dialychone* Claparède, 1869, *Paradialychone* Tovar-Hernández, 2008 and *Pseudobranchiomma* Jones, 1962 have been confirmed [68,71–74]. Members of the genera *Chone*, *Dialychone* and *Paradialychone* are still problematic due to their small size and because genera and species are delineated based on combination of features, such as details of uncini dentition (anterior and posterior abdominal chaetigers) and radiolar crown structures (lips and pinnular appendages) that are often difficult to interpret. As a result, the position of some species within either *Dialychone*, *Paradialychone* or *Chone* based on morphology is uncertain (e.g., *P. ambigua* Capa and Murray, 2015) and a molecular approach to this group is needed. The genera *Bispira* Krøyer, 1856 [2,69,74], *Euchone* [67,75,76] and *Perkinsiana* Knight-Jones, 1983 [68] appear to be paraphyletic, whereas monophyly of *Laonome* Malmgren, 1866, *Parasabella* Bush, 1905 and *Sabellastarte* Krøyer, 1856 should be assessed.

In the last two decades a number of sabellid genera have undergone major or partial taxonomic revisions (Table 3) that included morphological comparisons of congeners, as well as examination and re-description of types to detect potential synonyms or undescribed species. In a few of them, monophyly has been assessed through phylogenetic analyses of mainly morphological data.

3.1.3. Serpulidae

Monophyly of Serpulidae is supported by the presence of calcareous tubes with complex ultrastructures, distinct from the simple structure found in calcareous tubes of the unique sabellid *Glomerula piloseta* (Perkins, 1991). The serpulid thorax is surrounded by the thoracic membranes, which are absent in sabellids and fabriciids. Most serpulids have an operculum (or several), a modification of the distal part of a radiole, acting as a plug when animals hide in their tubes (Table 1, Figure 5).

The first formal phylogenetic analysis based on morphological data [43] recovered monophyletic Spirorbinae (as sister group to Serpulinae, including *Chitinopoma* Levinson, 1884, *Crucigera* Benedict, 1887, *Serpula* Linnaeus, 1758, *Hydroides* Gunnerus, 1768, *Ficopomatus* Southern, 1921, *Galeolaria* Lamarck, 1818, *Spirobranchus* Blainville, 1818) and paraphyletic Filograninae (*Filograna* Berkeley, 1835, *Microprotula* Uchida, 1978, *Protula* Risso, 1826). Phylogenetic studies using DNA data inferred two major clades within Serpulidae, e.g., [45–49]. The clade A comprised two clades: the *Serpula-Crucigera-Hydroides* (Clade AI ‘*Serpula*-group’) and the *Spirobranchus-Ficopomatus-Ditrupa* (Clade AII ‘*Spirobranchus*-group’). The Clade B included a monophyletic Spirorbinae as sister group to the *Protis-Protula-Vermiliopsis-Chitinopoma* (clade BI ‘*Protula*-group’). Position of serpulid genera, such as *Vermiliopsis* and *Chitinopoma* within clade BI along with typical filogranins, made both traditional Filograninae and Serpulidae paraphyletic.

Within Clade A, further assessment of AI ‘*Serpula*-group’ (*Serpula*, *Crucigera*, *Hydroides*) [77] supported monophyly of *Hydroides*, but *Serpula* was recovered as paraphyletic basal grade and *Crucigera* was polyphyletic. Later studies assessed relationships within the largest serpulid genus *Hydroides* [78–80]. Within AII ‘*Spirobranchus*-group’ several studies examined relationships within the genus *Spirobranchus* [81–84] and demonstrated sister group relationship between brackish-water genus *Ficopomatus* and freshwater monotypic *Marifugia* Absolon and Hrabě, 1930 [46].



Figure 5. Diversity within Serpulidae. (a) *Vermiliopsis glandigera/pygidialis*-complex sp., Lizard Island, Australia; (b) *Serpula* sp., Lizard Island, Australia; (c) *Hydroides lirs*, Lizard Island, Australia (d) *Spirobranchus corniculatus*, Lizard Island, Australia; (e) *Pomatostegus actinoceras*, Lizard Island, Australia.; (f) *Protula* sp., Lizard Island, Australia. ((a–e) by A. Semenov, (f) by G. Rouse).

Within clade B, studies focused on Spirorbinae, classification of which is based [85] on the six distinct types of brooding, two opercular (Pileolariini and Januini) and four tubular (Romanchellini, Paralaespirini, Circeini, Spirorbini). It has been repeatedly argued that tube incubation precedes opercular brooding [85–88], but Thorp and Segrove [89] advocated for an ancestral opercular incubation. Results of the first morphology-based phylogenetic analysis of spirorbins [44] confirmed the ancestry of tube brooding, but suggested that the opercular brooding arose once and the brooding cup of Januini is a simplification of the brooding structure of Pileolariini. Another analysis of morphological data [90] confirmed that opercular brooding is derived, but suggested that the two types arose independently. No molecular spirorbini phylogeny is available to test this arrangement. As neither traditional Serpulinae, nor Filograninae are monophyletic, re-classification based on a comprehensive integrative analysis and re-formulation of the subfamily diagnoses are needed. Meanwhile Spirorbinae is accepted as nested within Serpulidae, but other serpulid genera are not assigned into subfamilies. Most serpulid genera have not been revised (Table 4).

Table 4. Serpulid currently accepted genera that have undergone major or partial revisions and phylogenetic analyses (using morphological features, molecular data or both).

Genera	Number of Species *	Revision	Phylogenetic Analyses
<i>Bathyditrupa</i> Kupriyanova, 1993	1	Kupriyanova and Ippolitov 2015	NO
<i>Bathyvermilia</i> Zibrowius, 1973	7	Zibrowius 1973	NO
<i>Crucigera</i> Benedict, 1887	5	ten Hove and Jansen-Jacobs 1984	Kupriyanova et al. 2008
<i>Ditrupa</i> Berkeley, 1835		ten Hove and Smith 1990	NO
<i>Ficopomatus</i> Southern, 1921	6	ten Hove and Weerdenburg 1978	Kupriyanova et al. 2009; Styan et al. 2017
<i>Galeolaria</i> Lamarck, 1818	3	NO	Halt et al. 2009; Smith et al. 2012
<i>Hydroides</i> Gunnerus, 1768	99	Bastida-Zavala and ten Hove 2002, 2003; Sun et al. 2015; Sun et al. 2018	Sun et al. 2018
<i>Laminatubus</i> ten Hove and Zibrowius, 1986	3	Rouse and Kupriyanova 2021	Rouse and Kupriyanova 2021
<i>Marifugia</i> Absolon and Hrabec, 1930	1	Kupriyanova et al. 2009	Kupriyanova et al. 2009
<i>Metavermilia</i> Bush, 1905	15	Zibrowius 1971; Nishi et al. 2007	NO
<i>Pseudochitinopoma</i> Zibrowius, 1969	5	Kupriyanova et al. 2012	NO
<i>Pyrgopolon</i> de Montfort, 1808	3	ten Hove 1973	NO
<i>Serpula</i> Linnaeus, 1758	30	NO	Kupriyanova et al. 2008
<i>Spirobranchus</i> de Blainville, 1818	36	ten Hove 1970	Willette et al. 2015; Perry et al. 2019; Pazoki et al. 2020
<i>Spiraserpula</i> Regenhardt, 1961	18	Pillai and ten Hove 1994	NO
<i>Spirodiscus</i> Fauvel, 1909	2	Kupriyanova and Nishi 2011, Kupriyanova and Ippolitov 2015	NO

* Excluding subspecies.

3.2. Diversity and Species Discovery

3.2.1. Number of Genera and Species

Within Fabriciidae, 17 genera, 82 species and four subspecies are currently considered valid (Table S1). This revised dataset differs from that of Pamungkas et al. [91], who listed 21 genera and 91 species, but erroneously counted the genera *Eriographis* Grube, 1850, *Leiobranthus* Quatrefages, 1850, *Leptochoone* Claparède, 1870 and *Tuba* Renier, 1804, all of them already synonymised with the sabellid genus *Myxicola* (Fitzhugh 1989). Discrepancy in the number of species is due to synonymisations and new combinations, as recently updated in WoRMS.

The first fabriciid genus, *Fabricia* Blainville, 1828, was established to accommodate *Tubularia stellaria* Müller, 1774, a species with only 12 chaetigers and smaller than the sabellids described at that time [90]. In mid-19th century the genus *Manayunkia* was erected and *Fabriciolo* was established only in the 20th century. In the second half of the 20th century, 11 genera were established and four genera were erected at the beginning of the 21st century (Figure 6). It is remarkable that among the 17 currently valid Fabriciidae genera, eight were established by Fitzhugh alone (*Bansella* Fitzhugh, 2010, *Brifacia* Fitzhugh, 1998, *Fabricinuda* Fitzhugh, 1990a, *Novafabricia* Fitzhugh, 1990b, *Parafabricia* Fitzhugh, 1992, *Pseudoaugeneriella*, *Pseudofabriciolo* and *Raficiba* Fitzhugh, 2001) or with collaborators (*Echinofabricia* and *Rubifabriciolo*) [27].

According to Pamungkas et al. [91], whose data were collected in 2016, Sabellidae comprises 42 genera and 493 valid species. Since 2016, 20 new species have been described [74,92–103] and a new monotypic genus *Euchonoides* Magalhães, Bailey-Brock and Tovar-Hernández, 2020 was established. After the WoRMS database has been updated (see Materials and Methods section), the current count is 42 genera and 512 valid species in Sabellidae (Table S2). The first described genus was *Sabella* Linnaeus, 1767. From 1801 to 1850 only the genus *Myxicola* was established (Koch in [104]). The second half of the 19th century was a productive period, with 15 genera established. In the 20th century, six genera were erected in the first half, and nine in the second. Finally, from 2001, eight genera have been erected (Figure 6).

According to Pamungkas et al. [91], Serpulidae comprises 576 species in 77 genera, as they mistakenly included several fossil taxon names in the count of extant species. Serpulidae now comprises 562 species in 69 genera, which includes 48 genera with 374 extant species of Serpulinae *sensu lato* and 23 genera with 188 extant species of Spirorbinae (Table S3). These numbers, however, do not include those of fossil taxa (180 species, in 53 genera), not considered here. Out of 69 species of the genus *Spirorbis* Daudin, 1800, 46 were described before Bailey [85] re-classified spirorbins according to the incubation methods and never revised, so some of them upon a revision can be re-assigned to other genera.

The first serpulids described within the newly erected genus *Serpula* by Linnaeus [105] were *Spirobranchus triqueter* (non Linnaeus, *sensu* Fabricius, 1780), as *S. triqueter*, *Spirorbis spirorbis* (Linnaeus, 1758), as *S. spirorbis*, and *Circeis spirillum* (Linnaeus, 1758), as *S. spirillum*. *Serpula vermicularis* Linnaeus, 1767, the type species of the type genus, was described only nine years later. The monotypic genus *Hydroides*, with *H. norvegica* Gunnerus, 1768, was the second serpulid genus to be described in the 18th century. In the 19th century, 28 genera, eight spirorbins and 20 serpulins, were described. In 1900–1959, 22 genera (including three spirorbins) were described, while 48 genera were erected in the second half of the 20th century (1960–2000). Finally, from 2001, four genera, including three serpulins and one spirorbins, have been erected [49,106,107] (Figure 6).

3.2.2. Taxonomists and Species Discovery

Kirk Fitzhugh is the most productive author in terms of the number of discovered fabriciid species, with 27 species described alone and four in collaborations. Other authorities of fabriciid species include Karl Banse, Gesa Hartmann-Schröder and Greg Rouse, with six species described by each, all as single authors (Table S1).

The most prolific author in terms of sabellid species discovery is Adolph Eduard Grube, who described 40 species before 1881. Other productive taxonomists are María Ana Tovar-Hernández (42 species: 36 as first or single author, 6 as co-author); María Capa (29 species, all as first author or alone), Adriana Giangrande (29 species: 14 as first author or alone, and 15 as co-author), Olga Hartman (18 species) and Gesa Hartmann-Schröder (16 species) (Table S2).

The most productive serpulid taxonomist is Harry ten Hove who so far described 49 species, including seven alone. Gottfried Pillai described 46 species, including 31 species described alone and 15 in collaboration with ten Hove. Phyllis and Wynn Knight-Jones described 41 species, mostly spirorbins. Katherine Bush described 33 species, includ-

ing 25 alone. Helmut Zibrowius described 31 species, including 29 alone and Elena Kupriyanova authored 29 species, including eight alone. Other productive serpulid taxonomists (over 15 species described) are Minoru Imajima (21 species) and Alexander Rzhavsky (17 species, mostly spirorbins) (Table S3).

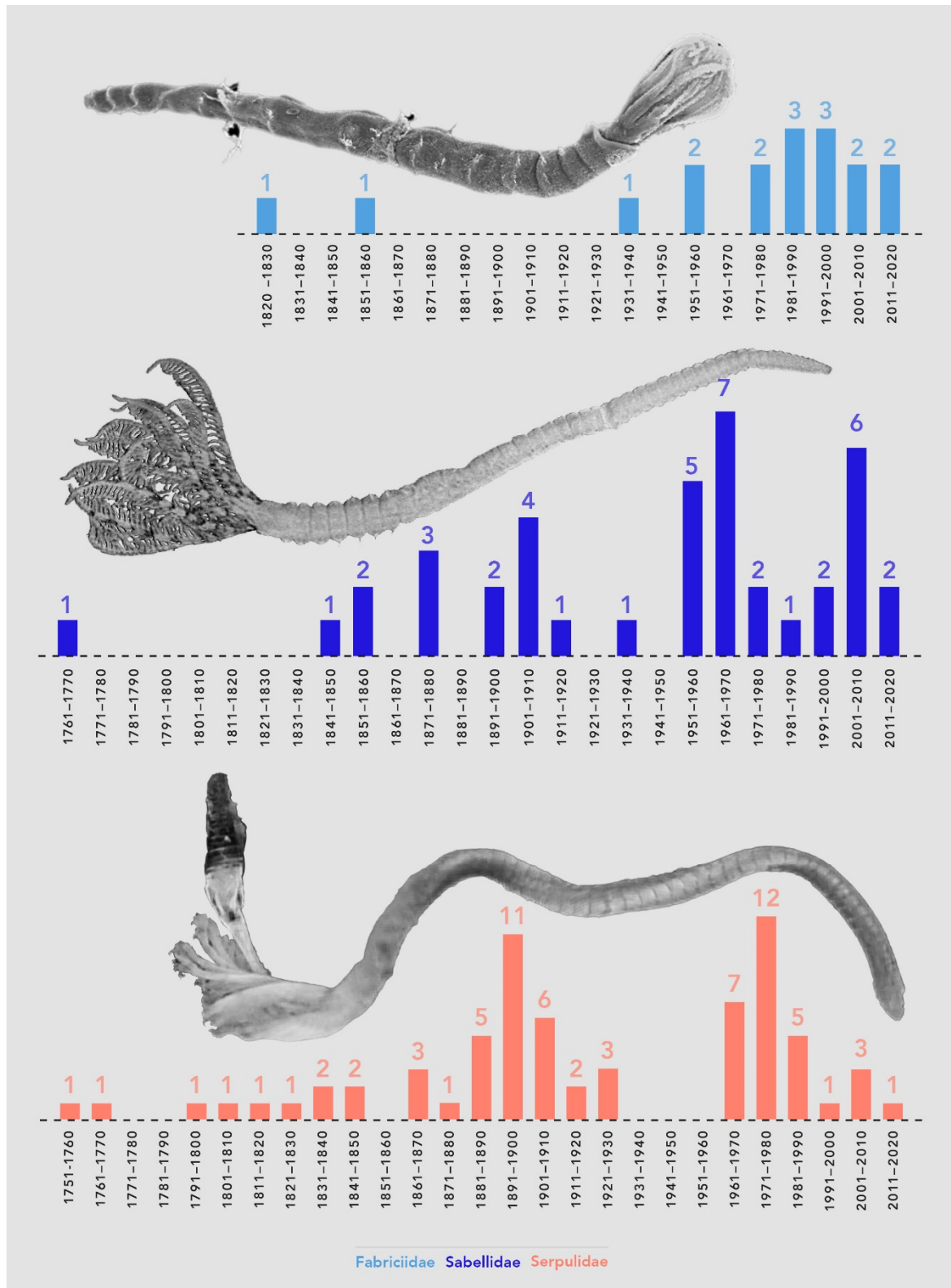


Figure 6. Number of genera erected each decade in Fabriciidae, Sabellidae, and Serpulidae.

3.2.3. Identification Keys, Diversity Assessments, and Recent Regional Taxonomic Studies

The key to all polychaete genera by Fauchald [12] includes all sabellids and serpulids considered valid at the time, but it is outdated and not recommended for taxonomic work anymore. A key to Fabriciidae genera recognized until 1998 was provided by Fitzhugh [57]. In that study, the currently accepted *Echinofabricia* was named Genus A. The most recently updated key to all fabriciid genera is that by Tovar-Hernández and Fitzhugh, in press. The keys to Sabellidae genera were provided by Fitzhugh [42], Tovar-Hernández [108] and most recently Tovar-Hernández and Fitzhugh [109]. The review by ten Hove and Kupriyanova [110] includes diagnoses and a key to all serpulid genera (excluding spirorbins) valid at the time.

Revision of literature reveals that intensive fieldwork and continuous taxonomic studies by a single scientist in a specific area have had a great impact in biodiversity knowledge of a region. However, large geographic regions have been scarcely studied, not only in difficult to access deep-sea environments, but even in the intertidal and subtidal zone either because not enough work has been put into taxonomic surveys, or members of Sabellida were not among targeted groups. It is expected that our understanding of species diversity will improve after efforts (financial, logistical, technological and taxonomic expertise) are devoted to fill those gaps. Herein, information about the most recent regional surveys and taxonomic revisions is provided, and the number of species described in these areas given as a rough approximation of their biodiversity knowledge.

The regions with the overall highest number of type localities of described species are the coastal areas of Europe, both coasts of North America, and Central and Western Indo-Pacific, while the areas with lower number of original descriptions are the majority of Africa, South America, as well as Tropical Eastern Pacific and Eastern Indo-Pacific (Figure 7).

The current state of biodiversity knowledge and a summary of the most recent (defined here as last 20 years) comprehensive checklists, faunistic and taxonomic regional studies (excluding single species descriptions) are organised below by marine realms. References to main comprehensive taxonomic studies are provided as recommendations for getting started with faunas of each realm.

Arctic

This realm covers the Arctic Ocean down to Newfoundland in the western Atlantic, including the northern half of Iceland, northern Russia, from the White Sea to the Bering strait, and all northern Alaska and Canada. One fabriciid, 16 sabellid species, and 16 serpulids have been described from the Arctic, most of them from the Western sector of the Arctic Ocean (Figure 7, Tables S1–S3). Knight-Jones et al. [111] reviewed species of *Pseudopotamilla* from Iceland, Greenland and the Canadian Arctic. Jirkov's book [112] on Arctic polychaetes, that includes diagnoses, illustrations, and keys to sabellids (including fabriciids) and serpulids (including spirorbins), as well as the recent comprehensive illustrated revisions with taxonomic keys to all Arctic Serpulidae (including Spirorbinae) by Rzhavsky et al. [113,114] are recommended for studies in this region.

Temperate Northern Atlantic

This realm is delimited in the north with the Arctic realm, and in the south reaches the coasts of Florida, including the northern half of the Gulf of Mexico, and is delimited in the east by the Cape Verde archipelago and the coasts of Mauritania. It also includes the Mediterranean and the Black Sea. Sixteen fabriciids, 124 sabellids, and 108 serpulids have been described from this realm (Figure 7). Of these, one fabriciid, 18 sabellid, and 12 serpulid species were from the Western coasts of the Atlantic Ocean and three sabellids were from northwest Africa. All the rest were described from European waters and the Mediterranean (Tables S1–S3).

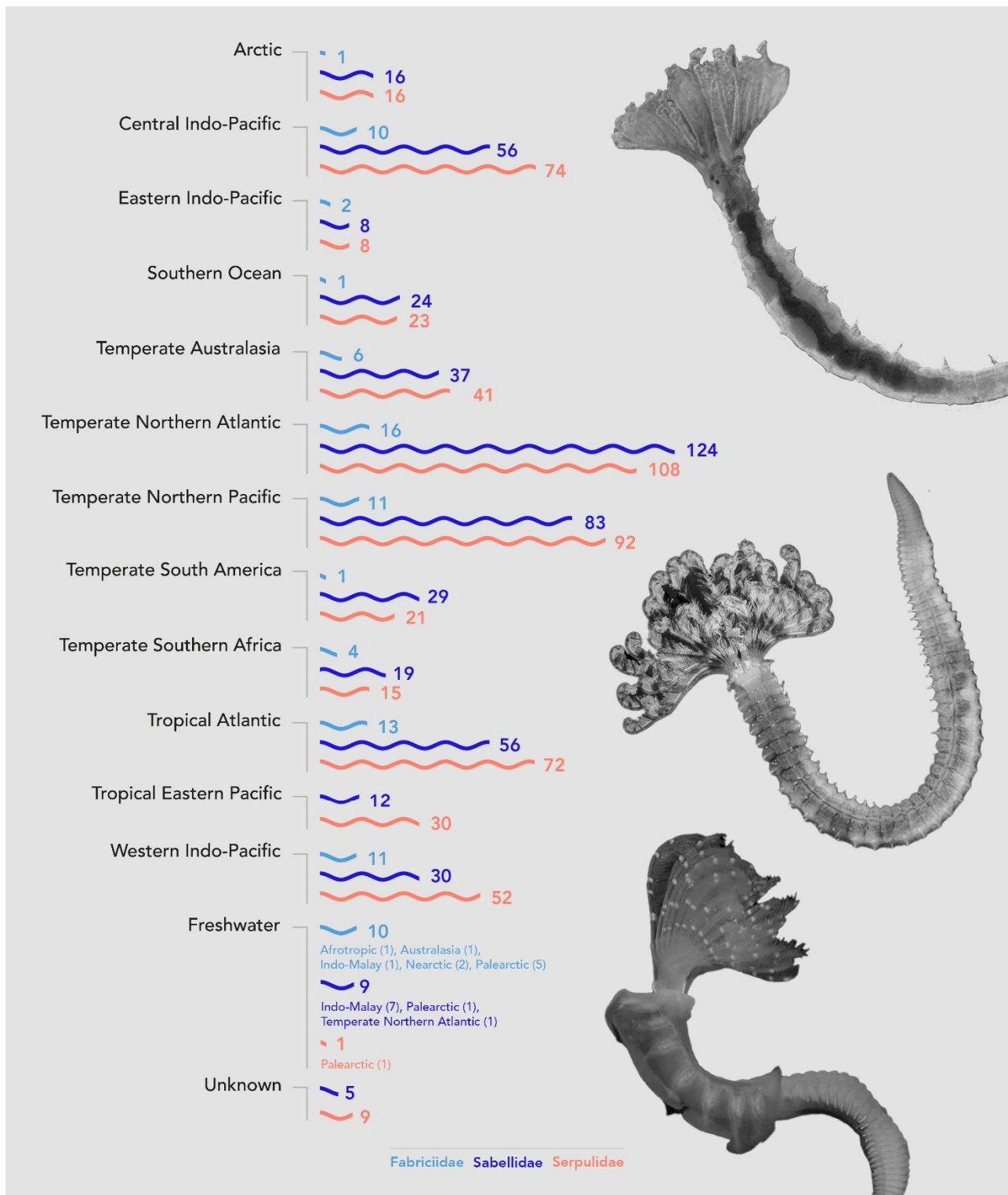


Figure 7. Number of species described for each marine realm (in alphabetical order, according to Spalding et al. [31]) and Udvardy 1975 for limnic realms.

The book by Fauvel on sedentary polychaetes of France [115] provide descriptions and illustrations of the common species of the north eastern Atlantic and western Mediterranean and is still been widely used despite being outdated. Relatively more updated sources of serpulid diversity data in the Mediterranean are books by Zibrowius [116] and Bianchi [117] that include keys, descriptions and illustrations. The illustrated key

by Knight-Jones [118] to the British Isles and North-West Europe is recommended as an initial source of data on Sabellidae, Fabriciidae and Serpulidae. The incoming book on Fauna Ibérica includes chapters on Fabriciidae and Sabellidae and will be a new standard reference for the region [119,120].

Despite the overall high number of species described from this region, only a few taxonomic and faunistic studies have been carried out on Sabellida in the last 20 years in the Atlantic provinces of this realm. In particular, fabriciids were studied by Bick [121], species of *Euchone* by Bick and Randel [122], *Chone* by Tovar-Hernández et al. [123,124] and *Pseudopotamilla* by Knight-Jones et al. [111]. However, the notable exception has been the Mediterranean, where much taxonomic activity, with particular emphasis on introduced species, has taken place recently. Some representative contributions dealing with Mediterranean fanworms include those by Çinar (on serpulids [125], on non-indigenous species [126]), the general annelid checklist of polychaetes from Turkey [127], Selim et al. (on *Dialychnone* and *Paradialychnone* [128]), Giangrande et al. (sabellids of the Ionian Sea [129], on *Acromegalomma* [130]), the general papers on annelid diversity of the Adriatic Sea [131,132] and the fabriciids and sabellids of the Adriatic [133], the checklist of Iberian species [134] and the most recent one by Tilic et al. [103] dealing with *Amphiglena*. A checklist of the polychaetes from the Black Sea includes three fabriciids, six sabellids, and 11 serpulids [135].

Temperate Northern Pacific

The western side of this realm is demarcated by the Bering Strait in the north, and an imaginary line from Taiwan to the south of Baja California Peninsula, in the south. The number of fabriciids described in this realm is 11, eight of them from the Eastern side (Table S1). The number of described sabellids is 83, 37 of which from the Western side, and 46 from the Eastern side (Table S2). Out of 92 serpulid species described from this region, 54 are from the western side (Table S3).

The catalogue of sedentary polychaetes from California [136], still widely used for the region, is outdated and is not recommended. The monograph of polychaetes of the Russian Far-East [136] and its English translation [137] that remains the main source of keys and information on polychaetes of the region, including Sabellida, is also outdated and thus should be used with caution. The revision of spirorbins from the east Pacific coast [137] is still the most recent source of information on this group.

The most recent literature-based annotated checklist of polychaetes from Pacific coasts of Russia lists 37 sabellids (including fabriciids) and 40 serpulids [138]. Sabellids from Japan were recently reported by Nishi et al. [95,139] and Yoshihara et al. [140]. Taxonomic studies on serpulids of Japan are summarized in the book by Imajima [141] that provides an illustrated key to 55 species of Serpulidae, but does not include sabellids. The most recent account of Chinese polychaetes [142] provides diagnoses and keys to 64 species of sabellids and 98 serpulid species, and is recommended as a source of biodiversity data and taxonomic keys for China. The complementary revision [143] includes a checklist of most annelid groups from the South China Sea, and lists three fabriciid, 33 sabellid and 72 serpulid species. Recent revisionary studies, including taxonomic keys, from the Pacific coast of North America have reported seven species of sabellids and more than 40 serpulids in the following contributions dealing with species of *Hydroides* from Northern Mexico [144], serpulids from the Eastern Pacific [145,146], sabellids and serpulids from northern Mexico [147,148], and sabellid *Acromegalomma* [149] and *Notaulax* species also from Northern Mexico [101].

Tropical Atlantic

This realm is delimited in the north by the Temperate Northern Atlantic realm and in the south by an imaginary line from Rio de Janeiro in the west to the southern border of Angola in the east. It also includes the southern half of the Gulf of Mexico and the Caribbean. Thirteen fabriciid species have been described from western side of the realm,

specifically from the Caribbean, and none from the eastern Atlantic (Table S1). Out of 56 sabellids described in the region, only one came from the African coasts (Table S2) and of the 72 serpulids, only 10 were described from Africa (Table S3).

Zibrowius [150] made the first study on Brazilian serpulids. Other recommended taxonomic studies of serpulids (other than *Hydroides*) of Caribbean are those by ten Hove [151–154].

Recent studies of the Caribbean fanworms included those describing fabriciids [27,155]; revisions of species in *Chone* [156] and *Branchiomma* [157]; records and new species of sabellids [155,158]; and selected serpulids, such as *Hydroides* [159], *Serpula* and *Spiraserpula* [160]. The tropical coasts of South America have been scarcely studied. The checklist of polychaetes of Brazilian Tropical Atlantic region reports 11 sabellid and 24 serpulid species for the area [161–164], with no fabriciids registered so far. However, several of those are records of species described from Europe, North America and South Africa, demanding further study. Additionally, Amaral et al. [163] checklist treated many already synonymised species as valid.

The illustrated key of Sabellidae and Fabriciidae by Tovar-Hernández and Fitzhugh [105] includes all species currently known for the Caribbean, whereas Caribbean Serpulidae are available in [165].

Western Indo-Pacific

This large realm covers most of East coast of Africa, Madagascar, Arabian (Persian) Gulf, the Red Sea, shelf of Bay of Bengal and Andaman Sea. The number of species described in this realm is 93, including 11 fabriciids, 30 sabellids, and 52 serpulids (Figure 7, Tables S1–S3). Out of 52 serpulids, only eight were described from African coasts.

An influential book on Indian polychaetes [166], unfortunately, lists European species (and even illustrates specimens collected in France) and therefore, is not recommended as an identification tool beyond the generic level. The most recent checklist by Sivadas and Carvalho [167] includes two fabriciids, 11 sabellids and 34 serpulids from India and critically evaluated annelid species richness in the region, stressing that native species diversity of India is severely underestimated. The relatively large number of serpulids described from Sri Lanka is due to the intense work of Pillai [40,168,169]. These publications still remain as the only source of faunal information for that region.

An annotated literature-based checklist by Wehe and Fiege [170] is the best compilation of annelid diversity in the area surrounding the Arabian Peninsula. The most recent checklist of intertidal polychaetes of Kuwait by Al-Kadari et al. [171], based on newly collected material, reported seven species of Sabellidae and 12 Serpulidae. A monograph on Serpulidae from the Suez Canal by Ben-Eliahu and ten Hove [172] included 16 species. In the Red Sea, Perry et al. [81] reviewed of serpulids of the genus *Spirobranchus* and sabellids have not been studied since Knight-Jones [173].

Central Indo-Pacific

This realm comprising the largest number of ecoregions (40) includes part of the coast of South-East Asia, from Taiwan to Malaysia, down to Tropical Australia from Coral Bay, in the West, to Brisbane, in the East. The eastern boundary of this region is delimited by an imaginary line from Fiji up to the south of Japan. The realm includes the Coral Triangle recognized as the global centre of marine biodiversity [174], and fanworms are also diverse in this region. Ten fabriciids, 56 sabellids, and 74 serpulids have been described from this realm (Figure 7), mainly from the Philippines and tropical Australia (Tables S1–S3). Other than newly described species, 78 species of Sabellidae have been reported only from the Gulf of Thailand, Indonesian Archipelago and the Philippine Seas [98,169], and at least 11 taxa are awaiting formal description [175,176]. Serpulidae from Hong Kong were most recently revised by Sun et al. [177], who provided illustrations, diagnoses and taxonomic keys. Tropical Australian sabellids belonging to 12 genera have been documented in a series of recent studies [68,69,72–74,178]. Serpulids from Kimberley (Western Australia) were revised by Pillai [106] and those from Lizard Island (Queensland) by Kupriyanova et al. [179], whereas the revision of the genus *Hydroides* in Australia [180]

includes both tropical and temperate species. The most comprehensive treatment of Australian sabellids and serpulids is still the interactive key by Wilson et al. [181], but it is outdated in the light of the recent studies. The digital guide [182,183] allows distinguishing 38 native and non-indigenous species of Serpulidae and 14 Sabellidae from Australia, and includes a glossary with main diagnostic features for members of both groups.

Eastern Indo-Pacific

This small in terms of the coastline length Pacific realm includes Hawaii, Marshall, Gilbert and Ellis Islands, Central and Southeast Polynesia, Marquesas, Eastern Island, and the shelf around them. It hosts type localities of 18 fanworms, including two fabriciids, eight sabellids, and eight serpulids (Figure 7, Tables S1–S3).

Fauna of this realm is poorly known beyond that of Hawaii. Out of eight serpulids described from this realm, five were described from Hawaii. The latest studies include those on serpulids of Hawaii (*Hydroides* [140], a key and records excluding spirorbins [145], records of 16 species with a key [142], and serpulids from Cross Seamounts in the Hawaiian chain [184]. Out of eight sabellids, five were described from Hawaii, and two species of *Branchiommma* were reported most recently [185]. A recent study of serpulids from atolls of Marshall Islands [186] reported 29 serpulids (including spirorbins). Small number of publications dealing with members of Sabellida highlights the need for taxonomic work in the area.

Tropical Eastern Pacific

This realm is delimited in the North by the Cape San Lucas, Baja California, by the northern border of Peru in the South and includes the Galapagos Islands in the West. No fabriciids have been described in this region (Table S1) and the number of described sabellids is 12, five of them originally reported from coast of Panama and the rest from further north (Figure 7, Table S2). The number of described serpulids is 30, most of them from Galapagos, Panama and Mexico (Figure 7, Table S3).

Recent studies of Sabellida from the region include those dedicated to Panamanian sabellids [187], some *Acromegalomma* [149] and *Chone* [124], and those focused on sabellids and serpulids from Mexico [145,148,188]. Three sabellids and two serpulid species introduced in the Galapagos Islands were reported by Keppel et al. [189].

Temperate South America

The realm covers both Pacific and Atlantic coasts of South America, from Peru to Rio de Janeiro, respectively. Only one fabriciid was described from this region (Table S1). Twenty-nine sabellids have been described (Figure 7), mainly from Chile and Argentina (Table S2), and 21 serpulids were described at a variety of localities from Brazil to Peru (Figure 7, Table S3).

The publication by Zibrowius [150] remains the most comprehensive study on Brazilian serpulids in both Tropical Atlantic and Temperate South America realms. More recent publications reported three species of fabriciids, 29 of sabellids and 22 species of serpulids for the Brazilian part of the Temperate South America realm [163] and 27 species of serpulids and 17 sabellids for Argentina [190]. Tovar-Hernández et al. [99] studied sabellids mainly from Argentina and Chile. A key to Sabellidae and Serpulidae from continental Chile is available in [191].

Temperate South Africa

This realm includes the coastline of Namibia and South Africa as well as Amsterdam and St. Paul Islands. It hosts type localities of 38 species of Sabellida, including four fabriciids, 19 sabellids and 15 serpulids (Figure 7, Tables S1–S3). Of these, 30 have been described in the littoral zone in South Africa, indicating that less taxonomic effort has been devoted to other areas within this region. The recent papers re-described two serpulid species based on type material (e.g., [192,193]).

Although South African polychaetes, including fanworms, were summarized in the influential book by Day [194], most of Sabellida included in the monograph are ‘cosmopolitan species’ with European type localities (e.g., of 27 serpulids only six have type localities in South Africa), so native Sabellida species diversity is severely underestimated. Spirorbins from South Africa have not been reviewed since studies of Knight-Jones [195] and Knight-Jones and Knight-Jones [196].

Temperate Australasia

The realm includes coasts of Southern Australia and New Zealand hosting type localities of 86 species of Sabellida. This number includes six fabriciids from Australia (Table S1), 37 sabellids (28 described from the Australia and nine from New Zealand (Table S2) and 41 serpulids (28 from Australia and 15 from New Zealand, Table S3) (Figure 7).

Spirorbins from southern Australia have not been studied since they were reviewed by Knight-Jones et al. [197]. In New Zealand, spirorbins were studied by Vine [198], who reported 24 species, nine of them new to science, while a list of sabellids and serpulids was provided by Glasby and Read [199].

Sabellids from Australian temperate waters have been well documented in a series of recent papers [68,69,72–74,200–202] along with records of temperate species. Most recent papers on temperate Serpulidae are Sun et al. [203] and Styán et al. [204], whereas the Australian *Hydroides* revision [180] also includes temperate species.

Southern Ocean

This large realm covers coasts of Antarctica and sub-Antarctic Islands. It hosts type localities of a single fabriciid, 24 sabellid and 23 serpulid species (six serpulins and 17 spirorbins) (Figure 7, Tables S1–S3). Many of these species were discovered and described as a result of Antarctic expeditions of the 19th and early 20th century (e.g., [205–210]).

The most recent contributions from the region are descriptions of two spirorbin species from Kerguelen and Bouvet Islands [211]; species of *Perkinsiana* [212] and reports of 19 still undescribed sabellids from Falkland Islands [213], demonstrating the underestimated diversity. There is no contribution summarizing Sabellida species diversity of this region.

3.3. Diagnostic Characters and Techniques Used for Species Discrimination

Most species within Sabellida are characterised by a unique combination of morphological features. The most useful morphological characters used for Sabellidae species identification are summarised in Capa et al. [24]; for Fabriciidae, see Bick [4]; for Serpulidae, see ten Hove and Kupriyanova [110] and Kupriyanova et al. [214]. Since detailed information is provided in these thorough revisions, only succinct identification guidelines are given below for each family.

3.3.1. Shortcuts to Identification of Fabriciidae

The small body size (most species are less than 5 mm long) and the absence of significant diagnostic characters make the identification of Fabriciidae difficult. All fabriciid species possess a radiolar crown with three pairs of radioles (Figure 8a–c). The branches are formed by successive longitudinal splitting of the radioles. The symmetrical branching of the radioles leads to bi-pectinated radioles, as found in most genera (Figure 8c), whereas pectinated radioles result in asymmetrical branching (Figure 8b), as in *Manayunkia* and *Monroika* only [4]. Ventral filamentous appendages, present in some genera, are associated with the radiolar crown (Figure 8b). These appendages have been described as non-vascularized (e.g., in all species of *Fabriciolo*, *Pseudofabricia* Cantone, 1972 and *Rubifabriciolo*) or vascularized (e.g., in all species of *Augeneriella*, *Echinofabricia*, *Manayunkia*, *Monroika* and *Pseudoaugeneriella*, and also some species of *Fabricinuda* and *Pseudofabriciolo*) [57]. These appendages are branched only among species of *Augeneriella*.

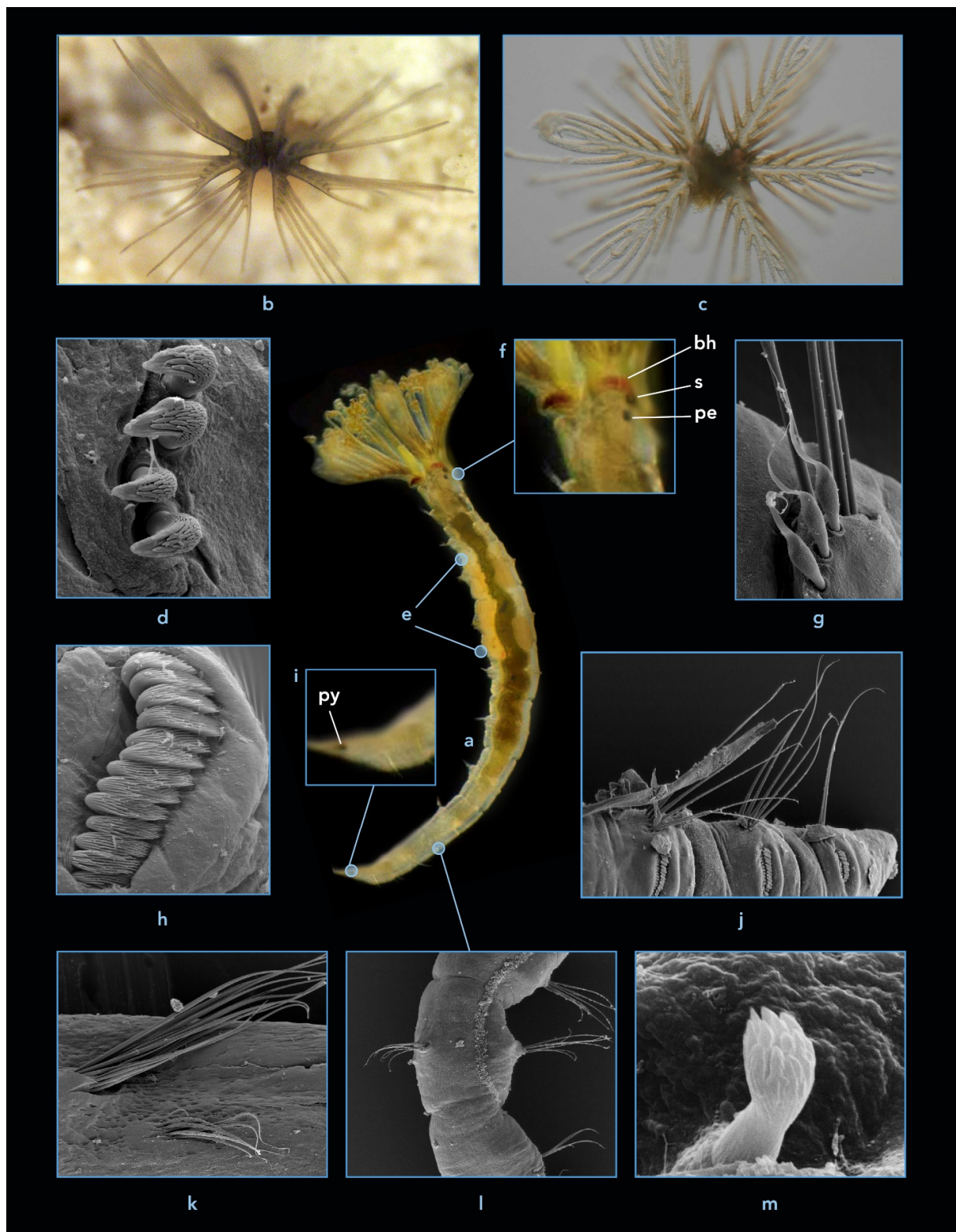


Figure 8. Main diagnostic characters for members of Fabriciidae. (a) *Fabricia stellaris*, dorsal view; (b) Pectinated radiolar branching pattern, *Manayunkia athalassia*; (c) Bi-pectinated radiolar branching pattern, *F. stellaris*; (d) Thoracic uncini of *Manayunkia zenkewitschii*; (e) Gamete bearing region in thorax; (f) Branchial heart (bh), spermathecal (s) and peristomial eye (pe), in this order; (g) Thoracic chaetae, *M. athalassia*; (h) Abdominal uncini, *Pseudoaugeneriella nigra*; (i) Pygidial eye (py); (j) Abdominal chaetae, *M. athalassia*; (k) Thoracic transitional chaetae (below), *Manayunkia godlewskii*; (l) Chaetal inversion, *M. athalassia*; (m) Abdominal pin-ead chaeta, *Rubifabriciola tonerella*. ((a,c) by A. Dietrich; (b) by G. Christie).

Peristomial eyes (Figure 8f) are developed among most species of Fabriciidae, black in most fabriciids, or red, as in *Echinofabricia* and *Rubifabriciola* [27].

The presence of thoracic pseudospatulate and transitional (=pilose, after Jones 1974) chaetae is of taxonomic significance [4] (Figure 8g,k). However, the distribution of pseudospatulate chaetae is not consistent within the genera. These chaetae occur on chaetigers 2–5 (some *Manayunkia* species), 2–8 (*Raficiba barryi* Fitzhugh, 2001), 3–5 (*Monroika africana* and most *Novafabricia* species), 3–6 (*Pseudoaugeneriella*, some species of *Augeneriella* and *Novafabricia*), 3–7 (*Brifacia metastellaris* Fitzhugh, 1998, *Fabricia stellaris*, *Parafabricia ventringulata* Fitzhugh, 1992, and some species of *Augeneriella* and *Fabricinuda*), or 3–8 (most *Fabricinuda* species) [4]. Pseudospatulate chaetae are absent in *Bansella*, *Echinofabricia*, *Fabriciola*, *Pseudofabriciola* and *Rubifabriciola* [4]. Species of *Rubifabriciola* have pin-head chaetae on the abdominal neuropodia [27] (Figure 8m). These chaetae have a blunt tip and a number of small teeth apically. Transitional chaetae (Figure 8k) replacing thoracic uncini occur on the last thoracic chaetigers (chaetigers 6–8) of *Brandtika* spp., *Manayunkia godlewskii* (Nusbaum, 1901), females of *M. occidentalis* Atkinson, Bartholomew and Rouse, 2020 and *M. zenkewitschii* Sitnikova, Shcherbakov and Kharchenko, 1997 [4,215–217].

The thoracic uncini are characterized by a long manubrium (homologous to handle in sabellids) and a main fang surmounted by a series of smaller teeth (Figure 8d). A slightly offset medium-sized tooth occurs between the large main fang and the smaller apical teeth in *Augeneriella*, *Fabricia*, *Fabricinuda*, *Monroika*, *Novafabricia*, *Parafabricia*, *Pseudofabricia*, *Pseudoaugeneriella* and some species of *Pseudofabriciola* [42]. The apical teeth can also be approximately of the same size in *Echinofabricia*, or may gradually decrease in size away from the main fang as in *Fabriciola*, *Manayunkia* and some species of *Pseudofabriciola* [57]. The abdominal uncini usually exhibit multiple rows of equal-sized teeth (Figure 8h). Only members of *Novafabricia chilensis* (Hartmann-Schröder, 1962) and *N. gerdi* (Hartmann-Schröder, 1974) have uncini with a single row of teeth.

Fabriciids usually have three abdominal chaetigers (Figure 8j). However, *Brandtika* spp., *Fabriciola minuta* Rouse, 1996, and *Monroika africana* have two abdominal chaetigers, while *Echinofabricia* spp. has four [215,218,219].

The pygidium is triangular or bluntly rounded in most species, but has a ventral depression in *Pseudofabriciola analis* Fitzhugh, Giangrande and Simboura, 1994. A pair of black or dark brown pygidial eyes is present in most species of Fabriciidae (Figure 8j). They are red in *Echinofabricia* (disappearing after fixation) and *Rubifabriciola* (persisting after fixation), but are always absent in all species of *Manayunkia* and *Monroika*, *Fabriciola parvus* Rouse, 1993 and two undescribed deep-sea species [220]. Unique among members of Sabellida, emergent spicules are present in the epithelium of *Echinofabricia* species [27].

3.3.2. Shortcuts to Identification of Sabellidae

Sabellids are relatively easily to visually identify to the generic level because genera are provided with unique and conspicuous diagnostic features (Figure 9). The diversity of radiolar eyes within members of Sabellidae is remarkable (e.g., Figure 9a), and the eye number, type and arrangement offer a very powerful taxonomic aid for genera and species identification [24,69,221]. The large compound eyes located in the tips of dorsal radioles are unequivocally characteristic of members of *Acromegalomma*, whereas the large single and bulging compound eyes arranged, in a longitudinal row on the outer margin of the radioles, are typical of members of *Pseudopotamilla* Bush, 1904 (Figure 9a). *Anamobaea* Krøyer, 1856 and *Notaulax* Tauber, 1879 are easily recognized due to the presence of long radiolar lobes with dorsal and ventral flanges. Other generic synapomorphies related to the radiolar morphology are the dichotomously branching radioles, found only in *Schizobranchia* Bush, 1905 and *Eudistylia* Bush, 1905 (most likely due to a regeneration processes [111,222]), and the external paired radiolar appendages, called stylodes, in members of *Branchiomma* (Figure 9e). *Euchone* is recognisable by the presence of a typical pre-pygidial depression with lateral wings, but this character is only visible in adults. Species of *Claviramus* Fitzhugh, 2002 have radiolar tips with expanded flanges, rolled inwards or bilobed, this feature is easily seen if radioles are

complete. *Potamethus* Chamberlin, 1919 is recognizable due the very long collar (2–4 times the length of next thoracic segment). Other genera are recognised by unique traits, which are not evident to a naked eye and require optic aids. These are the typical companion chaetae of members of *Parasabella*, the absence of posterior peristomial ring collar in members of *Amphiglena*, or the presence of a broad, oblique glandular (clitellum-like) ring on third abdominal segment in *Euchonoides*. Internal structures, such as the rows of vacuolated cells supporting radioles, dorsal lips and radiolar appendages, are of taxonomic significance and often used for species discrimination [64,102,122,223–226].

3.3.3. Serpulidae Diagnostic Characters

Within Serpulidae, body symmetry separates serpulins from spirorbins, as serpulins are bilaterally symmetrical, while spirorbins are curved in the direction of the tube coil. Specific identification has been based on a combination of characters such as morphology of the operculum and opercular peduncle, degree of development of the collar and thoracic membranes, and chaetal structures (Figure 10). Tube morphology and ultrastructure are important for identification of both extant and fossil taxa [227] (Figure 10a–c). Serpulid genera have been described on the basis of unique characters or on unique combinations of characters (or absence of characters), rather than on presence of shared derived characters. Mentioned here morphological characters used for serpulid identification have been described in details and illustrated in ten Hove and Kupriyanova [110], Wong et al. [228], Kupriyanova et al. [214].

The operculum that is present in most serpulins and in all spirorbins is one of the most important diagnostic characters (Figure 10d–h). The shape of the operculum varies significantly, ranging from soft transparent vesicles to complex structures reinforced with chitinous or calcareous endplates and spines. The distinct funnel-shaped opercula of *Crucigera* and *Serpula* are composed of numerous radii (Figure 10d), while in *Hydroides* the funnel is topped with a verticil of chitinous spines (Figure 10e). The operculum-bearing radiole can be identical to others (e.g., *Filograna*, *Apomatus* Philippi, 1844), but usually is modified into a smooth peduncle (Figure 10j). In cross-section, the peduncle is commonly cylindrical, but it is flat ribbon-like in members of the genus *Metavermlia* Bush, 1905. Below the operculum, the peduncle may bear diagnostic distal wings (e.g., *Spirobranchus*) (Figure 10h).

The collar segment bears only notopodial (collar) chaetae that may be absent (e.g., *Ditrupa* Berkeley, 1835, *Marifugia*, *Placostegus* Philippi, 1844). The collar chaetae may bear four types of diagnostic modified chaetae: bayonet-type (e.g., *Serpula*, *Hydroides*, Figure 10i), fin-and-blade (e.g., *Chitinopoma*, *Protis* Ehlers, 1887), *Spirobranchus*-type (e.g., *Spirobranchus*, *Laminatubus* ten Hove and Zibrowius, 1986) and *Ficopomatus*-type (see [214]). Tonguelets, located between collar lobes, are diagnostic of the genera *Spirobranchus* and *Pyrgopolon* de Montfort, 1808. The thoracic membranes (Figure 10l) may be ending at the first (*Ditrupa*) or the second thoracic chaetiger (*Chitinopoma*), or may continue to the mid-thorax (e.g., *Pomatostegus*, *Vermiliopsis* Saint-Joseph, 1894), to the last thoracic chaetiger (some *Spiraserpula* Regenhardt, 1961 and *Metavermlia* spp.), or past the end of the thorax forming the ventral apron (e.g., *Ficopomatus*, *Serpula*, *Hydroides*, *Protula*, *Spirobranchus*) (Figure 10m). In most genera the thorax consists of seven chaetigerous segments (first with collar chaetae only and six with both notopodia and neuropodia). The number of thoracic segments varies from five (*Tanturia* Ben-Eliahu, 1976 and *Bathyditrupa* Kupriyanova, 1993) or six (*Laminatubus*, *Hyalopomatus* Marenzeller, 1878, *Spirodiscus* Fauvel, 1909) to 10 (*Kimberleya* Pillai, 2009), while spirorbins have three to five thoracic segments.

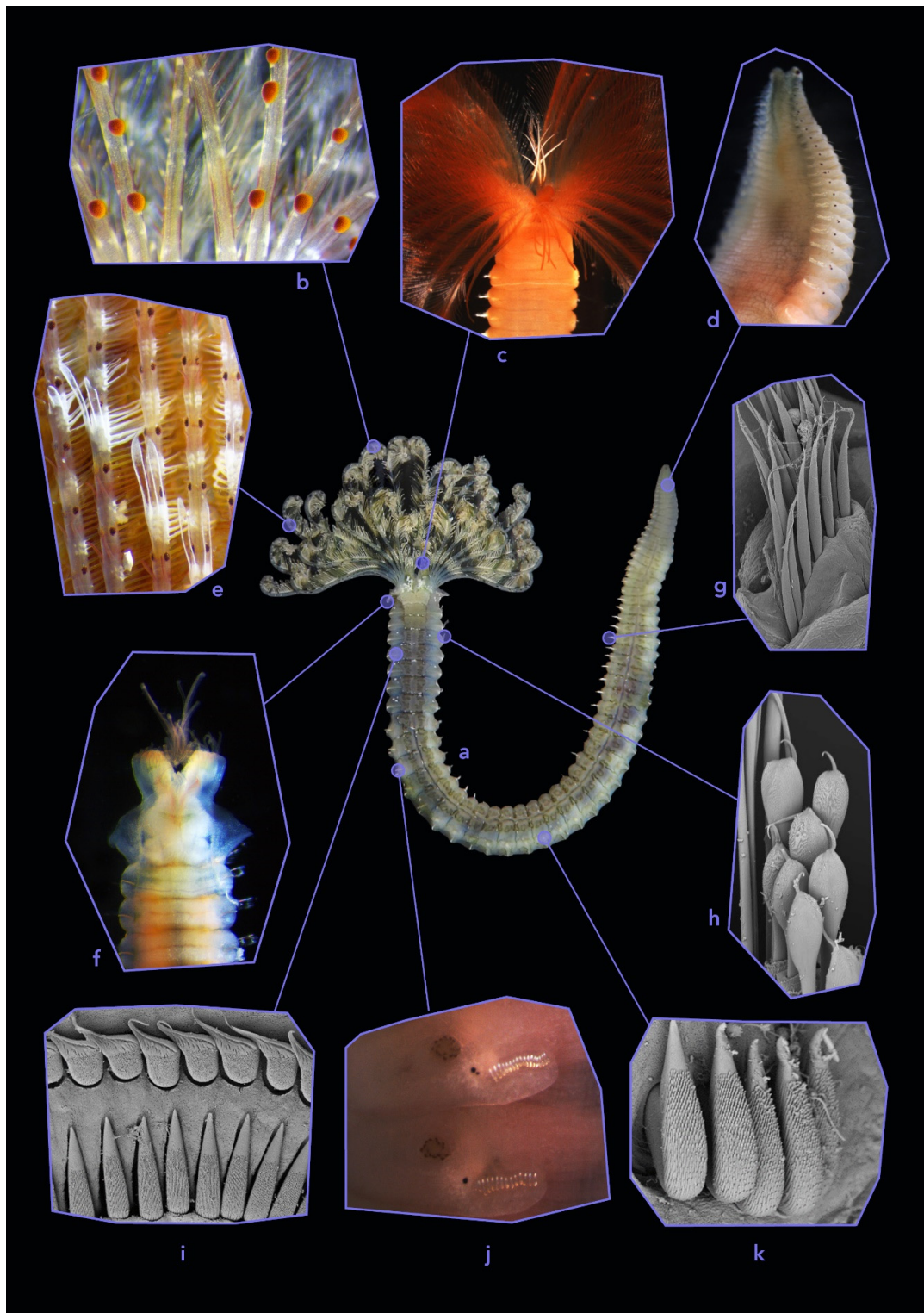


Figure 9. Main diagnostic characters for members of Sabellidae. (a) *Parasabella microphthalmma*, ventral view; (b) Compound eyes on dorsal radioles, *Pseudopotamilla* sp.; (c) Radiolar internal structures, *Chone infundibuliformis*; (d) Pygidial morphology, *Bispira* sp.; (e) Radiolar stylodes, *Branchiomma* sp.; (f) Collar, radiolar lobes and glandular girdle in second chaetiger, *Jasmineira* sp.; (g) Abdominal chaetae, *Parasabella* sp.; (h) Thoracic chaetae, *Parasabella* sp.; (i) Thoracic uncini and companion chaetae, *Notaulax* sp.; (j) Parapodia morphology and arrangement of chaetae, *Bispira* sp.; (k) Abdominal uncini, *Notaulax* sp.

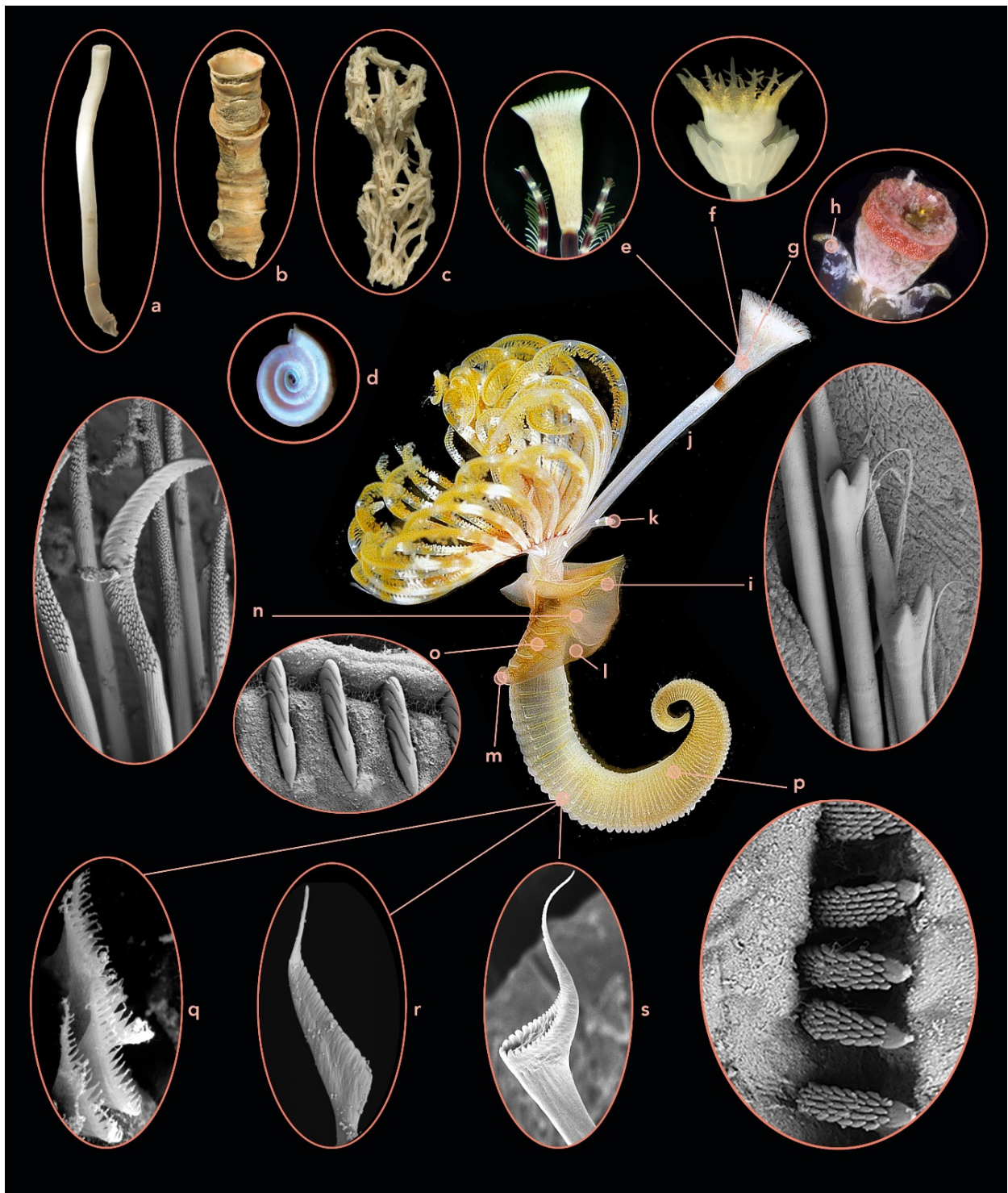


Figure 10. Main diagnostic characters for members of Serpulidae. Centre: lateral view of a *Serpula* specimen removed from the tube; (a–d) Tubes: *Hyalopomatus biformis* (a), *Serpula vermicularis* (b), *Filograna implexa* (c), *Circeis armoricana* (d); (e–h) Opercula: *Serpula* (e), *Hydroides* (f), *Spirobranchus* (g) showing distal wings (h); (i) Special (bayonet) collar chaetae of *Hydroides*; (j) Peduncle; (k) Pseudopericulum; (l) Thoracic membranes; (m) Apron; (n) Thoracic *Apomatus* (sickle-shaped) chaetae of *Vermiliopsis*; (o) Thoracic saw-shaped uncini of *Hydroides*; (p) Posterior abdominal rasp-shaped uncini of *Hydroides*; (q–s) Abdominal chaetae: flat trumpet-shaped of *Serpula*; (q), flat geniculate of *Vermiliopsis*; (r) true trumpet-shaped of *Spirobranchus* (s). (a–c,f) by E. Wong, (d) by A. Rzhavsky, (e) by G. Rouse, (g,h) by A. Semenov, (j–m) (central photo of *Serpula*) by F. Verbiest, (n–s) (SEM images) by S. Lindsay).

In the posterior thoracic segments chaetae are supplemented by diagnostically important *Apomatus* or sickle-shaped chaetae (Figure 10n). The number of vertical teeth rows in the thoracic and anterior abdominal uncini (saw-shaped, with one row of teeth, e.g., *Hydroides*, *Serpula* (Figure 10o); rasp-shaped, with several rows of teeth, e.g., *Hyalopomatus*, *Placostegus*, *Marifugia*; or saw-to rasp-shaped, from with one tooth distally to a row of up to five teeth near the peg, e.g., *Filogranula* Langerhans, 1884) is diagnostic. Posterior abdominal uncini are always rasp-shaped (Figure 10p). Even more important is the shape of the anterior tooth of uncini. The anterior teeth are either pointed fangs (e.g., *Filograna*, *Hydroides*, and *Serpula* (Figure 10o,p), and pileolarii spirorbins), or a wide variety of blunt 'wedge' shaped pegs (e.g., *Pseudovermilia* Bush, 1907, *Spirobranchus*, *Galeolaria*, *Ficopomatus*, *Hyalopomatus*, *Chitinopoma*, *Pyrgolopon*, *Vermiliopsis*, *Protula*).

The shape of abdominal chaetae is very important for generic diagnostics (Figure 10q–s). The simplest forms are capillary (*Bathyditrupa*) and acicular (*Paumotella* Chamberlin, 1919). The flat trumpet-shaped chaetae with a single row of teeth are found in *Crucigera*, *Hydroides*, *Serpula* (Figure 10q). Abdominal chaetae previously referred to as 'geniculate' are two distinct types of chaetae, true trumpet-shaped, typical for, e.g., *Ficopomatus*, *Galeolaria*, *Placostegus*, *Spirobranchus* (Figure 10s) that lack thoracic '*Apomatus*' chaetae, and flat geniculate are found in taxa with *Apomatus* chaetae, e.g., spirorbins, *Apomatus*, *Chitinopoma*, *Vermiliopsis* (Figure 10r).

3.3.4. Data and Techniques Used for Species Identification and Systematics

Initial Collection, Observation and Fixation in the Field

To identify individuals to the species level, specimens are first examined under a stereomicroscope. If conditions in the field permit, they should be examined and photographed alive to document colouration. Removing individuals from their tubes, specially serpulids, without any tube or specimen damage is rarely possible unless 0.05% phenol-seawater solution is used for several hours [229–231]. This method does not work in spirorbins (Bick pers. obs.) and it is unknown whether DNA is affected by phenol. It is important to examine and photograph intact tubes if they are broken to extract animals.

Fixation and preservation of specimens vary depending on further purposes of samples. Specimens aimed for a morphological study only are commonly fixed in a 4% solution of formaldehyde in sea water for 24–48 h, if possible after relaxation of individuals (in magnesium chloride). Animals are then rinsed in distilled water and preserved in 70–80% ethanol. For scanning electron microscopy (SEM) osmium tetroxide is preferable as a fixative.

Specimens aimed for genetic sequencing should avoid all contact with formaldehyde as it degrades DNA, impeding amplification of the usual size fragments to be sequenced. Best procedures for DNA sequencing include fixation of fresh specimens in high concentration ethanol (the higher the better) and storing samples at 4–6 °C, or at least not in direct sunlight at room temperature. The ethanol should be changed at least once, preferably more often. RNA sequencing may need other protocols such as fixing with RNAlater. For integrative (morphological and molecular) studies, a tissue sample taken from a specimen should be fixed in ethanol and stored in a fridge or a freezer, while the rest of the specimen should be fixed in formalin and preserved in ethanol. Further reading on fixation and preservation of samples is found at Rouse and Pleijel [232].

Morphological Studies of Preserved Specimens

When examining freshly preserved or museum material lacking natural pigmentation, staining with methyl (or methylene) green (blue) helps to increase contrast and to reveal glandular patterns, including thoracic ventral shields and glandular girdles [24]. Examination of chaetae requires higher magnification (>100×), therefore, chaetae and noto- and neuropodia are dissected from the specimen, placed on a slide in a drop of ethanol, glycerin or permanent media, and covered with a cover glass. Applying gentle pressure on the cover glass ensures that uncini and chaetae lay in a lateral position. Using SEM is essential to reveal details of external features, such as ciliation, chaetal morphology and

body wall microstructure, as well as anatomical features not easily distinguished in small specimens (appendages of the radiolar crown, for example). SEM is also an indispensable tool to examine tube ultrastructure, important for taxonomy of serpulids (reviewed by Ippolitov et al. [227]).

Structures of the radiolar crown, e.g., the rows of vacuolated cells supporting the radioles, dorsal and ventral lips, dorsal radiolar and pinnular as well as ventral radiolar appendages, and a parallel lamella in Sabellidae, dorsal lips and ventral filamentous appendages in Fabriciidae, are examined after fine sections with a sharp blade or, better, histological semi-thin sections are made and mounted on temporary or permanent slides, and stained with solutions, such as Mallory or Cason (e.g., [226]).

Morphometric characters such as counts (e.g., numbers of radioles or pinnules), measurements and proportions of soft body parts (e.g., thorax to abdomen ratio, length of dorsal lips) have traditionally been considered diagnostic for some taxa, but individuals may show sexual dimorphism [216], size and age-related variability ([70,233] or their size may be affected by anaesthetization and fixation techniques [234], which needs to be considered when comparing material.

For drawings to be made to scale, a camera Lucida attached to both the stereo- and the compound scopes is used. Traditional ink drawing (pencil sketching followed by India ink tracing) is currently supplemented or replaced by digital tracing of scanned pencil sketches, using a drawing pad (e.g., [235]). Advances in digital photography and universal availability of microscope-mounted digital cameras and Z-stacking software also resulted in photographs of live or preserved specimens, rather than line drawings being used in species descriptions. Use of SEM micrographs helps to illustrate both chaetal and soft body diagnostic features characters with precision and objectivity. Micro-computed tomography techniques have been proved useful in studies of internal anatomy in sabellids and serpulids ([49,236,237], and may offer taxonomically useful information.

Genetic Data

Genetic methods have been used in studies of Sabellida for nearly 20 years. The earliest publication by Patty et al. [238] used the C1 regions of 28S (123 bp) of 16 species to assess evolutionary relationships among Sabellidae. Kupriyanova et al. [45] published the first phylogeny of Serpulidae based on analyses of 18S rDNA, 28S rDNA, and morphological characters of 29 taxa. Combination of molecular (18S rDNA, the D1 region of 28S rDNA, and histone H3) and morphological datasets have been used to assess for the first time the relationships within Fabriciidae [27]. Other studies of Sabellida have used a limited number of molecular markers commonly used in polychaete systematics [239]. Currently, the number of sequences in GenBank is 246 for Fabriciidae, 814 for Sabellidae, and 2880 for Serpulidae, figures that indicate the relative larger effort put into molecular studies in serpulids compared to the other two families (Figure 11). In addition, "BOLD Systems [36] includes 443 barcodes (fragments of COI gene) of Serpulidae, 349 of these records are mined from GenBank and 19 different BOLD records are also shared with GenBank. Similarly, BOLD holds 692 COI sabellid barcodes, 399 of which are mined from GenBank and 148 BOLD records that were also uploaded in GenBank. Among the unidentified 105 sabellids there is an unknown number of sequences that belong to fabriciids as this database still follows the old classification. Summarising, there are 75 serpulid and 145 sabellid/fabriciid COI sequences available in BOLD, in addition to those found in GenBank.

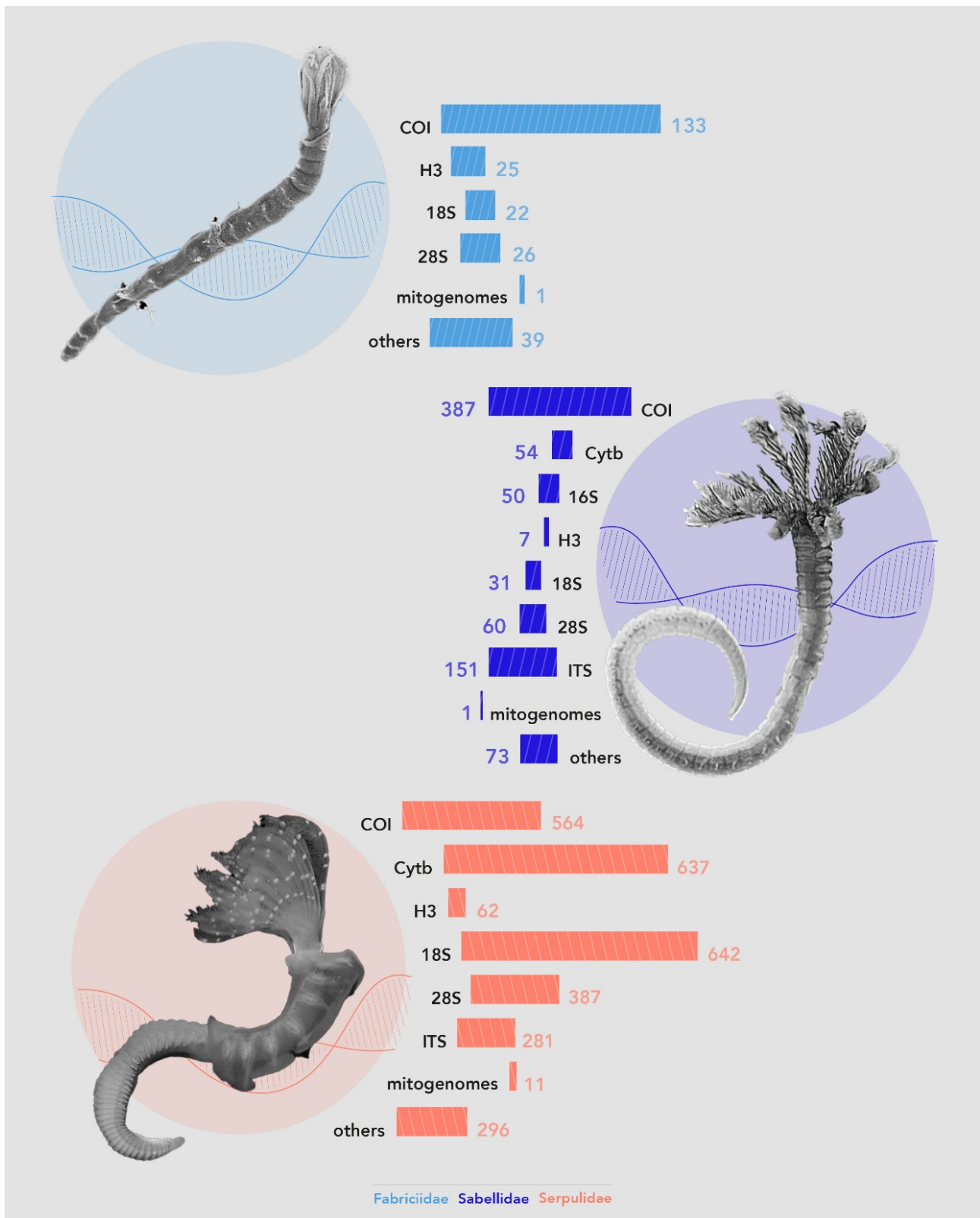


Figure 11. Number of sequences available in Genbank for Fabriciidae, Sabellidae; and Serpulidae.

The universal DNA barcoding fragment of COI gene is by far the most popular marker for the Fabriciidae, accounting for 54% (133 sequences) of the sequences available for this group (Figure 11), and Sabellidae, 38% (387 sequences) (Figure 11). For Serpulidae, despite all efforts (reviewed in Sun et al. [78]), no COI sequences had been available until

Carr et al. [240] reported six. However, Sun et al. [76], who developed genus-specific primers to generate COI sequences for 11 species of *Hydroides*, showed that “serpulid” sequences in Carr et al. [240] are likely from bacteria. Progress in COI barcoding in serpulids is mainly a result of new primer development [77]. Currently, the number of COI sequences for members of Serpulidae in Genbank is 564 (not including those mentioned problematic sequences [240], Figure 11).

Other markers widely used in systematics studies of Sabellida are nuclear 18S (642 sequences for Serpulidae, 31 for Sabellidae, 22 for Fabriciidae), 28S RNA (387 for Serpulidae, 60 for Sabellidae, 26 for Fabriciidae), mitochondrial cytochrome b (cytb) (637 for Serpulidae and 54 for Sabellidae), nuclear internal transcribed spacer (ITS2), ATP synthase, and Histone H3 (Figure 11). Mitochondrial 16S, widely used in sabellids (50 sequences in Genbank), has not been successfully amplified for serpulids.

Manayunkia is the fabriciid genus with most sequences in GenBank (179). The Sabellidae genera with most available sequences are *Branchiommia* (259), followed by *Sabella* (86) and *Sabellastarte* (61). Among the serpulids, *Hydroides* is the genus with the highest number of sequences in GenBank (1366), followed by *Spirobranchus* (601); all the rest have at least one order of magnitude less sequences available (Figure 12).

Although Sabellida are still behind other annelids in terms of genomic approach, several studies recently reported mitochondrial genomes and used transcriptomes for resolving systematics and evolutionary questions within this group. The first Sabellida mitochondrial genome was published for the serpulid *Spirobranchus giganteus* (Pallas, 1776) [241]. Mitochondrial genome sequences of ten *Hydroides* species have been reported in Sun et al. [242]. The mitochondrial genomes of *Sabella spallanzanii* (Gmelin, 1791) and freshwater fabriciid *Manayunkia occidentalis* were recently published [243,244]. The phylogeny by Tilic et al. [3] includes transcriptome sequences of 20 species of Sabellida (three fabriciids, 15 sabellids, and two serpulids), containing up to 3015 orthologous genes. Several other studies have also dealt with expressed sequence tag (EST) libraries and transcriptomes to address molecular mechanisms of larval settlement, or gene order and loss [245] in serpulids, adding up to 4205 sequences of mRNAs of larval cDNA library. With current fast adoption of the genomic approach, the number of sequences is expected to raise dramatically in the near future.

Species Delimitation and Identification

Application of molecular methods in combination with traditional morphological techniques or alone have expanded in the last two decades with regard to species delimitation in annelids in general, and in Sabellida, in particular. These methods are sustained by the definition of species as independently evolving entities (metapopulations), that are genetically (and often phenotypically) distinct [246,247]. Thus, species are expected to be reciprocally monophyletic clusters, morphologically distinct and/or genetically divergent, as a result of evolutionary forces applied to closely related lineages. Molecular-based approaches have not only improved species delimitation by providing additional evidence to morphological taxonomy, but also helped to reveal cryptic (only genetically distinct) species [248].

In Fabriciidae, even though species appear morphologically similar due to the animal's small size and the diagnostic features being difficult to recognize by non-specialists, molecular approach to species identification and delimitation is still uncommon. Only one species, *Manayunkia occidentalis*, has been described based mainly on genetic data [216].

In Sabellidae, boundaries between species within the genera *Amphiglena*, *Branchiommia*, *Parasabella*, *Pseudobranchiommia* Jones, 1962, *Sabellastarte* and *Sabellomma* Nogueira, Fitzhugh and Rossi, 2010 were assessed with molecular and morphological data [70,72–74]. Results revealed cryptic diversity hidden in species complexes and helped to assess the diagnostic features traditionally used for morphological species identification [2,27,72–74,103,140].

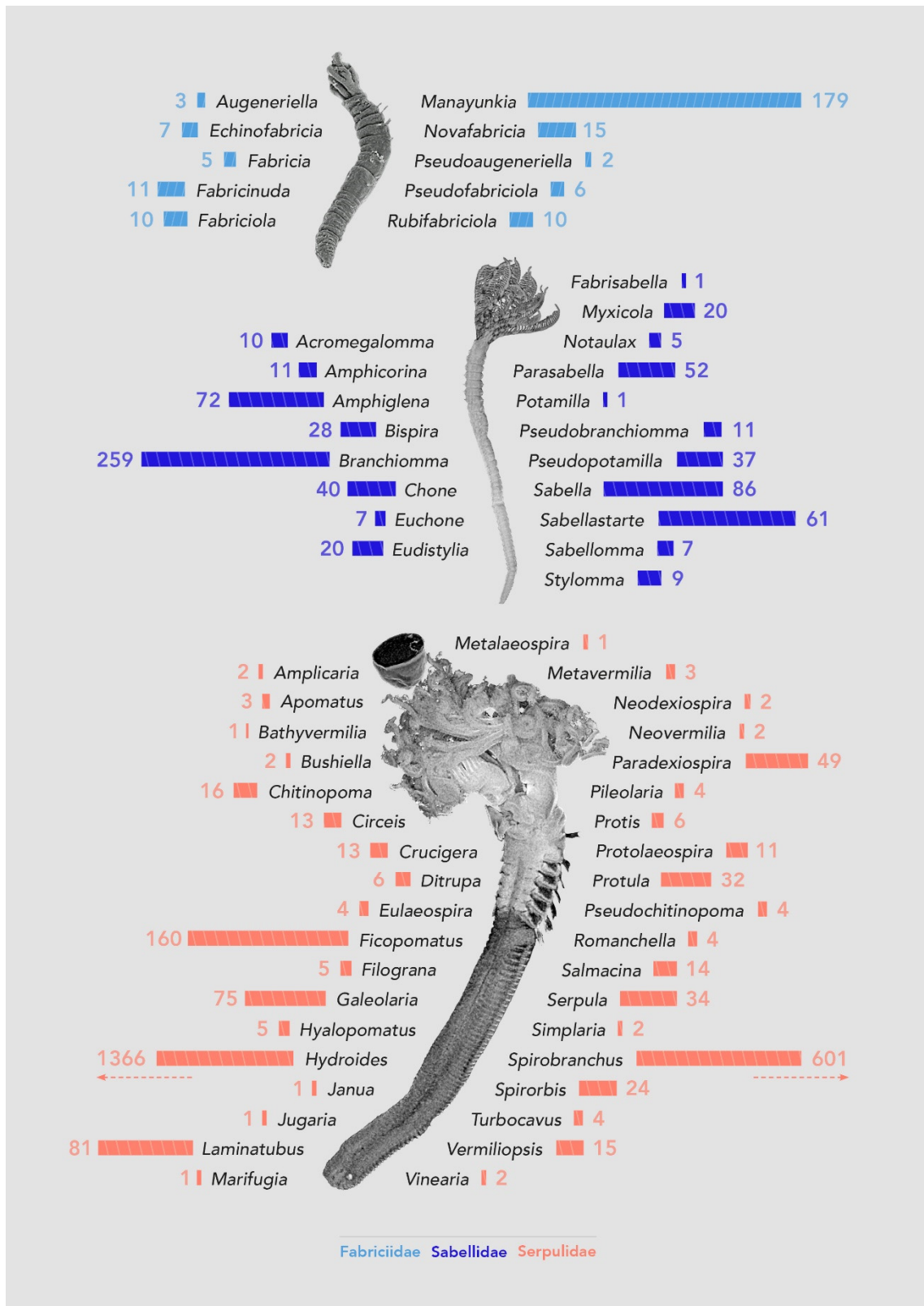


Figure 12. Number of DNA sequences available in GenBank for genera in Fabriciidae, Sabellidae, and Serpulidae.

In Serpulidae, the study of Halt et al. [249] was the first to name a new species in Sabellida without morphological indicators, after analyses of DNA revealed two cryptic species with non-overlapping distributions within *Galeolaria caespitosa* Lamarck, 1818. Another

study revealed three genetic species with overlapping distributions within *Ficopomatus enigmaticus* (Fauvel, 1923), two cryptic and one morphologically distinct [204]. A combination of molecular and morphological data helped to partially resolve species complexes within the genera *Hydroides* [203,250,251] and *Spirobranchus* [84,193,252].

The idea of ‘DNA barcoding’ is that a species can be uniquely characterised by a short DNA fragment and then identified by comparing such a fragment from an unknown specimen to a reference DNA sequence [253]. Initially, a 650 base pair fragment of the mitochondrial COI was proposed as a standard barcoding gene for animals [253] because of its variability among closely related taxa and supposed ease of amplification. Later, however, a number of other mitochondrial markers (cytb, e.g., [81–84,193,204,249,252] and nuclear (ITS, [82,249]) have been used, especially in serpulids where amplification of COI proved to be challenging. The first attempts to use DNA data alone while ignoring any morphological and biogeographic evidence to identify potentially invasive serpulids [254], were rather a failure. The authors mistakenly claimed discovery of an Australian species *Spirobranchus taeniatus* (Lamarck, 1818) (mostly likely *Spirobranchus triqueter*) and North American *Serpula columbiana* Johnson, 1901 (almost certainly *Serpula vermicularis*) attached to drifting marine litter in the Mediterranean, after comparing (minimum 97% nucleotide identity was accepted) partial sequences of the conservative (thus unsuitable for species-level barcoding) 18S gene with the limited set of sequences available in GenBank. Similarly, Langeneck et al. [255] criticised another paper by the same authors (Rech et al. [256]) who identified specimens associated with floating debris in the Lagoon of Venice as *Hydroides sanctaerucis*, suggesting its presence in the Mediterranean might have been overlooked due to misidentification as common *H. dianthus*. Rech et al. [256] again did not examine the morphology of the specimens and used 18S sequences for identification, accepting an identity $\geq 97\%$ with sequences of *H. sanctaerucis* in GenBank. However, 18S rDNA sequences are ill-suited for molecular identification because they have identity close to 100% in closely related species. The low sequence identity shows that the specimens in Rech et al. [256] study did not belong to *H. sanctaerucis*, and the species name should be removed from checklists of species non-indigenous for the Mediterranean [255].

3.4. Ecology, Distribution and Biogeography

3.4.1. Ecology

Fabriciidae

A review of the ecology and biology of Fabriciidae was published recently [4]. Most fabriciids occur in intertidal and subtidal zones, mainly in sheltered areas on sandy, muddy or rocky sediments, in mangroves, on red and green algal mats, and in seagrass beds, with low benthic species richness.

Fabriciids are mainly distributed in marine and brackish ecosystems worldwide, but species of the genus *Manayunkia* are also common in freshwater, and even hypersaline lakes, where they survive salinities of 82 psu for several months [257]. The abundance of some species tends to be very high in habitats with low biodiversity. The highest abundances of *Fabricia stellaris* and *Manayunkia aestuarina* (over 10^6 ind. m^{-2}) have been reported in physiologically stressful conditions, such as sediments with a high organic matter content and waters of highly variable salinities [258–261]. A reduction in organic matter content from 1.8% to 1.0% in the Baltic Sea was followed by a reduction in fabriciid abundance from 16 000 to 6000 ind. m^{-2} [262]. Giangrande et al. [263] found five fabriciid species in a coastal Mediterranean system naturally acidified by carbon dioxide vent emissions. Among these, *Parafabricia mazzellae* Giangrande, Gambi, Micheli and Kroeker, 2014 and *Brifacia aragonensis* Giangrande, Gambi, Micheli and Kroeker, 2014 were most abundant even in the extremely low pH zone (pH 6.6–7.2).

Fabriciidae species produce flexible tubes consisting of the finest sediment particles stabilized by mucus. Detritus might also be deposited on the outside of the tubes. Fabriciids are not obligatory tube dwellers and they can voluntarily leave their tubes and build new

ones. When outside, they crawl with the posterior end in front, while the radiolar crown is folded up and dragged behind [264,265].

Fabriciids are suspension-feeders like other Sabellida, but *Manayunkia* spp. are deposit feeders. In addition to detritus, they ingest bacteria, heterotrophic protozoa, cyanophytes and diatoms. The sizes of the ingested particles range from 1–2 µm to 2–7 µm and occasionally reach up to 20 µm [265].

Some fabriciids are commensals of molluscs, e.g., the freshwater *Brandtka asiatica* Jones, 1974 and *Monroika africana* [215,266], or the marine *Rubifabriciola tonerella* (Banse, 1959) and *Novafabricia infratorquata* (Fitzhugh, 1983) [231], but these species have been also found in other substrates. Another example of commensalism is the occurrence of peritrichous ciliates on anterior chaetigers in *Manayunkia aestuarina* [4]. *Manayunkia speciosa* Leidy, 1859 is an obligate invertebrate host of the myxozoan parasites *Ceratonova shasta* (Noble, 1950) and *Parvicapsula minibicornis* Kent, Whitaker and Dawe, 1997, which cause ceratomyxosis in salmon and trout in North America [267,268].

Sabellidae

A review of ecology and biology of sabellids was recently published [24]. Sabellids are able to inhabit either hard or soft sediments. Species of *Amphiglena*, *Bispira*, *Perkinsiana*, *Pseudobranchiomma*, *Sabellomma*, *Sabellastarte* and *Stylomma* Knight-Jones, 1997 mainly inhabit littoral hard substrates, as epibionts of algae, or associated with biogenic structures, including live coral or rubble [2,68,73,74,269,270]. Some species of *Perkinsiana* and *Pseudopotamilla* associated with dead coral and limestone sediments are capable of actively boring into the calcium carbonate [271,272].

Several species of *Acromegalomma*, *Amphiglena*, *Branchiomma*, *Eudistylia*, *Notaulax*, *Parasabella*, *Pseudobranchiomma* and *Sabella* are abundant in biofouling communities [72, 74,101,147,273–276]. Some of the soft bottom species need large and stable enough surface (shell, rock, holdfast or root) to attach to build their tubes. This is characteristic of species of *Branchiomma*, *Parasabella*, *Bispira manicata* (Grube, 1878), *Acromegalomma*, or the Mediterranean *Sabella spallanzanii*, a species associated, in natural conditions, to *Posidonia* K. Koenig seagrass roots [73,129,133,277,278]. However, other soft-bottom species can build tubes within the sediment grains, like *Euchonoides meone* Magalhães, Bailey-Brock and Tovar-Hernández, 2020. This species is found near a sewage outfall in Hawaii, reaching 141,046 ind/m², the highest densities ever reported for Sabellidae [279].

Sabellids have been only recently found in chemosynthesis-based environments, such as hydrothermal vents, methane seeps and organic falls, and their diversity in such habitats is poorly understood. *Bispira wireni* (Johansson, 1922) was reported from a hydrothermal vent from Okinawa, Japan [280]. *Jasmineira* sp. and an undetermined sabellid colonized bone and sunken wood in the southwestern Indian Ridge [281]. Unidentified sabellids have been reported from methane seeps in the Gulf of Mexico [282] and Chile [283]. Recently, an undescribed species of *Bispira* was found at a deep-sea cold seep off the Pacific coast of Costa Rica [284].

Although the group is typically marine, a few exceptional species have adapted to brackish and even fresh water environments. The most remarkable example is the exclusively freshwater genus *Caobangia*. Euryhaline sabellids are, for example, the Australian *Desdemona aniara* Hutchings and Murray, 1984 and *Laonome triangularis* Hutchings and Murray, 1984, Indian *Potamilla leptochaeta* Southern, 1921, American *Aracia sinaloae* Tovar-Hernández, 2014, and the cryptogenic *Desdemona ornata* Banse, 1957, *Euchone limnicola* Reish, 1959, and *Laonome xeprovala* Bick and Bastrop, 2018 [68,102,285–290]. Some species typically found in fully marine conditions are tolerant to brackish water conditions, e.g., members of *Euchone*, *Branchiomma* and *Parasabella* [147,291], while *Laonome calida* Capa, 2007 and *L. albicingillum* Hsieh, 1995 have been reported in environments ranging from fully marine to freshwater [68,292–294].

With the exception of *Glomerula piloseta*, that inhabits calcareous tubes, all sabellids build tubes by secreting the mucous base and enforcing it with different size particles they

attach, including mud, sand, feces or biogenic fragments [24]. Smaller species are more liable to leave the tubes if disturbed and can build new ones [295], but larger species, even if capable to build new tubes, tend to inhabit the same one for longer periods or their whole lives [270,296,297].

Until very recently, sabellids have been found mostly in areas of high productivity and assumed to be obligatory suspension feeders [298]. However, a sabellid-bacterial symbiosis, fueled by methane, between a still undescribed species of *Bispira* and methane-oxidizing Methylococcales bacteria, has recently been reported from a methane seep [284]. This makes *Bispira* a new addition to the list of annelids (including Siboglinidae and two new serpulids of the genus *Laminatubus*, see below) relying on chemosynthetic symbionts for nutrition.

Associations of sabellids with other organisms relate to their ability to bore into calcium carbonate. The seven species of *Caobangia* are commensals or parasites of freshwater gastropods and bivalves in rivers of southeastern Asia [289,299]. *Terebrasabella heterouncinata* Fitzhugh and Rouse, 1999 bores into the shells of marine gastropods, including abalones and limpets, in South Africa and California [66,300,301]. *Notaulax montiporicola* Tovar-Hernández and ten Hove, 2020 associated with the living coral *Montipora nodosa* (Dana, 1846) does not bore into coral, but uses crevices to settle and allows coral tissue to grow around its tube [101].

Serpulidae

A review of ecology and biology of serpulids was recently published [214]. Serpulids are typical on hard substrates in all marine environments. Inhabitants of areas with predominantly soft-sediments always attach to rocky outcrops, stones and shells, and can deal with high sedimentation rate by building their tubes upwards to avoid being buried in the sediment [302]. Many serpulids are notorious opportunistic foulers, capable of colonising any available hard substrates. The ability to settle and build large aggregations on human-made surfaces makes serpulids important and troublesome members of fouling communities. However, some show high habitat selectivity, resulting from non-random larval settlement and juvenile survival (reviewed by Kupriyanova et al. [303]). A few unusual serpulids are pre-adapted to living unattached on soft substrates in subtidal-shelf (*Ditrupa*) [110] or bathyal-abyssal (*Bathyditrupa* and *Spirodiscus*) environments [107]. However, larvae of free-living *Ditrupa* need to attach initially to small particles during settlement and metamorphosis to start building the tube [304].

Serpulids are some of recognizable animals to inhabit the periphery of seeps and hydrothermal vents. *Laminatubus alvini* ten Hove and Zibrowius, 1986 and *Protis hydrothermica* ten Hove and Zibrowius, 1986 were the first serpulids to be formally described from vent communities of East Pacific Rise and *Laminatubus* is known from other seeps (e.g., Pescadero Transform Fault, Gulf of California) and vents, e.g., Alarcon Rise, Gulf of California [305]. *Hyalopomatus mironovi* Kupriyanova, 1993 and *Protis* sp. were reported from hydrothermal vents of North Fiji [306]. Less is known about seep-associated serpulids, as more species have been reported from fossil than modern hydrocarbon seeps [307]. Serpulids (tentatively identified as members of *Neovermilia* Day, 1961) have been reported from cold seep communities in Nankai Trough [308], the Peruvian active margin [309], the Terevaka ridge [310], the Peru Trench, Middle American Trench off Mexico [311], and the Barbados prism [312].

Although serpulids are predominately marine, some species of *Hydroides* tolerate mixohaline conditions (e.g., [313], for *H. elegans* (Haswell, 1883)), while representatives of *Ficopomatus* can cope with a wide range of salinities and are common in brackish-water environments world-wide [110]. *Marifugia cavatica* Absolon and Hrabě, 1930, closely related to *Ficopomatus*, is the only known truly fresh-water serpulid, inhabitant of subterranean caves of the Dinaric Alps [46].

Serpulids produce their calcareous tubes using a pair of calcium carbonate secreting glands located on the collar. As obligate tube dwellers, they never leave their tubes and

cannot build new ones if removed. Adult serpulids lie in the tube with their dorsum facing the substrate and locomotion is limited to partial emergence from and withdrawal into the tube [314]. Hiding behaviour is a common antipredator tactic, and animals may adjust the durations of such behaviour to current benefits and costs [315].

As suspension-feeders, serpulids show varying abilities in particle sorting and clearance rates. High planktonic biomass removal (>50% of initial standing stock) and significant differences in clearance for different components of the community by reef-building *Ficopomatus enigmaticus* indicate that the serpulid can regulate planktonic biomass and promote changes in plankton community structure [316]. *Ditrupa arietina* (Müller, 1776) lives unattached in soft sediments and ingests diatoms, haptophytes, bacteria and cyanobacteria ranging from 1 to 50 µm in size, and the origin of the food is both planktonic and benthic [317]. Recently metanotrophy (similar to that found for members of *Bispira* sp.) has been reported, as a result of symbiosis between two species of the genus *Laminatubus* (*L. joicebrooskae* Rouse and Kupriyanova, 2021 and *L. paulbrooksi* Rouse and Kupriyanova, 2021) and methane-oxidizing Methylococcales bacteria, from a seep off Costa Rica [284].

While a large number of serpulids is found in coral reefs on coral rubble (e.g., [318]: Fiji, [319]: Okinawa, Japan, [179]: Queensland, Australia), only some taxa, such as *Floriprotis* Uchida, 1978, *Pseudovermilia*, *Spirobranchus* and *Vermiliopsis* spp., are found in association with live corals. Some *Spirobranchus* species are reported as obligate associates of corals to the extent that their successful settlement occurs only on live corals (e.g., [320–322]), although recent observations indicate that while *Spirobranchus* larvae have a preference for live corals, they will survive on other substrates [83]. Many serpulids form epizootic associations with other invertebrates, mostly molluscs, crustaceans, bryozoans, and sponges. For example, *Hydroides spongicola* Benedict, 1887 occurs symbiotically in the chemically aggressive do-not-touch-me sponge *Neofibularia nolitangere* (Duchassin and Michelotti, 1864), while *Circeis paguri* Knight-Jones and Knight-Jones, 1977 is associated with hermit crabs (reviewed in [303]). Spirorbins are commonly found in specific epiphytic associations with macrophytes and their settlement can be stimulated by algal extracts [323,324].

3.4.2. Biogeography, Distribution and Bathymetry

Members of the Sabellida are found world-wide and, like most polychaetes, for much of the 20th century were assumed to have naturally wide, even cosmopolitan, distributions (e.g., [166,194,325]). Darling and Carlton [326] use the term eucosmopolitan to refer to the species with naturally broad distribution (found in two or more oceans). However, recent studies overwhelmingly show that ‘cosmopolitan’ taxa represent complexes of either morphospecies or cryptic species (reviewed in [327]). All evidence to date suggests that polychaetes have restricted natural geographic and bathymetric distributions, thus taxa reported with wide ranges should be treated as potential species complexes. Two general exceptions to the rule of restricted distributions are deep-sea and invasive species. Ranges of deep-sea polychaetes are expected to be wider than those found in shallow seas as a result of stable environmental conditions over wide distances, a traditional view (e.g., [328]) also supported by recent studies (e.g., [329,330]). Annelids that are easily translocated by anthropogenic means can establish and become invasive in remote localities, consequently expanding their ranges [327]).

Biodiversity patterns may be influenced not only by intrinsic ecological and historical factors, but also by ‘extrinsic factors’ *sensu* Giangrande and Licciano [331]. When a group is studied by a few specialists working in a particular area, species distribution may correlate with that of the specialists (‘author effect’). The concentration of taxonomic expertise in some regions may increase the number of species in those areas compared to less studied areas (‘concentration effect’).

Fabriciidae

Fabriciids have been described from all marine realms except for the Tropical Eastern Pacific (Table S1). Temperate Northern Atlantic is the province with the highest number

of fabriciids (16 species), followed by Tropical Atlantic (13 species), Temperate Northern Pacific and Western Indo-Pacific (11 species each), Central Indo-Pacific (10 species) and Temperate Australasia (six species), Temperate Southern Africa (four species), Eastern Indo-Pacific (two species), and Actic, Southern Ocean, and Temperate Southern America, each with a single species (Table S1). Most of the 4739 georeferenced occurrences in GBIF are also from the Temperate North Atlantic Realm and the Tropical Atlantic (Figure 13) and refer to members of *Fabricia*, *Fabricinuda* and *Manayunkia* [34]. There are records from neither Tropical Eastern Pacific nor from Western Indo-Pacific, the west coast of South America, and the west coast of Africa. The historical records until 1999, compiled by Giangrande and Licciano [331], showed 55.8% of the total fabriciid species are found in the tropics. Interestingly, the currently available information, based on species type localities show sthat most species were described from the Atlantic Ocean, at all latitudes. Explanation to latest results could be ‘concentration effect’, with taxonomic expertise accumulated at both sides of the Atlantic, and poor state of knowledge elsewhere.

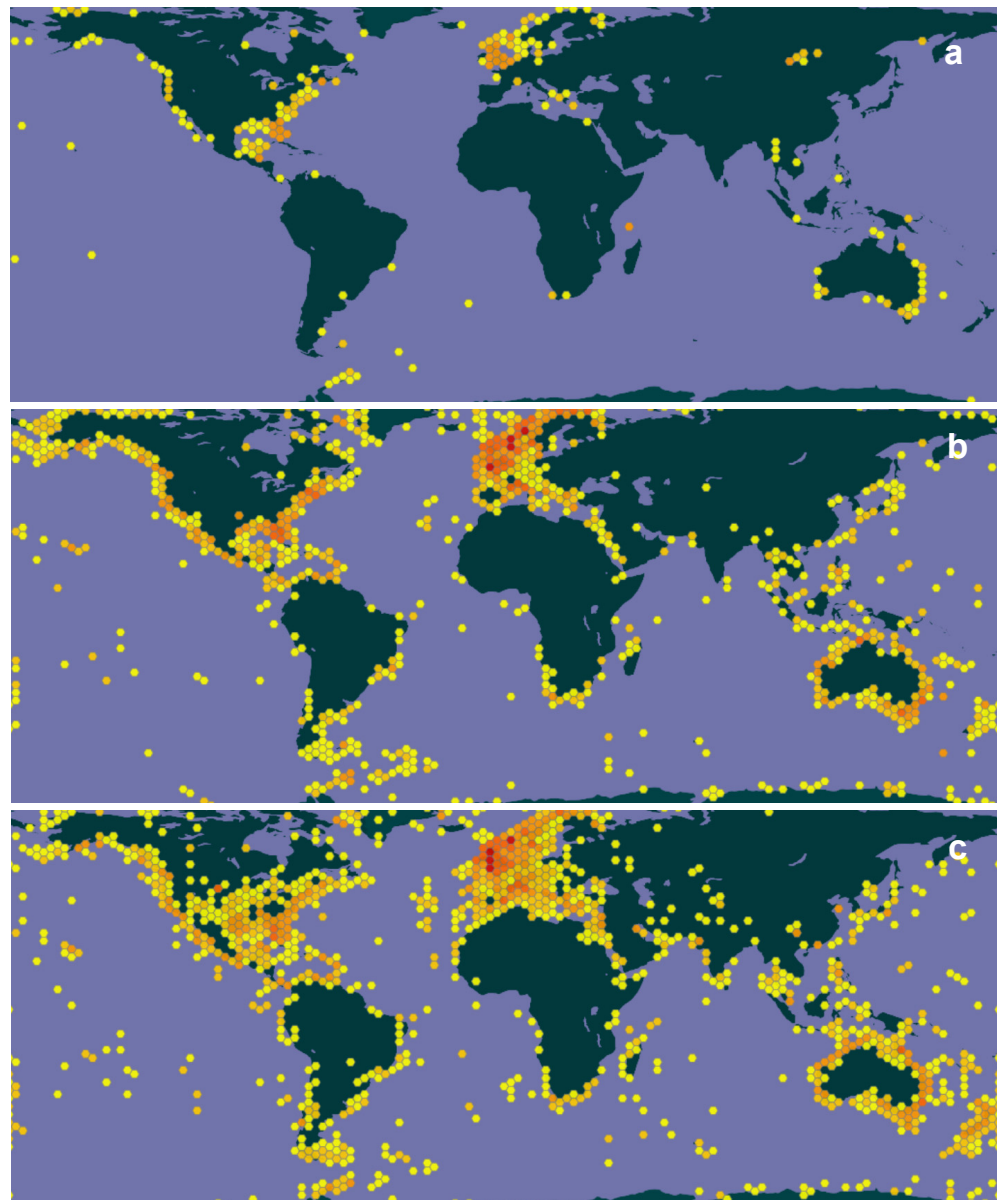


Figure 13. Georeferenced occurrences from GBIF. (a) Fabriciidae; (b) Sabellidae; (c) Serpulidae.

The species of most genera are distributed almost worldwide. The adaptability of Fabriciidae to different environments and the wide distribution of some taxa can be shown by the example of the genus *Manayunkia*. The ten extant *Manayunkia* species occur worldwide in marine, brackish and freshwater habitats, as well as hypersaline lakes. Their common ancestor was most likely already present in marine habitats [4]. There are ten species adapted to freshwater conditions: *M. speciosa* and *M. occidentalis* (Nearctic); *M. zenkewitschii*, *M. baicalensis* (Nusbaum, 1901) and *M. godlewskii* (Palearctic) [216,217]. One species, *M. athalassia* Hutchings, Dekker and Geddes, 1981, was found in hypersaline lakes in Australia [257], another species, *M. mizu* Rouse, 1996, in marine habitats [219,332] and three species, *M. aestuarina*, *M. caspica* Annenkova, 1928), *M. brasiliensis* Banse, 1956, in brackish environments [333,334] (Nogueira pers. obs.).

Most Fabriciidae occur in intertidal and subtidal waters. Only certain *Pseudofabriciolo* species (e.g., *P. californica* Fitzhugh, 1991, *P. filamentosa* (Day, 1963), *P. filaris* Fitzhugh, 2002, and *P. longipyga* Fitzhugh, Giangrande and Simboura, 1994), *Fabricinuda longilabrum* Fitzhugh, 2002 and *Raficiba barryi* occur between depths of 50 m and 335 m [53,58,63,335]. The record of *Fabricia sabella* (Ehrenberg, 1937) reported by Hartman (1965) from 1000 m off New England needs a revision because the nominal *F. stellaris* is a brackish-water species from the Baltic Sea. In the southwest Atlantic, exceptionally, two yet undescribed species provisionally assigned to the genera *Fabriciolo* and *Novafabricia* have been found at 4500 m [220] and one other of *Fabriciolo* from the Okhotsk Sea below 2000 m (Table 5).

Table 5. Deepest records for members of Sabellida below 1000 m.

Taxon	Depth (m)	References
FABRICIIDAE		
<i>Fabriciolo</i> sp. (Okhotsk Sea)	>2000	Alalykina 2020
<i>Fabriciolo</i> sp.	4600	Baumhaker 2012
<i>Novafabricia</i> sp.	4600	Baumhaker 2012
SABELLIDAE		
<i>Jasmineira bermudensis</i> Hartman, 1965	1000	Original description
<i>Potaspina australiensis</i> Capa, 2007	1000	Original description
<i>Euchone magna</i> (Fauchald, 1972)	1071	Original description
<i>Perkinsiana assimilis</i> (McIntosh, 1885)	1100	Original description
<i>Chone gracilis</i> Moore, 1906	1244	Méndez 2006
<i>Bispira wireni</i> (Johansson, 1922)	1335	Capa et al. 2013
<i>Potamethus filiformis</i> Hartmann-Schröder, 1977	1430	Original description
<i>Pseudopotamilla intermedia</i> Moore, 1905	1682	Original description
<i>Bispira</i> sp. (Costa Rica)	1887	Goffredi et al. 2020
<i>Chone</i> sp. (Okhotsk Sea and N. Pacific abyss)	>2000	Alalykina 2020
<i>Euchone</i> sp. (Okhotsk Sea and N. Pacific abyss)	>2000	Alalykina 2020
<i>Jasmineira</i> sp. (Okhotsk Sea and N. Pacific abyss)	>2000	Alalykina 2020
<i>Potamethus</i> sp. 1 (Okhotsk Sea and N. Pacific abyss)	>2000	Alalykina 2020
<i>Potamethus</i> sp. 2 (Okhotsk Sea)	>2000	Alalykina 2020
<i>Potamethus singularis</i> Hartman, 1965	2000	Original description
<i>Potamilla neglecta</i> (Sars, 1851)	2030	Hansen 1882
<i>Potamethus malmgreni</i> (Hansen, 1878)	2222	Original description
<i>Euchone</i> cf. <i>incolor</i> Hartman, 1965	2500	Alalykina 2020
<i>Fabrisabella similis</i> Fauchald, 1972	2520	Original description
<i>Potamethus scotiae</i> (Pixell, 1913)	2578	Original description
<i>Euchone papillosa</i> (Sars, 1851)	2900	Uschakov 1955; Levenstein 1969
<i>Jasmineria pacifica</i> Annenkova, 1937	2900	Original description
<i>Jasmineira schaudinni</i> Augener, 1912	3500	Augener 1912 (abyssal, no depth given); Jirkov 1982, 2001
<i>Chone infundibuliformis</i> Krøyer, 1856	3521	Wesenberg-Lund 1950
cf Sabellidae species 1 (Clarion-Clipperton Zone)	4029	Amon et al. 2017
<i>Potamethus mucronatus</i> (Moore, 1923)	4131	Original description, as <i>Notaulax</i>

Table 5. Cont.

Taxon	Depth (m)	References
<i>Potamilla abyssicola</i> Uschakov, 1952	4200	Original description; Levenstein 1961 1969; Alalykina 2020
<i>Potamethus spathiferus</i> (Ehlers, 1887)	4360	Fauvel 1914
<i>Euchone incolor</i> Hartman, 1965	4862	Original description; Hartman 1971
? <i>Potamethus</i> sp. Mozambique Basin	5068	Hartman 1971
<i>Potamethus dubius</i> (Eliason, 1951)	5860	Original description
<i>Jasmineira</i> sp. Japan	6207	Levenstein 1961b
<i>Potamethus singularis</i> Hartman, 1965	6023	Original description; Hartman 1971
Sabellidae sp. Pacific Ocean	8042	Levenstein 1969; Lemche et al. 1976
<i>Potamilla</i> sp. Kurile-Kamchatka Trench	8100	Uschakov 1952; Belyaev 1989
<i>Jasmineira</i> sp. Kermadec Trench Trench	8300	Kirkegaard 1956; Hartman and Fauchald 1971; Belayev 1972
<i>Potamethus</i> sp. Izu-Bonin Trench	8735	Belayev 1989
<i>Jasmineira filitovae</i> Levenstein, 1961 (as <i>Potamethus</i>)	9735	Levenstein 1969, 1973; Belyaev 1989
SERPULIDAE		
<i>Laminatubus joicebrooksae</i> Rouse and Kupriyanova 2021	1011	Original description
<i>Hyalopomatus madreporae</i> Sanfilippo, 2009	1146	Original description
<i>Neovermilia falcigera</i> (Roule, 1898)	1580	Zibrowius and ten Hove 1987
<i>Metavermilia ogasawaraensis</i> Nishi, Kupriyanova and Tachikawa, 2007	1603	Original description
<i>Zibovermilia zibrowii</i> Kupriyanova and Ippolitov, 2015	1710	Original description
<i>Hyalopomatus dieteri</i> Kupriyanova and Ippolitov, 2015	1980	Original description
<i>Hyalopomatus biformis</i> (Hartman, 1960)	1982	Kupriyanova and Nishi 2010
<i>Metavermilia zibrowii</i> Bailey-Brock and Magalhães, 2012	2013	Original description
<i>Vermiliopsis notialis</i> Monroe, 1930	2016	Averintsev 1974
<i>Bushiella</i> (<i>Jugaria</i>) <i>atlantica</i> (Knight-Jones, 1978)	2100	Original description
<i>Bathyvermilia islandica</i> Sanfilippo, 2001	2399	Original description
<i>Filogranula stellata</i> (Southward, 1963)	2464	Ben-Eliahu and Fiege 1996
<i>Hyalopomatus variorugosus</i> Ben-Eliahu and Fiege, 1996	2474	Original description
<i>Laminatubus paulbrooksi</i> Rouse and Kupriyanova, 2021	2478	Original description
<i>Protis browni</i> (Pixell, 1913)	2585	Original description
<i>Protis hydrothermica</i> ten Hove and Zibrowius 1986	2620	ten Hove and Zibrowius 1986
<i>Hyalopomatus marenzelleri</i> Langerhans, 1884	2800	Zibrowius 1968, 1969, 1977
<i>Laminatubus alvini</i> ten Hove and Zibrowius, 1986	2842	Original description
<i>Neovermilia</i> cf. <i>sphaeropomata</i> (Benham, 1927)	3261	Rouse and Kupriyanova 2021
<i>Apomatus globifer</i> Théel, 1878	3384	Uschakov 1957
<i>Hyalopomatus clapedii</i> Marenzeller, 1878	3550	Kupriyanova and Jirkov 1997
<i>Hyalopomatus jirkovi</i> Kupriyanova, 1993	3949	Kupriyanova et al. 2011
<i>Spirodiscus grimaldii</i> Fauvel, 1909	4124	ten Hove and Kupriyanova 2009
<i>Bathyvermilia kupriyanovae</i> Bastida-Zavala, 2008	4190	Original description
<i>Apomatus similis</i> Marion and Bobretzky, 1875	4400	Fauvel (1909), Fauvel (1914)
<i>Spirodiscus groenlandicus</i> (McIntosh, 1877)	4440	Kupriyanova and Ippolitov 2015
<i>Bathyvermilia zibrowiisi</i> Kupriyanova, 1993	4550	Kupriyanova et al. 2011
<i>Hyalopomatus sikorskii</i> Kupriyanova, 1993	4550	Kupriyanova et al. 2011
<i>Protis simplex</i> Ehlers, 1887	4810	Knight-Jones et al. (1997)
<i>Protis polyoperculata</i> Kupriyanova, 1993	5110	Original description
<i>Hyalopomatus mironovi</i> Kupriyanova, 1993	5216	Rouse and Kupriyanova 2021
<i>Protis arctica</i> (Hansen, 1879)	5300	Zibrowius 1969
<i>Bathyvermilia challengerii</i> Zibrowius, 1973	5719	Original description
<i>Bathyvermilia langerhansi</i> Fauvel, 1909	5987	Eliason 1951
<i>Bathyvermilia gregrousei</i> Kupriyanova and Ippolitov, 2015	6050	Original description
<i>Nidificaria levensteinae</i> (Bailey-Brock and Knight-Jones, 1977)	6096	Original description
<i>Bathyditrupa hovei</i> Kupriyanova, 1993	6330	Kupriyanova et al. 2011
<i>Protis</i> sp. 2	8345	Kupriyanova et al. 2014
<i>Protis</i> sp. 1	9735	Kupriyanova et al. 2014

Sabellidae

Sabellids have been described from all marine realms and all seven members of *Caobangia* are known so far are from the Indo-Malay limnic realm. In the current analysis, the Temperate Northern Atlantic is the realm with the highest number of sabellids described (125 species), which represents 24% of the sabellids described worldwide, followed by the Temperate Northern Pacific (79 species, 15%), Central Indo-Pacific (58 species, 11%), Tropical Atlantic (56 species, 11%), Temperate Australasia (37), Western Indo-Pacific (20 species), Temperate South America (28 species), Southern Ocean (24 species), Temperate Southern Africa (18), Arctic (16 species), Tropical Eastern Pacific (15 species), Eastern Indo-Pacific (8), 23 species non-marine and eight species with unknown type locality (Table S2). Most of the 117 073 georeferenced occurrences in GBIF are from the Temperate Northern Atlantic and the Tropical Atlantic realms, and records belong to members of genera *Euchone*, *Jasmineira*, *Chone* and *Sabella* [34] (Figure 13). Other realms with large representation of sabellids records are Tropical Atlantic, the Arctic and Temperate Australasia. The number of described species and number of records is higher in the Atlantic than in any other ocean, the result that contradicts the patterns showing an increase in sabellid species richness towards the tropics, and mainly in the Indo-Pacific [331].

Some genera with few species, such as *Anamobaea* or *Stylomma*, and the freshwater *Caobangia*, are exclusive of tropical environments [69,158,229], and others, such as *Branchiomma*, *Bispira*, *Acromegalomma*, *Notaulax*, *Sabellastarte*, and *Sabellonga*, have either tropical or temperate distribution [149,157,336–338]. A few genera show a significant preference for colder waters and are either well represented at greater depths or in higher latitudes (e.g., members of *Chone*, *Euchone*, and *Jasmineira*). The Antarctic region is richer in number of genera and species than the Arctic [24] (Figure 7), and genera, such as *Perkinsiana*, are mainly distributed in the Southern Ocean [212].

Sabellids found below 6000 m have all been reported from the Western Pacific Ocean (Table 5) and include species of the genera *Jasmineira*, *Potamethus* and *Potamilla* Malmgren, 1866 [339–344]. Species reported in the abyssal zone (2000–6000 m deep) include members of the genera *Chone*, *Euchone*, *Fabrisabella*, *Jasmineira*, *Potamilla*, and *Potamethus* (Table 5). The genus *Potamethus* is the most speciose deep-sea taxon (Table 5). *Jasmineira filitovae* Levenstein, 1961 is the deepest record (9735 m). Sabellids reported from between 1000 and 2000 m depths include species of *Bispira*, *Chone*, *Euchone*, *Jasmineira*, *Perkinsiana*, *Potamethus*, *Potaspina* and *Pseudopotamilla* [280,284,345–348]. Among all sabellids recorded below 1000 m, 13 have been identified to the genus level only, most probably constituting new species.

Serpulidae

Serpulids have been described from all marine realms. The realm with highest number of species is the Temperate Northern Atlantic (108 species), followed by the Temperate Northern Pacific (92), Central Indo-Pacific (74), Tropical Atlantic (71), Western Indo-Pacific (52), Temperate Australasia (41), Tropical Eastern Pacific (28), Southern Ocean (23), Temperate South America (21), Arctic (16), Temperate Southern Africa (15), Eastern Indo-Pacific (8), and nine species with unknown type locality (Table S3). Of the 107 859 georeferenced records in GBIF (2020), more than half are within the Temperate Northern Atlantic (mainly identified as *Spirobranchus*, *Hydroides*, *Ditrupa* and *Spirorbis*) and following realms with highest occurrences are the Temperate Australasia (mainly *Spirobranchus*, *Hydroides*, *Galeolaria* and *Serpula*) and the Tropical Atlantic (*Hydroides*, *Spirobranchus*, *Vermiliopsis* and *Pseudovermilia*) (Figure 13). There were no previous analyses of global serpulid distribution patterns to compare with these data.

Serpulids are common inhabitants of intertidal, subtidal and shelf locations, but they can occur at all latitudes from intertidal to hadal depths. *Spirorbis* bathymetric distribution ranges from littoral to abyssal depths, but they are most commonly found in the sublittoral zone. The best known representatives of the genera *Ficopomatus*, *Galeolaria*, *Hydroides*, *Salmacina* Claparède, 1870, *Serpula*, *Spirobranchus* and *Vermiliopsis* are inhabitants of shal-

lower waters (below 500 m), and so are representatives of less known and more cryptic genera, such as, for example, *Chitinopoma*, *Floriprotis*, *Josephella* Caullery and Mesnil, 1896, *Metavermilia*, *Pomatostegus*, *Pseudochitinopoma* Zibrowius, 1969, *Pseudovermilia*, *Rhodopsis* Bush, 1905, *Semivermilia* ten Hove, 1975 and *Spiraserpula*. Some genera, e.g., *Apomatus*, *Filigranula*, *Neovermilia* and *Protula* may include both subtidal and bathyal species.

Serpulids found below 2000 m were reviewed by Zibrowius [349], who corrected Hartman's [339] compendium of abyssal polychaetes by removing taxa typical of subtidal and shelf depths (*Hydroides*, *Ditrupa*, *Placostegus*, *Serpula*, *Spirobranchus*). As a result, he listed 25 species, including one unidentifiable specimen from Kermadec Trench (6620–6730 m, [350]). Belyaev [344] added two unidentified hadal specimens from 6410–6757 m (Aleutian Trench) to 9715–9735 m (Izu-Bonin Trench), the latter being the deepest record for a serpulid. In their review, Paterson et al. [351] list only 26 serpulids from over 2000 m world-wide, including five species from depths beyond 3500 m, all described by Kupriyanova [352,353] from Kuril-Kamchatka Trench alone. Sanfilippo [354], Kupriyanova et al. [355,356] Kupriyanova and Nishi [357], Bailey-Brock and Magalhães [184], Kupriyanova and Ippolitov [107], and Rouse and Kupriyanova [358] recently provided additional records and descriptions of new deep-sea serpulid taxa. Kupriyanova et al. [356] reviewed and revised hadal records below 5000 m, demonstrating that the deepest serpulid records (8345 and 9735 m) reported in Belyaev's book [344] belong to the genus *Protis*.

Currently, 36 named species have published records below 1000 m, 28 of them are reported from below 2000 m (Table 5), although Kupriyanova et al. [356] lists eight records in open nomenclature (*Bathyvermilia* sp., *Hyalopomatus* sp., *Protis* sp., Serpulidae gen. sp. A and B). In summary, serpulids from bathyal and abyssal depths (>1000 m) are found in the genera *Apomatus*, *Bathyditrupa*, *Bathyvermilia* Zibrowius, 1973, *Bushiella* (*Jugaria*) Knight-Jones, 1978, *Filigranula*, *Hyalopomatus*, *Laminatubus*, *Metavermilia*, *Neovermilia*, *Nidificaria* Knight-Jones, 1984, *Spirodiscus*, *Protis*, and *Zibrovermilia* Kupriyanova and Ippolitov, 2015, but only species of *Bathyditrupa*, *Bathyvermilia*, *Hyalopomatus*, and *Protis* are found in the abyss, also penetrating into the hadal zone. Non-operculate *Protula* and operculate *Apomatus* are often confused with non-operculate and operculate *Protis* sp., so that abyssal records of supposed *Protula* and *Apomatus* might belong to *Protis* [356].

3.5. Non-Indigenous and Invasive Species

Shallow-water Sabellida, due to their sedentary tubicolous lifestyle, are common members of biofouling communities and are easily translocated by anthropogenic means, i. e., on ship hulls and floating marine debris [147]. Distribution as larvae in ballast water has been suggested [359–362] and is the most plausible hypothesis for *Sabella spallanzanii* [363,364], but larvae of sabellids and serpulids have never been reported from ballast water samples. If become established in remote localities, such translocated taxa significantly expand their ranges. However, some reported broad distributions are a reflection of uncertain taxonomic status. Such species remain as widely distributed or even 'cosmopolitan' only as long taxonomic uncertainty persists, and a molecular investigation usually split them into a number of geographically restricted species.

According to the literature survey of polychaetes reported outside their natural ranges, Serpulidae and Sabellidae account for 22% of the total number of non-native polychaetes world-wide [365]. However, a critical assessment of non-indigenous species records is needed. The number of such species is a function of the research effort put into distinguishing non-native and native taxa, which in turn depends on the knowledge of native diversity and the state of taxonomy of a group. Integrative taxonomic revisions of species with reportedly global distributions are important because such taxa may include cryptic invaders that are particularly difficult to track because they are often assumed to be native species or wrongly assigned to other invasive species [366].

Several criteria for distinguishing non-indigenous from native species have been proposed as lines of indirect evidence, such as a new record for an area, a new localised occurrence showing a population explosion, species with disjoint distribution, with insufficient

natural dispersal capabilities to account for observed distribution range, or species associated with means of human-made transport, e.g., found on ship hulls (e.g., [172,367,368]). In the last two decades, molecular genetics tools have proved indispensable direct lines of evidence for assessing the status of a reportedly invasive taxon. The population genetics studies allow testing if distant populations belong to same species, and also if genetic variability of suspected new arrivals is lower than that observed in the native range, which indicates a recent translocation (e.g., [72,74,204,294,368–370]). Molecular data can also help to determine the origin of non-native populations. For example, haplotype variability analysis suggests that although serpulid *Hydroides dianthus* (Verrill, 1873) was originally described from New England, its native range may be the Mediterranean [250].

A good example of a sabellid with an uncertain invasive status is *Laonome calida* described from the Calliope River, Australia, and later reported as introduced in the Netherlands [294], Odra River and the Sea of Azov [371,372]. Simultaneously, the morphologically similar *Laonome xeprovala* was described from the Baltic Sea, and DNA sequences from specimens from the Netherlands and Sea of Azov showed that they belong to the same species [102]. Neither *L. calida* nor *L. xeprovala* had been reported from Europe before 2014, and increased occurrences suggest a recent invasion [373]. Molecular analyses, however, are needed to determine whether the European populations belong to the same species found in Australia (implying that *L. xeprovala* could be a junior synonym of *L. calida*) or a distinct non-indigenous species of unknown origin is found in Europe (in which case *L. xeprovala* would be valid). Similarly, *Branchiomma* species are easily translocated outside of their native ranges [72,129,147,374–379], but members of this genus are so morphologically homogenous that species identification using morphological characters only is problematic. Therefore, assessing the identity of *Branchiomma* spp. with invasive potential requires a comprehensive generic revision, including DNA-based species delimitation analyses [72,379]. Other records still to be confirmed by molecular studies are the sabellids *Euchone variabilis* Hutchings and Murray, 1984, *Laonome triangularis*, *Desdemona aniara* and the three species of *Pseudobranchiomma* reported from Australia [74,126,380,381].

Table 6. List of translocated species, with presumed origin indicated by provinces or ecoregions (*sensu* Spalding et al. [31]). Those species that are included as unresolved, require confirmation and two are not cosmopolitan (*Branchiomma curtum* and *Parasabella pallida*). NA: not applicable.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Acromegalomma claparedei</i> (Gravier, 1906)	Djibouti, Gulf of Aden	Red Sea	? Non-indigenous	Western Mediterranean	none	Listed in the Mediterranean [382] but needs confirmation [130].
<i>Amphicorina pectinata</i> (Banse, 1957)	Masked Island, New Zealand	Southern Island New Zealand	? Non-indigenous	Western and Central Mediterranean	none	Redescribed from Italy and Spain without examination of types from New Zealand [383]. Included in the Mediterranean checklists [365,381,384] but requires confirmation.
<i>Bispira polyomma</i> Giangrande and Faasse in Faasse and Giangrande, 2012	Yerseke Marina, the Netherlands	Unknown	? Non-indigenous	NA	none	Found among cultured oysters, presumably as an introduction [385].
<i>Branchiomma bairdi</i> (McIntosh, 1885)	Bermuda	Tropical Northwestern Atlantic	Non-indigenous	Gulf of California, Australia, Mediterranean, Suez Canal, northeastern Atlantic Ocean, California, Hawaii, Galapagos, Madeira	COI, Cytb, 16S, 28S, ITS	Widest distribution reported for a sabellid [72,126,129,147,185,189,376,377,379,386–388]. Some records need confirmation [185].
<i>Branchiomma boholense</i> (Grube, 1878)	Bohol, Philippines	Western Coral Triangle	Non-indigenous	Mediterranean	COI	Reported from the Mediterranean [375,389,390]. Çınar [126] corrected his records as <i>B. bairdi</i> . Many records of <i>B. bairdi</i> in the Mediterranean are <i>B. boholense</i> [379].

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Branchiomma coheni</i> Tovar-Hernández and Knight-Jones, 2006	Panama, Pacific	Tropical Eastern Pacific	Non-indigenous	Florida, Gulf of California	none	Records from Tampa Bay and Gulf of California [391] first since description. In Florida it was an early detected non-indigenous species [391].
<i>Branchiomma conspersum</i> (Ehlers, 1887)	Key West, Florida, USA	Floridian	Non-indigenous	Hawaii	ITS	Reported from Hawaii [185]. Caribbean records may be erroneous [391]. Both syntypes of <i>B. curtum</i> and Caribbean specimens were juveniles produced by fission [392]. See comments in [391].
<i>Branchiomma curtum</i> (Ehlers, 1901)	Juan Fernández Island, Chile	Juan Fernández	Not translocated	? Mexican Caribbean	none	Common in the Mediterranean as Lessepsian migrant [129,389,390,393–401], and Brazil [234,402]. Reported as introduced in Australia [403], Spain [404], UK [405], Marmara Sea [406], Portugal [407] and the Netherlands [408], but types of <i>D. ornata</i> were not examined.
<i>Branchiomma luctuosum</i> (Grube, 1870)	Red Sea	Red Sea	Non-indigenous	Mediterranean, Brazil	none	
<i>Desdemonia ornata</i> Banse, 1957	South Africa	Agulhas	? Non-indigenous	Iberian Peninsula, UK, Marmara Sea, Portugal	none	

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Euchone limnicola</i> Reish, 1959	Los Angeles, California, USA	Warm Temperate Northeast Pacific	? Non-indigenous	Dunkerke, Australia	none	Reported from Australia by McArthur [409] and included in Hewitt et al. [380] based on McArthur dissertation. Reported by Guyonnet and Borg [410] from the French coast of North Sea.
<i>Laonome calida</i> Capa, 2007	Queensland, Australia	Unknown	? Non-indigenous	Australia (Queensland, Northern Territory, Western Australia), ? Europe (the Netherlands, Sea of Azov, Baltic Sea, Mosel River)	none	Reported in Australian in fully marine but also estuarine conditions, in both pristine and port environments [68]. Bick et al. [102] suggest that European records belong to <i>Laonome xeprovala</i> , not <i>L. calida</i> .
<i>Laonome elegans</i> Gravier, 1906	Red Sea	Red Sea	? Non-indigenous	East Mediterranean	none	Listed in Zenetos et al. [383]. Presence in the Mediterranean area as Lessepsian migrant needs to be confirmed.
<i>Laonome triangularis</i> Hutchings and Murray, 1984	New South Wales, Australia	East Central Australian Shelf	? Non-indigenous	Turkey	none	Reported as introduced in Turkey [126].
<i>Laonome xeprovala</i> Bick and Bastrop in Bick et al. 2018	Estonia, Baltic Sea	Unknown	Non-indigenous	the Netherlands, Sea of Azov, Baltic Sea, Mosel River	COI, 16S, 18S	Specimens from the Baltic Sea, the Netherlands and the Sea of Azov possessed identical genotypes, but unknown origin [102]. Confirmation that it is not the same as <i>L. calida</i> is needed.

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Myxicola infundibulum</i> (Renier in Meneghini, 1847)	Devon, UK	Northern European Seas	Non-indigenous	Australia, ?North America	COI, 16S	Analysed sequences of specimens from European and Australian waters belong to same species; sequences from Maine showed some differences [411].
<i>Parasabella fullo</i> Grube, 1878)	Northern Japan	Temperate Northwest Pacific	Non-indigenous	Santa Barbara and San Diego, California, USA	none	Collected on ship hulls in California, and a resident population appears to exist in the region [412].
<i>Parasabella pallida</i> Moore, 1923	California, USA	Warm Temperate Northeast Pacific	Not translocated	NA	none	Included in the list of translocated species by mistake [294], as it was described from California [143] not the Caribbean, as later fixed in [73].
<i>Parasabella rugosa</i> (Moore, 1904)	San Diego, California, USA	Warm Temperate Northeast Pacific	Non-indigenous	Australia	none	It was reported in Australia near an international port as sp. cf. <i>P. rugosa</i> Capa and Murray [73].
<i>Pseudobranchiomma emersoni</i> Jones, 1962	Port Jackson, Jamaica	Tropical Northwestern Atlantic	Non-indigenous	Australia	none	As cf. <i>P. emersoni</i> in Capa and Murray [74].
<i>Pseudobranchiomma orientalis</i> (McIntosh, 1885)	Hong Kong	Unknown	Non-indigenous	Australia	none	As cf. <i>P. orientalis</i> in Capa and Murray [74]. Ethanol fixed specimens are need for molecular analysis.

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Pseudobranchiomma schizogenica</i> Tovar-Hernández and Dean, 2014	La Paz, Mexico	Tropical Northwestern Atlantic	Non-indigenous	Australia, Galapagos	ITS, Cytb	As cf. <i>P. schizogenica</i> in Capa and Murray [74] from Australia, also reported in Galapagos [183].
<i>Sabella spallanzanii</i> (Gmelin, 1791)	Malta	Mediterranean	Non-indigenous	Australia, New Zealand	COI, H3, 18S, 28S, 16S, ITS	Considered an invasive pest in Australia and New Zealand [202,364,370,413].
<i>Sabellastarte spectabilis</i> (Grube, 1878)	Bohol, Masalac, Philippines and Singapore	Western Coral Triangle	? Non-indigenous	Sri Lanka, Solomon Islands, Mauritius, Japan, Taiwan, Hawaii, Malaysia, Saipan, Pakistan	COI, 16S	Reports of accidental introductions to Hawaii [414–416] rely on invalid morphological features [70]. Evidence for wide distribution exists [70]. Parasite of red abalone. Reported from abalone farms from California and Chile [66,300–419]. Reviewed by Dittmann [420]. Styan et al. [204] revealed three species (not formally described) with overlapping ranges in Australia, one of which is morphologically distinct from the other two. Grosse et al. [421] found two other species within the complex Spain.
<i>Terebrasabella heterouncinata</i> Fitzhugh and Rouse, 1999	South Africa	Unknown	Non-indigenous	California, Chile	none	
<i>Ficopomatus enigmaticus</i> (Fauvel, 1923)	France, native range is unknown, likely southern Australia	Unknown	Non-indigenous	Europe, New Zealand, Japan, USA (both coasts), Argentina, Tunisia, Egypt, Côte d’Ivoire, South Africa	Cytb, COI	

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Ficopomatus uschakovi</i> (Pillai, 1960)	Sri Lanka	Unknown	? Non-indigenous	Indo-Pacific, Western Africa (Nigeria, Ivory Coast), Brazil, Venezuela, Colombian Caribbean and southern Mexican Pacific ?Australia	none	Several records given outside the native range [422–425]. Likely a species complex [204].
<i>Hydroides brachyacantha</i> Rioja, 1941	Pacific coast of Mexico	Warm Temperate Northeast Pacific	Native	Likely restricted to Pacific coast of Mexico, no evidence of translocations	18S, cytb, ITS	Belongs to a complex of species, records from warm-temperate and tropical localities world-wide likely belong to other species of <i>H. brachyacantha</i> complex [203].
<i>Hydroides dianthus</i> (Verrill, 1873)	New England, USA	Either East Coast of the USA or the Mediterranean	Non-indigenous	Brazil, China, Japan, West Africa, the Mediterranean (or US East Coast), the Black Sea, Texas	COI	Observed higher haplotypes diversity in the Mediterranean contradicts the accepted native range of <i>H. dianthus</i> in the USA. The cryptic lineage found in Texas was evidently introduced to the Black Sea recently [250].
<i>Hydroides dirampha</i> Mörch, 1863	St. Thomas Island, US Virgin Islands	Tropical Northwestern Atlantic	Non-indigenous	Australia, Brazil, Japan, Hawaii, New Zealand, Panama, the Pacific from Mexico and California, and the Mediterranean	18S, cytb, COI, 28S, ITS	Several records given outside the native range [426–429]. Molecular data from Australia, Brazil, Panama [78,79].

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Hydroides elegans</i> (Haswell, 1883)	Sydney, Australia	Unknown	Non-indigenous	Sub-tropical world-wide: Mediterranean-Atlantic, Indo-West Pacific, tropical Pacific America, West Atlantic, East Atlantic, South Africa	Microsatellites, 18S, cytb, COI, 28S	See [106]. Biofouling has been shown as a major mode of dispersal for this species [430]. Molecular data from Panama, California, Australia, Brazil, Italy and Spain [79,421]. Imported from Japan with oysters to the Atlantic coast of France [431,432] then the UK and Australia [359,432,433]. Molecular data from China, Japan [79].
<i>Hydroides ezonesis</i> Okuda, 1934	Northern Japan	Warm Temperate Northwest Pacific	Non-indigenous	France, UK, Australia	18S, 28S	Reports from South and East Africa, India, Pakistan, Sri Lanka, Hong Kong, tropical Australia, and the eastern Mediterranean likely belong to other species of the <i>H. operculata</i> complex [251]. Records outside of the native range include [78,180,362,434].
<i>Hydroides operculata</i> (Treadwell, 1929)	Gulf of Aden	Western Indo-Pacific	Native, some species in the complex maybe non-indigenous	A complex of species, no evidence of translocations for any species of the complex	18S, cytb, COI, 28S, ITS	Molecular data from Florida [77], Panama, Australia, India [79], Pacific Mexico [80].
<i>Hydroides sanctaecrusis</i> Krøyer [in] Mörch, 1863	Saint Croix, Virgin Islands	Eastern Caribbean	Non-indigenous	Singapore, tropical Australia, Hong Kong, Taiwan, Florida, India. Not found in the Mediterranean [240]	18S, COI, 28S, ITS	

Table 6. Cont.

Species	Type Locality	Presumed Origin	Category	New Occurrences (Outside of Expected Natural Range)	Molecular Markers	Comments
<i>Spirobranchus kraussii</i> (Baird, 1865)	Cape of Good Hope, South Africa	Agulhas	Native, some species in the complex non-indigenous, but not <i>S. kraussi</i>	Restricted to South Africa, no evidence of translocations	18S, cytb	Reports from warm-temperate and tropical localities in the Indo-Pacific and Mediterranean Sea belong to other species of <i>S. kraussii</i> complex [84,193].
<i>Spirobranchus tetraceros</i> (Schmarda, 1861)	NSW, Australia	East Central Australian Shelf	Native, some species in the complex likely non-indigenous, but not <i>S. tetraceros</i>	Likely restricted to south-eastern Australia, no evidence of translocations.	cytb	Reports from warm-temperate and tropical localities world-wide belong to other species of the <i>S. tetraceros</i> complex. At least one of these species was introduced and established in the Mediterranean [252].

One of the best examples of a sabellid with the invasive status confirmed through a combination of morphological and genetic data is *Sabella spallanzanii*. This large conspicuous Mediterranean native was introduced to Australia in 1965 and to New Zealand in 2008 [364,435,436]. Analyses of COI sequences from the native and non-indigenous populations proved that the New Zealand incursion originated from Australia rather than from the Mediterranean [370]. Other examples of sabellids with invasive status (but of unknown origin) confirmed with DNA analyses are *Parasabella crassichaeta* Capa and Murray, 2015 and *Pseudobranchiomma* cf. *schizogenica* Tovar-Hernández and Dean, 2014, reported from both Hawaii and Australia [73,74]. Out of seven nominal species of the serpulid genus *Hydroides* reported as translocated outside of their natural range, five are confirmed invaders (Table 6). One of them, *H. elegans*, is the best-known cryptogenic polychaete, reported from most sub-tropical locations world-wide [110], and biofouling as the major mode of its dispersal was supported by DNA data [430]. *Ficopomatus enigmaticus* is another cryptogenic serpulid, because, although it was described from France, its native range is enigmatic (hence the name), likely to be southern Australia [420]. This typical species has invaded warm-temperate estuaries world-wide, as confirmed by DNA studies [204,437,438].

Ficopomatus uschakovi (Pillai, 1960), described from Sri Lanka, a tropical species with supposedly wide distribution in Indo-Pacific, was recently reported as introduced to South America [422–425]. The invasive status of the species has not been examined with DNA, but preliminary molecular data (Kupriyanova unpubl.) suggest that this taxon is a complex of species. Two nominal *Hydroides* species, *H. brachyacantha* Rioja, 1941 and *H. operculata* (Treadwell, 1929), are examples of complexes of morphologically similar species [180,251]. Similarly, the invasive status attributed to serpulids *Spirobranchus kraussii* (Baird, 1865) and *S. tetraceros* (Schmarda, 1861) [365,439] is unjustified, as both are members of species complexes [84,193,252].

The Mediterranean Sea leads the rank when it comes to reported introductions, with 13 serpulid and 10 sabellid non-indigenous species reported, mainly as a result of Lessepsian migration from the Red Sea [125,365,440,441]. In this region, 11 species of sabellids and serpulids, mainly of the genera *Branchiomma*, *Ficopomatus*, and *Hydroides*, have been listed among the top 100 worst invasive species, based on their economic and ecological impacts [442]. However, taxonomic and invasive status of many of these taxa needs to be revised.

3.6. Fanworms Are Important: Some Applications

3.6.1. Nuisance Fouling Species

Several serpulid species, predominantly of the genera *Hydroides*, *Ficopomatus*, and *Spirobranchus*, are capable of colonizing a wide range of natural and artificial substrates and settling gregariously, which makes them economically and ecologically important fouling nuisance species.

Serpulid foulers constitute a significant financial burden due to costs associated with the removal of tubes from artificial structures. Millions of dollars are spent annually to prevent the fouling of marine organisms, especially of *Hydroides*, on human-made structures [443]. Dense tube aggregates attach to underwater seawater intake pipes of power plants reducing water flow and causing blockages. Fouled docks require cleaning maintenance in harbours around the world. Fouling interferes with navigation and shipping industries by decreasing ship speed, while increasing the weight and drag of buoys [444,445].

In marine aquaculture the key impact is the direct fouling of stock causing physical damage, biological competition and environmental modification, while infrastructure, such as aquaculture nets and cages, is also damaged. The conservative estimates of economic loss to the aquaculture industry are 5–10% of production costs attributed to biofouling [446].

Manayunkia speciosa and/or *M. occidentalis* (see [216]) are obligate hosts of the myxozoan parasites *Ceratonova shasta* and *Parvicapsula minibicornis*, which cause ceratomyxosis in salmon and trout in North America [267,268,447]. Management actions, such as flow

manipulations to increase the mortality of *M. speciosa* and disturbance of its habitat, have been implemented [268].

3.6.2. Non-Indigenous and Invasive Species

Non-native to a region species translocated to another region can expand and have significant impact on human health, economic interests or environmental values. Such translocations of fouling species of Sabellida are well documented (e.g., [448–452]). Countries around the world have established biosecurity systems, aimed to prevent the introduction and/or spread of non-indigenous organisms. Some Sabellida have been listed in individual countries' Laws and Regulations, indicating its status as unwanted non-indigenous species (invasive, pests, parasites, pathogens). For example, in New Zealand, *Sabella spallanzanii* has been registered as a notifiable organism, subject to targeted surveillance work, including study of population dynamics and reproduction, under the New Zealand Biosecurity Act 1993 [364]. In Australia, non-indigenous marine species already found and those not yet found but have demonstrated significant impacts elsewhere are ranked according to their invasive impact and potential. For example, *S. spallanzanii* is regarded as a high impact, notifiable invasive species, while *Hydroides dirampha* Mörch, 1863, *H. dianthus*, *H. sanctaecrucis* Krøyer in Mörch, 1863, *H. ezoensis* Okuda, 1934 are listed as medium or low priority species [433]. In Mexico, sabellids *Branchiommma bairdi* (McIntosh, 1885) and *Terebrasabella heterouncinata* and six serpulids (*Ficopomatus enigmaticus*, *F. miamiensis* (Treadwell, 1934), *F. uschakovi*, *Hydroides elegans*, *H. bispinosa* Bush, 1910 and *H. dirampha*) are regulated under the Diario Oficial de la Federación [453]. *Ficopomatus enigmaticus* is the only annelid registered in the Spanish Catalogue of Exotic Invasive Species [421]. In Brazil, the only species of Sabellida reported as invasive is *Branchiommma luctuosum* (Grube, 1870) [401].

3.6.3. Indicators of Pollution

Manayunkia speciosa is an indicator of moderate organic pollution, but is intolerant of severe pollution or anoxic sediments [447,454,455]. Decrease of the organic content of the sediment from 1.8% to 1.0% leads to reduction in abundance of its congener, *M. aestuarina*, from 16 000 to 6000 ind.m² in the Baltic Sea [262]. *Euchonoides moeone* was proposed as an indicator of sediment organic enrichment in a sewage outfall in Hawaii [279].

Sabella spallanzanii can trap anthropogenic micro-particles and glue these to their tubes, and it has been proposed as an indicator of microlitter pollution in sheltered and polluted environments such as ports [456]. Larvae of *Hydroides elegans* have been used as indicators for biomonitoring and ecotoxicology tests (e.g., [457–459]).

Some sabellids and serpulids have been suggested as bioindicators of heavy metal pollution. For example, the tube of *Sabella spallanzanii* is an important compartment in metal retention and suitable for evaluation of the pollution by traced elements [460], while *Branchiommma bairdi* and *B. luctuosum*, invasive sabellids in the Mediterranean, can accumulate high concentrations of arsenic (As), cadmium (Cd), chromium (Cr) and lead (Pb), considered to be priority toxic or ubiquitous persistent, bioaccumulative and toxic (PBT) substances under the EU Water Framework Directive [461]. Some studies have focused on the effects of heavy metals on larval development and metamorphosis using serpulid larvae (*Hydroides elegans*: [462,463]); *Galeolaria caespitosa*: [464]).

3.6.4. Bioremediators

As suspension feeders, *Sabella spallanzanii*, *Branchiommma luctuosum* and *B. bairdi* have been tested as bioremediators for aquaculture waste-water treatment in polluted coastal areas [273,274,465–470]. However, these three taxa are invasive in some areas, and may pose a threat to native ecosystems. Nevertheless, the use of non-indigenous species as bioremediator may allow to transform a potential risk into a benefit, with high potential commercial gain and economic feasibility [470]. Due to their important role in organic sediment bioremediation, the Food and Agriculture Organization of the United Nations

(FAO, Roma, Italy) recommended *Sabella* as one of organisms with most potential for the development of integrated multi-trophic aquaculture systems [471].

Ficopomatus enigmaticus is a dominant species in estuaries and lagoons, where it can affect the community structure and contribute to the invertebrate biomass [472,473]. Due to its ability to build extensive reefs, *F. enigmaticus* is considered an ecosystem engineer that can modify estuarine ecosystem, changing water flow, sedimentation rates, and creating a structured hard substrate habitat in a soft-sediment environment. Large aggregations of *F. enigmaticus* remove suspended particulate matter, reduce excess nutrient loads and improve oxygen levels in enclosed waters, thereby improving the water quality and environmental conditions for other benthic species (reviewed in [420]). Davies et al. [474] stressed that because of the fundamental role *F. enigmaticus* played in the maintenance of water quality of an enclosed system near Cape Town, South Africa, eradication of this non-indigenous species should not be a management option.

3.6.5. Models Organisms in Research

Sabellids are used as models in regeneration biology, most notably in studies examining the developmental basis and functional ecology of regeneration [222,475–477]. Members of the genus *Myxicola* are known for the giant axon [478] that directly innervates the worm's muscles, presumably aiding in super-fast retraction into the tubes [479]. The outsized nerves make this species a model organism for studies of neuroanatomy, neuroactivity and electrophysiology [480–482]. *Myxicola*'s giant axons were also used for testing the effects of the anticonvulsant Carbamazepine on the ionic conductance [483]. Moreover, the mucus of *Myxicola infundibulum* (Renier in Meneghini, 1847), with natural antibacterial and antioxidant compounds, showed potential for drug prospecting [470].

Hydroides elegans is easily adapted for laboratory research because of its rapid generation time (three weeks) and ease of propagation. The adults spawn and eggs easily fertilise, their larvae become metamorphically competent in several days and readily settle in the laboratory. Thus, *H. elegans* has been declared an important model organism [484] and has been used routinely during last two decades in hundreds of experimental embryological, larval ecology and biofouling studies, including tests of newly formulated marine coatings (e.g., [485–490]). Other *Hydroides* species, such as *H. ezoensis* and *H. dianthus*, have also acted as model organisms for larval ecology research (e.g., studies of mechanisms of gregarious settlement by [491–493]). *Spirobranchus lamarcki* (Quatrefages, 1866) has provided an important model system for molecular and embryological work, including studies on the organization and expression of its developmental genes (e.g., [494–497]). Recently *H. elegans* and *S. triqueter* have served as models in ocean acidification and biomineralization research (e.g., [498–500]).

3.6.6. Objects of Ornamental Trade

Sabellida includes some of the most beautiful marine invertebrates due to their colourful radiolar crowns. They are listed among the ten most imported ornamental invertebrates [501] and are amongst the most photographed polychaetes found in marine guides and featured on postcards, stamps, calendars, T-shirts and even tattoos. Largest sabellids (*Anamobaea*, *Bispira*, *Notaulax*, *Sabella* and *Sabellastarte*) and serpulids such as Christmas tree worms (*Spirobranchus*) and coco worms (*Protula*) are popular in the aquarium trade. The vast majority of ornamental sabellids and serpulids are tropical species, although a market for cold-water species has been growing [502,503]. Efforts to culture sabellids (e.g., *Sabellastarte spectabilis* (Grube, 1878) [504–506], *Sabella pavonina* Savigny, 1822 [270,507] and *Bispira brunnea* (Treadwell, 1917) [508] are well under way. Aquaculture can provide environmental benefits by reducing collecting pressure on highly traded species.

3.7. Future Perspectives in Fanworm Research

As it is clear from this review, knowledge of Sabellida biodiversity is incomplete and the reported species numbers appear to be an underestimation of the true diversity.

This review highlights that some of the lesser known coastal and continental shelf areas including Hudson complex, the Atlantic coast of South America (especially the tropical Atlantic region, excluding the Caribbean Sea), the coastlines along the Arabic Sea and Gulf of Bengal, and the Far East of Russia. However, Africa, with the exception of South Africa and Morocco, is by far the most neglected continent when it comes to taxonomic studies.

More surveys into deep-sea (abyssal and hadal), chemosynthesis-based (hydrothermal vents, methane seeps and organic falls) and freshwater habitats are needed for a better understanding of the Sabellida diversity and adaptations to these habitats. The fact that undescribed species have been collected in recent deep-sea cruises along several worldwide regions (e.g., [284,509,510]) provides evidences for deep sea fanworms still awaiting to be discovered. Studies of symbiotic/commensal relationships with other organisms, e.g., molluscs, corals, sponges, or examinations of bacterial microbiomes may reveal not only new taxa, but also new ecological relationships and trophic networks (e.g., [284,490]).

Importantly, the diversity of some remote areas, including deep sea environments, is poorly known not only because of the obvious logistical difficulties with collecting, but also due the insufficient number of experts and their unbalanced distribution across the globe known as ‘taxonomic impediment’ (e.g., [94,511]). We need to train and sustain more systematists able to discover, describe, identify and classify species and also to increase efforts directed to manage and curate existing research collections [355].

As many more species are yet to be discovered, either in the field or in museum collections, particular attention should be paid to setting a high standard for the new species descriptions, which would include use of modern microscopic techniques (e.g., SEM, Phase Contrast), assessment of intra- and interspecific variability, and preparation of quality informative illustrations (digital drawings and high-quality digital photographs of stained fixed or live specimens, when possible). Exploration of both new characters, e.g., ultrastructure of calcareous serpulid tubes that proved useful for species delimitation [107,227,512], and new techniques to examine existing morphological characters, e.g., tomography and 3D reconstructions (e.g., [237]) should significantly improve species descriptions in the future and aid species delimitations.

Although multivariate morphometrics have been used to analyse differences among annelid species and populations (e.g., [513,514]), this technique is not very common for species delimitation because body shapes of these soft-bodied organisms vary depending on the fixation or anaesthetization methods [234]. We suggest that application of morphometrics to chaetal or opercular traits should be explored. However, regardless of availability DNA data, morphological studies must include statistical assessment of intraspecific variability and its sources (such as size-dependent, ontogenetic, environmental) (e.g., [72,278,515]).

Understanding of true species diversity of Sabellida requires world-wide revisionary studies of existing species and their distribution ranges. As early species descriptions are often very short and sometimes poorly illustrated, further re-descriptions of older species (especially described before mid-20th century) are needed, ideally based on topotypical material (as, e.g., done for serpulid *Spirobranchus kraussii* by Simon et al. [193]). For the species with lost or lacking types, neotypes should designated (e.g., as for *Pseudopotamilla reniformis* (Bruguère, 1789) by Knight-Jones et al. [111]), preferably accompanied by DNA sequence data (e.g., as done for *Hydroides brachyacantha* by Sun et al. [197]). It is imperative that the type material (holotype, type series, additional specimens showing intraspecific variability, and DNA extractions) is always deposited in properly curated permanent museum collection(s) where it is maintained in optimal conditions [516].

Contrary to previous conceptions that the ocean has no boundaries and that polychaetes more often than other organisms have cosmopolitan distributions [327], it now became clear that the genetic and species diversity of marine invertebrates is highly structured geographically and significant species diversity is hidden in former ‘cosmopolitan polychaete species’. Therefore, resolution of ‘cosmopolitan species’ should be one of the main goals of revisionary studies of Sabellida. This goal is only achieved with application

of fast-developing molecular tools such as DNA sequencing and genomics/transcriptomics. Molecular tools and analytical methods are indispensable to further improve our understanding of the species diversity, but also to trace the pathways and origins of invasive species, to determine biogeographic boundaries between species, and to provide reliable phylogenetic hypotheses. Robust well-resolved phylogenies with significant taxon coverage using transcriptome and mitochondrial genome data are important to address important character evolution questions (e.g., photoreceptor evolution and evolution of the reproductive and larval strategies in Sabellidae and Serpulidae). Finally, in the future molecular identification of species by non-specialists might replace morphology-based identifications only if reliable databases of reference sequences supported by voucher specimen depositories are built.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/3/130/s1>, Table S1: Fabriciidae, species and type localities; Table S2: Sabellidae, species and type localities; Table S3: Serpulidae, species and type localities.

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Appendix A

Fabriciidae and Sabellidae species with doubtful identity requiring further investigation (*inquirenda*), indeterminable or incorrect assignment.

Fabriciidae

1. *Manayunkia siaukhu* Annenkova, 1938 *inquirenda*. Based on the description, *M. siaukhu* has pygidial eyes [517] and thus does not fulfill diagnostic features for the genus.

Sabellidae

2. *Clymeneis* Rathke, 1843 *inquirenda*

Clymeneis and its type species *Clymeneis stigmosa* Rathke, 1843 are of doubtful identity requiring further investigation. Description was based in specimens inquirenda (?) apparently without crown and types have not been found. It has not been reported over more than a century, but recently mentioned in the paper about original specimens and type localities of early described polychaete species from Norway [518].

3. *Sabella aculeata* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
4. *Sabella ammonita* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
5. *Sabella arenaria* Montagu, 1803 *indeterminable*

Described based on the tube only, the worm is unknown [42] (pp. 552).

6. *Sabella arundinacea* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
7. *Sabella clavata* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
8. *Sabella compressa* Montagu, 1803 *indeterminable*

Original description was based only in the tube. Hartman [325] (pp.559) suggested that the tube is perhaps from a pectinariid.

9. *Sabella conica* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
10. *Sabella corticalis* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
11. *Sabella dimidiata* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
12. *Sabella flabellata* Savigny, 1820 *inquirenda*

Declared as *inquirenda* by Knight-Jones and Perkins [337] (pp. 398).

13. *Sabella fixa* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
14. *Sabella grossa* Baird, 1865 *inquirenda*

Declared as *inquirenda* by Knight-Jones and Mackie [338] (pp. 2296).

15. *Sabella helicina* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
16. *Sabella nigra* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
17. *Sabella sabulosa* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
18. *Sabella setiformis* Montagu, 1803 *indeterminable*

The tube was the only structure described, the worm is unknown [519] (pp.553).

19. *Sabella stagnalis* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
20. *Sabella subcylindrica* Montagu, 1803 *indeterminable*

Only the tube was described, animal unknown [519] (pp. 552-553).

21. *Sabella teredula* Chiereghini in Siebold, 1850 *indeterminable*

Only the tube was described [520] (pp. 369).

22. *Sabella trigona* Chiereghini in Siebold, 1850 *indeterminable*

Only the tube was described [520] (pp. 369).

23. *Sabella uncinata* Gmelin in Linnaeus, 1788. Insecta: Trichoptera.
24. *Sabella vegetabilis* Gmelin in Linnaeus, 1888. Insecta: Trichoptera.
25. *Sabella zonalis* Stimpson, 1854 *inquirenda*

Declared *inquirenda* by Knight-Jones and Perkins [337] (pp. 405).

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