

Review

On the Systematics and Biodiversity of the Opheliidae and Scalibregmatidae

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Abstract: In this paper we review the systematics, diversity, and ecology of two related annelid families: Opheliidae Malmgren, 1867 and Scalibregmatidae Malmgren, 1867. Opheliids are deposit-feeders and that are mainly found as burrowers in sandy sediments. Morphologically, opheliids are characterized by the smooth cuticle, as well as the presence of a conspicuous ventral groove, reduced parapodia, and a tubular-shaped structure often projecting from the posterior end. Scalibregmatids are also deposit-feeders, but compared to opheliids, they have a characteristic arenicoliform body, a T-shaped anterior end and a glandular, reticulated epidermis. For each family, we summarize the available information about the evolutionary relationships, taxonomic history, geographical distribution, ecological preferences and diversity of life strategies along with the techniques most commonly used for their study. By highlighting the main gaps in knowledge on each of these topics, this review ultimately aims at stimulating further research into members of these two families in the future.

Keywords: Opheliidae; Scalibregmatidae; diversity; taxonomy; anatomy; biology



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1. Introduction

Opheliidae Malmgren, 1867 is a well-known family of annelids distributed throughout the world mostly in sandy sediments [1–3]. Most of the described five to six genera and ca. 160 species of opheliids include elongate, deposit-feeding burrowing worms, which are easily recognized by the smooth cuticle and the presence of a conspicuous ventral groove along at least the posterior half of the body (Figure 1). Opheliids usually have a conical to pointed prostomium that lacks lateral antennae, whereas their pygidium often develops a tubular-shaped prolongation that may bear cirri and marginal papillae. Although some species may reach 100 mm in length, most opheliids range between 5–70 mm and their trunk comprise about 30–60 segments [4].

The knowledge on opheliid taxonomy and systematics has been substantially improved in the last two decades, including the delineation of subfamilies and phylogenetic affinities [1]. However, further work is still needed in order to assess the validity of the genus *Ammotrypanella* McIntosh, 1879 and some species of *Ophelia* Savigny, 1822 and *Ophelina* Örsted, 1843, as well as the status of the many synonymies attributed to the presumably cosmopolitan *Polyopthalmus pictus* (Dujardin, 1839). The opheliid fauna of some geographic areas is well known (e.g., North Atlantic, California) whereas other regions remain clearly understudied and may potentially hold many undescribed species (e.g., Tropical Atlantic, Indo-Pacific and Australasia). The biology, ecology, and burrowing behavior of some species were studied in detail due to their ecological importance in the intertidal and shallow subtidal of sandy beaches at temperate and tropical latitudes (e.g., [5–10]).

Some of these shallow water opheliids represent promising bioindicator species and have been even the target of experimental toxicological studies [11,12]. In contrast, we know virtually nothing on the biology of the opheliid species found at greater depths, despite their numerical importance in many macrofaunal assemblages in the deep-sea [13].

Traditionally, opheliid taxonomy has been based on conspicuous morphological characters, such as the number of branchiate chaetigers and different features associated to the anal tube. However, the branchiae and the anal tube are easily detached or damaged, leading to the wrong assessment of their absence or presence during species descriptions and identification and producing too much taxonomic confusion in the past (e.g., [1,2,14,15]). On the other hand, recent studies based on scanning electron microscopy (SEM) have revealed that the extended presence of lateral organs as well as a variety of nuchal organs features [1,15] may represent reliable taxonomic characters in those animals with simple bodies, reduced parapodia, and apparently similar simple chaetae. The internal anatomy of several opheliids has been studied in detail during the first half of the 20th century [16,17], when much attention was paid, for instance, to the structure of the sensory organs (e.g., [18,19]) and the arrangement of the body musculature (e.g., [20,21]). Methodological approaches such as the use of microcomputed X-ray tomography (Micro-CT) may update some of the results from these studies and provide further morphological support for the described genera (e.g., features of the digestive tract) by revealing new phylogenetically informative characters.

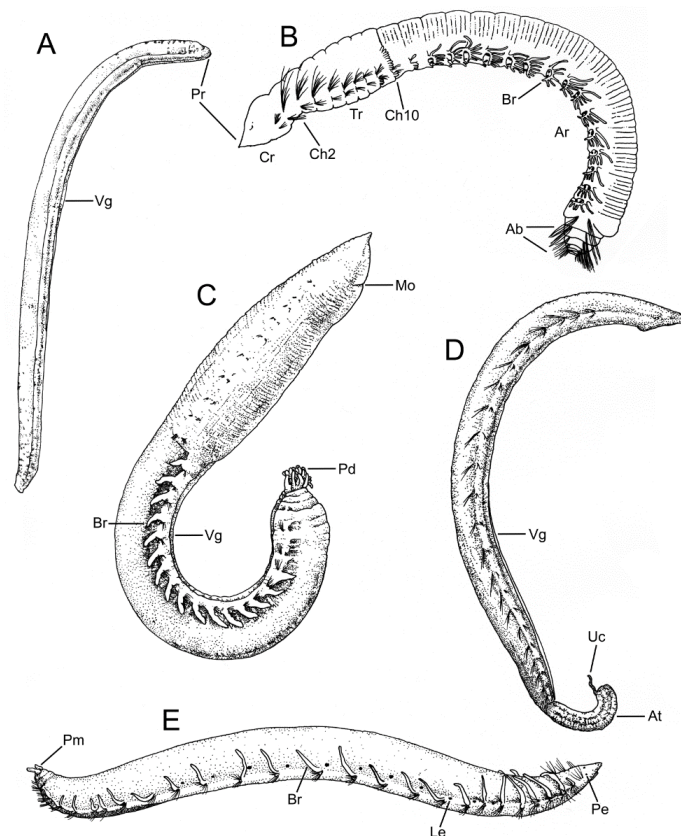


Figure 1. Stylized drawings of opheliids of the subfamily Opheliinae (B,C) and Ophelininae (A,D,E). (A) *Polyophthalmus pictus* in latero-ventral view; (B) *Thoracophelia japonica* in lateral view (chaetiger numbers mark limit between body regions); (C) *Ophelia bicornis* in lateral view; (D) *Ophelina abbranchiata* in lateral view; (E) *Armandia cirrhosa* in lateral view. (A,C–E) redrawn after Parapar [4]; (B) modified after Misaka and Sato [22]. Abbreviations: Ab—abranchiate chaetigers; Ar—abdominal region; At—anal tube; Br—branchia; Ch—chaetiger; Cr—cephalic region; Le—lateral eye; Mo—mouth; Pd—pygidium dorsal papillae; Pe—prostomial subdermal eye; Pm—pygidium marginal papillae; Pr—prostomium; Tr—thoracic region; Uc—unpaired anal cirrus; Vg—ventral groove.

Scalibregmatidae is a worldwide distributed family of sedentary annelids currently including ca. 70 described species classified in 14 genera (see below) [3,23]. Most species are subsurface deposit-feeders and prefer muddy bottoms at considerable depths or in high latitudes. Typically, they range between 5–70 mm in body length, exhibiting a vividly red pigmentation and a relatively simple external morphology [24]. Traditionally, the body shape has been categorized either as arenicoliform, i.e., more or less elongated and tapering towards the posterior end, or as maggotlike, i.e., relatively short and stout [25]. The epidermis is thick and glandular, and each trunk segment is often divided in one to six annulated rows of elevated pads that give the body a characteristic tessellate appearance. The prostomium is usually small and forms a pair of lateral or frontal prostomial appendages, which give the anterior end a characteristic T-shaped appearance. The pygidium is typically simple and possesses a variable number of cirri. However, there are several exceptions to this body plan within morphologically divergent species classified in the genera *Axiobregma*, *Speleobregma*, and *Scalibregmella* [26,27].

Scalibregmatids have been known for a relatively long period of time, and indeed, quite extensive monographs on the group were already published during the 19th and the early 20th centuries [28–30]. However, despite this early interest, the phylogenetic position of the family as well as the relationships amongst its genera remain poorly understood. This is despite the several taxonomic revisions that the family has undergone during the last few decades, notably involving the rearrangement of several genera [25,31,32] and the transference of the genus *Travisia* to the newly erected family Travisidae [33]. While most Scalibregmatidae has been described from the Northern Atlantic [34,35], the family is unusually diverse in the Antarctic Ocean, from where 16 species have been described so far [31,36,37]. Most of those Northern Atlantic and Antarctic species have been recorded from muddy bottoms, where they might become very abundant and even locally dominate the benthic community. Records of scalibregmatids in lower latitudes are scarcer but often come from a wider range of environments, including sandy bottoms, *Posidonia* and *Zostera* seagrass meadows [38], corals and sponges [25,39], mussel beds [40], or even marine and anchialine cave systems [26].

Despite that the internal anatomy of Scalibregmatidae has long been known [28,41], no recent studies have revisited these early anatomical studies using modern imaging techniques. This has hampered our understanding of both the phylogenetic position of the family as well as its internal relationships insofar as the homology of many scalibregmatid characters in relation to other annelids [36,42,43], as well as the character evolution within the group remain obscure. Consequently, both the family Scalibregmatidae as well as many of its genera are diagnosed without any synapomorphies [24,44], but rather based on combinations of few external morphological characters [23,24,30,44] whose inter- and intraspecific variability remain, in general, poorly understood. The fact that many scalibregmatids have been described from limited or fragmented material has aggravated this situation [27,40], also because many traditional characters vary substantially across life stages of the same species [26,36]. This situation can be improved integrating different microscopical techniques in future taxonomic descriptions. This approach has already been followed by recent studies, which have successfully included previously overlooked characters, such as arrangement of ciliary bands, glands, or patterns of the epidermal ornamentation, in the diagnoses of several new species [26,36].

In this contribution, an updated revision of the current biodiversity knowledge of the families Opheliidae and Scalibregmatidae is provided, and an update in taxonomy, classification, and systematics of the members of both taxa, highlighting where major gaps in knowledge lie and where future efforts could be made.

2. Methods

Published literature on opheliids and scalibregmatids was reviewed thoroughly aiming for information on diversity, ecology, and distribution. The World Register of Marine Species [3] database was mostly used as the basis for systematic arrangement, syn-

onymies and valid genera and species, as well as Blake and Maciolek [1] for Opheliidae and Blake [23] for Scalibregmatidae. Furthermore, brief accounts on systematics and general morphology of these families are also provided as well as tables with valid nominal species including type locality, depth (from original description) and marine realms (*sensu* [45]) (Tables A1 and A2 in Appendix A).

3. Results

3.1. Opheliidae Malmgren, 1867

3.1.1. Systematics

Until recently, the Opheliidae comprised three subfamilies: Opheliinae Hartman-Schröder, 1971, Ophelininae Hartman-Schröder, 1971 and Traviinae Hartmann-Schröder, 1971. The latter only included the genus *Travisia* Johnston, 1840 that differed from other opheliids in having a grublike appearance and a papillated cuticle. Indeed, recent molecular phylogenetic analyses have demonstrated the monophyly of opheliids if the Traviinae are excluded [46], subsequently motivating the establishment of Traviinae as a family by Blake and Maciolek [33]. In fact, this possibility had been already proposed by Blake [47], Bleidorn et al. [48] and Hall et al. [49]. The morphological differences between Traviinae and the other two subfamilies were further supported by Belova and Zhadan [50]. These authors suggested that the presence of several shared anatomical and ultrastructural features of the gills amongst several opheliid genera but absent in *Travisia*, might support the exclusion of the latter from Opheliidae and would constitute synapomorphies of the Opheliinae and Ophelininae. The Traviidae is now considered the sister group to the Scalibregmatidae, while molecular analyses have highlighted the affinities of opheliids to capitellids and echiuroids [51,52] and to other “sedentary” families as well (e.g., Arenicolidae). Therefore, today Opheliidae includes only the subfamilies Opheliinae and Ophelininae [1,46]. The two subfamilies are represented only by species with elongated bodies and smooth cuticle, all sharing the presence of a conspicuous ventral groove [1].

According to Blake and Maciolek [1], Opheliidae comprises five genera distributed in the subfamilies Opheliinae (*Ophelia* and *Thoracophelia* Ehlers, 1897) and Ophelininae (*Armandia* Filippi, 1861, *Ophelina* and *Polyophthalmus* Quatrefages, 1850). However, there has been much confusion with the generic arrangement within the Opheliidae (e.g., synonymies and changes in diagnosis of genera). Sene-Silva [53] performed a cladistic morphological analysis of the family that have led to a redefinition of the previously established genera. In this context, *Lobochesis* Hutchings and Murray, 1984 was synonymized with *Thoracophelia*, which subsequently replaced *Euzonus* Grube, 1866 (a homonym of the diplopod myriapod *Euzonus* Menge, 1854 [54]). According to Blake and Maciolek [1], the genera *Tachytrypane* McIntosh, 1879 and *Ammotrypanella* would fall within the current diagnosis of *Ophelina* because the presence and distribution of branchiae seemed much variable within the latter. However, *Ammotrypanella* was retained by Wiklund et al. [2] who also amended the redefinition of the genus as given by Schüller [55]. Furthermore, the abranchiate *Antibactrum* Chamberlin, 1919 is regarded as a valid genus in the World Register of Marine Species [3] but considered, in turn, as a synonym of *Ophelina* by Blake and Maciolek [1]. In this context, Paul et al. [46] have provided a phylogenetic analysis of the family but considering only a limited number of species; therefore, an analysis based on molecular and morphological characters including a greater taxa sampling would be desirable to assess the actual definition of genera.

3.1.2. Taxonomic History

The first described species was *Ophelia bicornis* Savigny, 1822. The number of newly described taxa increased gradually during the second half of the 19th century and along the first two decades of the 20th century. After WWII new species were described at a rate of about 10 per decade, whereas in the last decade (2010–2019) 30 new species were added to the family from all around the globe (Figure 2A). This overall tendency closely resembles those exhibited by each of the most speciose genera (Figure 3).

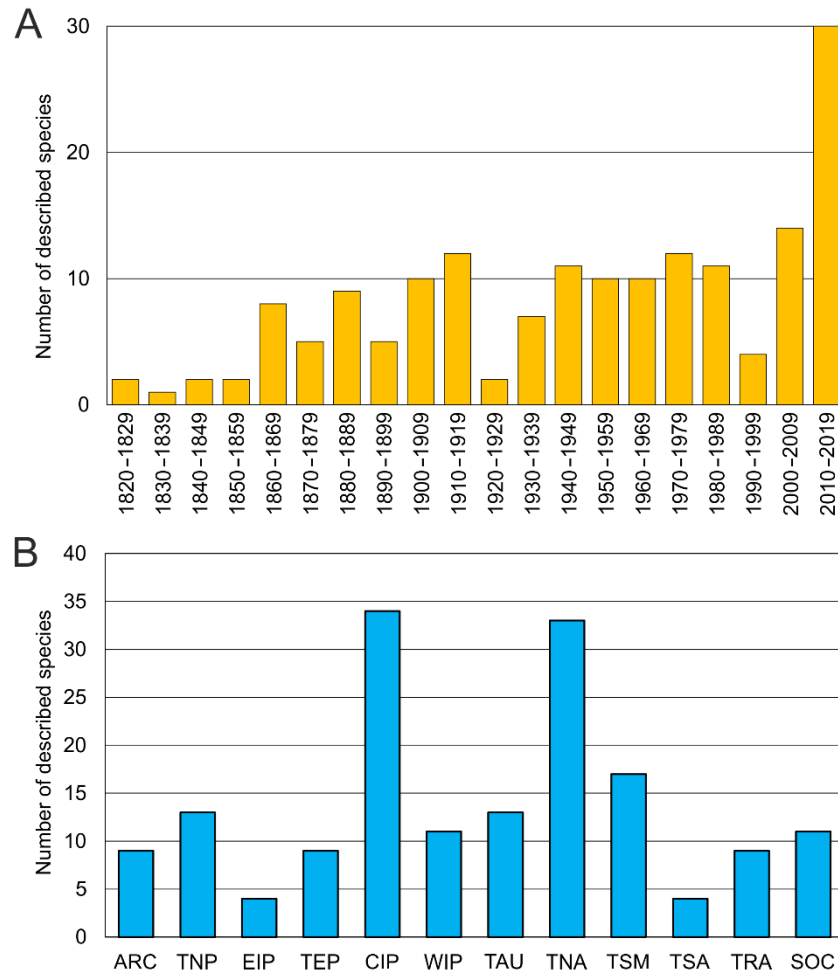


Figure 2. (A) number of opheliid species described per decade; (B) number of valid opheliid species listed under the bioregion (*sensu* Spalding et al. [45]) according to type locality. Abbreviations: ARC—Arctic; TNP—Temperate North Pacific; EIP—Eastern Indo-Pacific; TEP—Tropical Eastern Pacific; CIP—Central Indo-Pacific; WIP—Western Indo-Pacific; TAU—Temperate Australasia; TNA—Temperate Northern Atlantic; TSM—Temperate South America; TSA—Temperate South Africa; TRA—Tropical Atlantic; SOC—Southern Ocean.

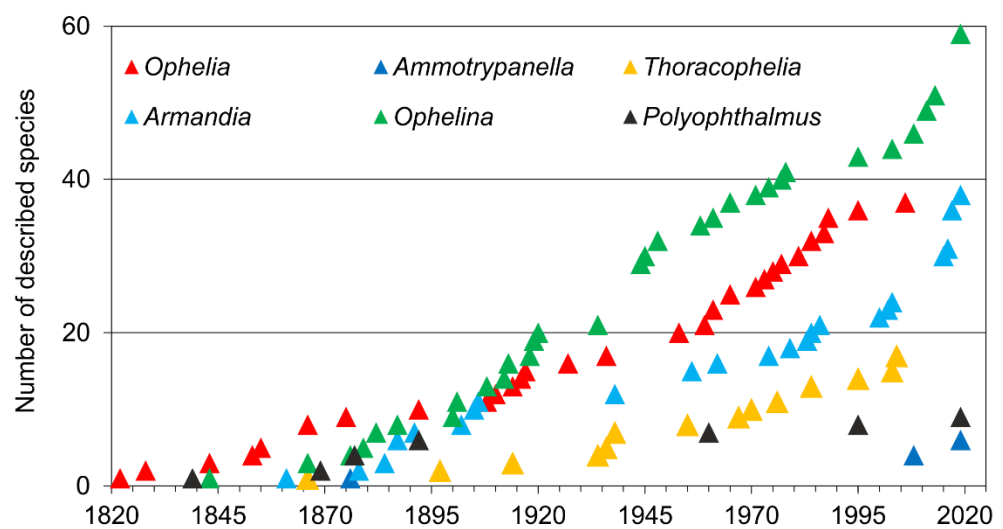


Figure 3. Number of described species (accumulated) of each opheliid genus (including *Ammotrypanella*) from 1820 to 2020.

There are a number of identification keys for Opheliidae from regions such as South Africa [56], California [47], the United Kingdom [54], and the Iberian Peninsula [4]. Some papers also provided tables that compile morphological features for species of the genus *Thoracophelia* (as *Euzonus* and *Lobochesis*; [57]), *Ophelina* from Australia [58], *Armandia* [59] and *Polyophthalmus* [60], and identification keys for *Ophelina* from NE Atlantic [61] and *Armandia* from Australasia and Central Indo-Pacific [62,63].

3.1.3. Taxonomic Characters and External Morphology

The opheliid body is usually elongated and divided into a defined number of segments, usually ranging between 30–70. The anterior end is inflated in the Opheliinae, but typically sleek and more elongate in the Ophelininae [1,4]. The trunk may be entire, as in Ophelininae (Figure 1A,D,E), or divided in two (e.g., *Ophelina*) (Figure 1C) or three regions (e.g., *Thoracophelia*) (Figure 1B). In *Thoracophelia*, the modified chaetiger 10 marks the limit between the thoracic and the abdominal region (Figure 1B). A conspicuous ventral groove is always present, but it may extend continuously throughout the trunk, as in Ophelininae (Figure 1A,D and Figure 4B,H,I), or be restricted to its posterior half, as in Opheliinae (Figure 1C). Some species present two additional longitudinal lateral grooves, one on each side of the body (Figure 4H). Paired lateral branchiae attached dorsally to the parapodia are present in many species, either along the entire trunk or limited to its posterior 1/2–2/3 portion. Branchiae are always absent in last few chaetigers (Figure 1B,E, Figure 4I,J and Figure 5A,C,H). Branchiae are bifurcate or pectinate in some *Thoracophelia*, but simple and cirriform in the remaining genera (Figure 1B).

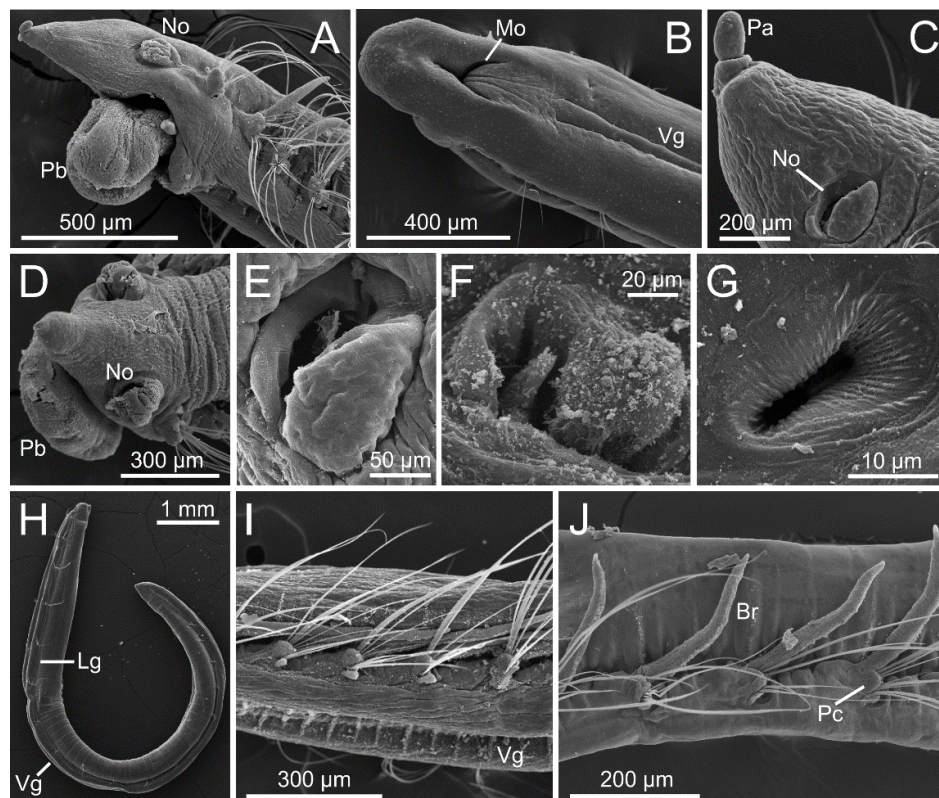


Figure 4. SEM micrographs of several Opheliidae showing main diagnostic characters. (A) *Ophelina breviata*, anterior end in lateral view, showing pointed prostomium; (B) *Polyophthalmus pictus*, anterior end in ventral view, showing the distally rounded prostomium; (C) *Ophelina helgolandiae*, anterior end in lateral view; (D) *O. breviata*, anterior end in dorsal view; (E) *O. helgolandiae*, nuchal organ; (F) *Armandia buccina*, nuchal organ; (G) *Ophelina abranchiata*, nuchal organ; (H) *O. abranchiata* in lateral view; (I) *A. buccina*, anterior chaetigers in lateral view; (J) *Armandia opisthoculata*, mid-body chaetigers in lateral view. Abbreviations: Br—branchia; Lg—lateral groove; Mo—mouth; No—nuchal organ; Pa—palpode; Pb—proboscis; Pc—prechaetal lobe; Vg—ventral groove.

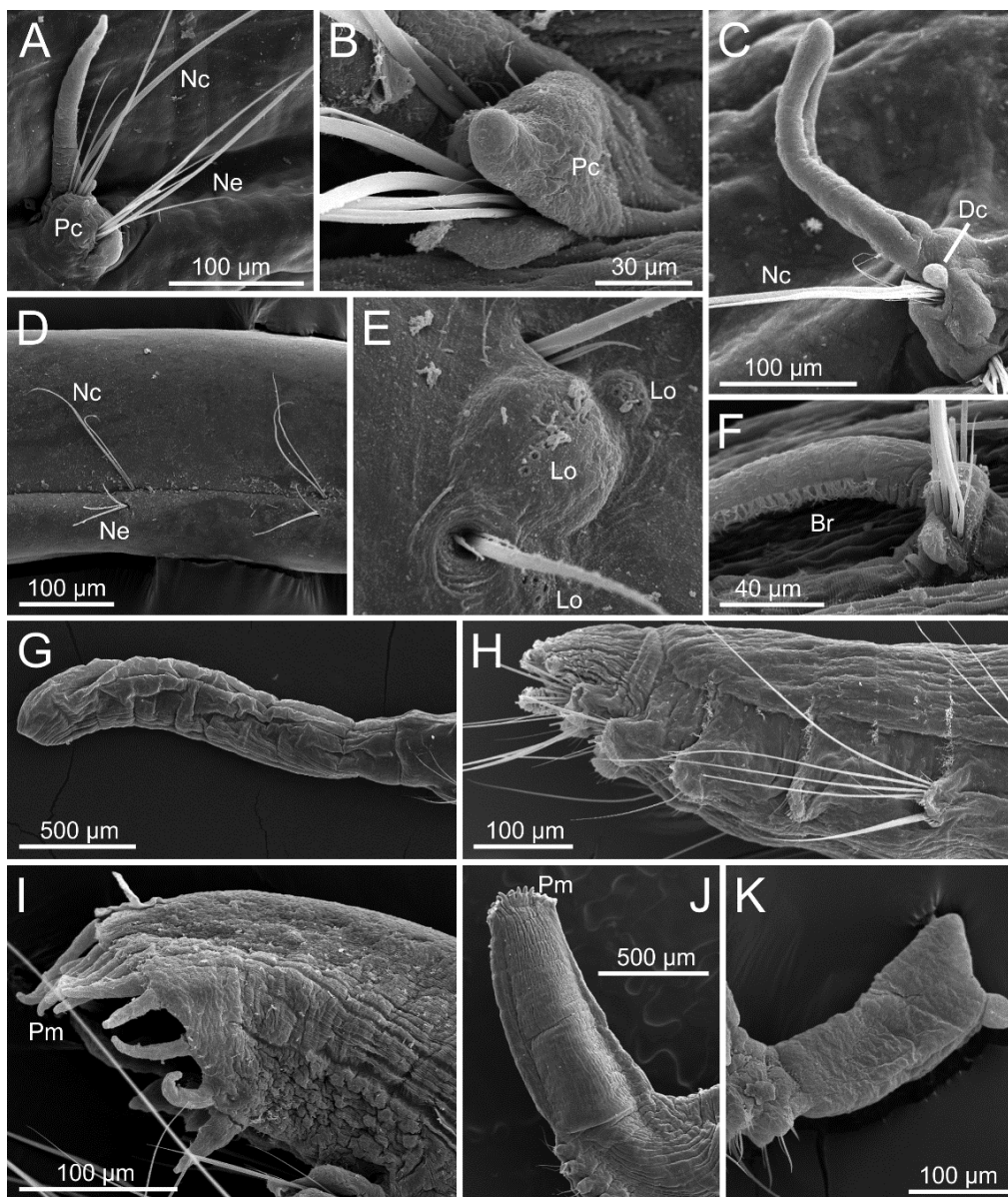


Figure 5. SEM micrographs of several Opheliidae showing main diagnostic characters. (A) *Ophelina basicirra*, parapodium and branchia; (B) *Armandia laminosa*, parapodium; (C) *Ophelina helgolandiae*, parapodium and branchia; (D) *Ophelina abranchiata*, mid-body parapodia; (E) *Polyophthalmus pictus*, lateral organs; (F) *Armandia paraintermedia*, parapodium and branchia; (G) *O. abranchiata*, anal tube in lateral view; (H) *Armandia parva*, posterior end in lateral view; (I) *Armandia tubulata*, anal tube in lateral view; (J) *Ophelina bowitzi*, anal tube in lateral view; (K) *Ophelina cylindricaudata*, anal tube in lateral view. Abbreviations: Br—branchia; Dc—“dorsal cirrus”; Lo—lateral organs; Nc—notochaetae; Ne—neurochaetae; Pc—prechaetal lobe; Pm—pygidium marginal papillae.

The prostomium is elongated, tapered, or conical in most species (Figure 4A,C), but rounded in *Polyophthalmus* (Figure 4B). It lacks lateral appendages, but a terminal palpode (sometimes biarticulated) is present in *Armandia* and several *Ophelina* species (Figure 4A,C). The proboscis is often an axial, nonmuscular eversible structure (Figure 4A,D and Figure 6A,B), but it might consist of several retractable ciliated tentacles in some species of *Armandia* [63,64]. Nuchal organs are eversible and represented by one pair of conspicuous ciliated pits/slits of various shapes depending on the species [65] (Figure 4A,C–G). Exceptionally, two pairs of nuchal organs are present in *Polyophthalmus* spp. and *Armandia polyophthalma* Kükenthal, 1887 (see [65]), often slightly pigmented [2]. Subdermal pigmented eyes (two to three) are present in several species [66] (Figure 1E); these simple eyes are present in larvae

and may be retained in the adult [67]. Additional pairs of segmentally arranged pigmented eyes are present in *Armandia* and *Polyophthalmus*, at least on several midbody segments (Figure 1E).

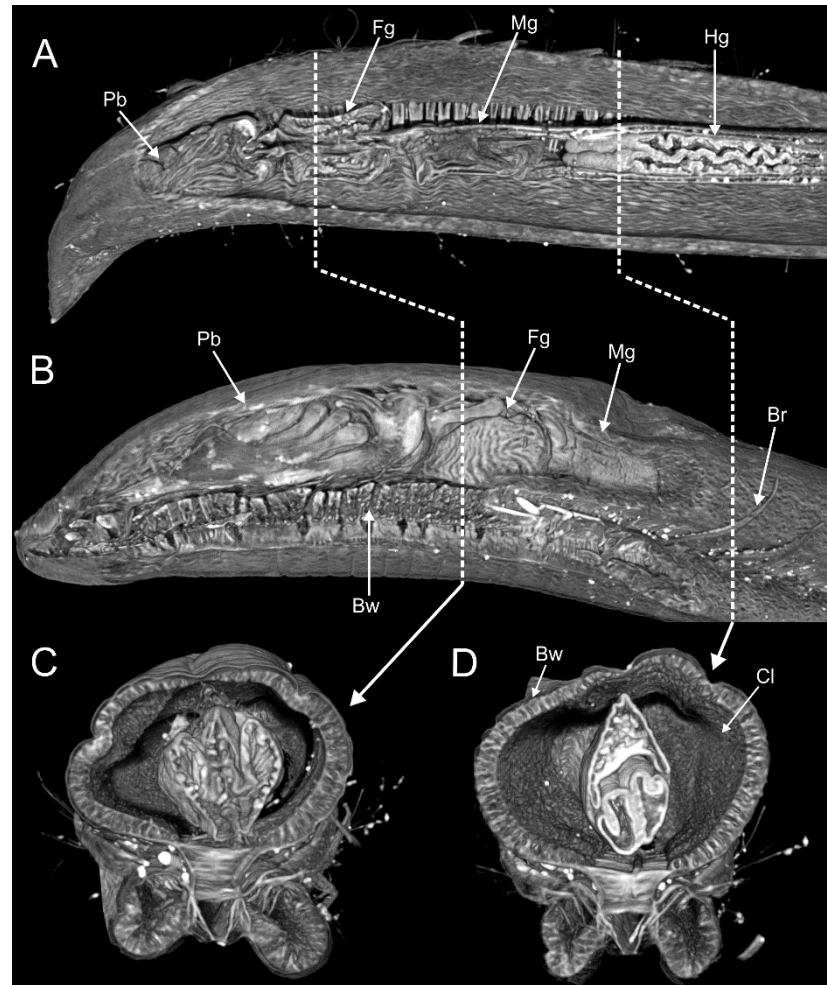


Figure 6. Microcomputed tomography (μ CT) sections of *Ophelina acuminata* from Iceland. (A) frontal, (B) right sagittal and (C,D) transversal body sections showing internal anatomy. White discontinuous lines in (A,B) marking regions showed in (C,D). Abbreviations. Br—branchia; Bw—body wall musculature; Cl—coelomic space; Fg—foregut; Hg—hindgut; Mg—midgut; Pb—proboscis.

Parapodia are biramous and consist of small lobes or tori provided with simple capillary chaetae (Figure 4I,J and Figure 5A–F). A ventral cirrus is present and a small spherical projection may be also found dorsally on the prechaetal lobe in *Armandia* (termed as “dorsal cirrus”: [15,62]; Figure 5C). Parapodial ciliated sensory organs were reported on the prechaetal lobe in several species of *Armandia* [62]. Lateral organs are usually present as ciliated pits in between noto- and neuropodia and may also occur in the anterior achaetous segments [15] (Figure 5E).

The last segments may be achaetous and are often retractile. The pygidium typically prolongs into a tubular funnellike structure (termed anal cone, funnel, or tube) that may be quite long in comparison to body length in some species of Ophelininae (Figures 1D and 5G–K). The shape of the funnel, as well as the presence of accessory structures, such as dorsal/marginal papillae and unpaired/paired cirri, diagnoses few genera and species (Figure 1C–E and Figure 5G–K).

Most opheliids have a relatively simple body, reduced parapodia, and simple chaetae. Therefore, the taxonomy of the family has traditionally relied on the limited number of available external characters. This is particularly evident among *Polyophthalmus*, a

genus in which most described species are nearly identical morphologically (e.g., [19]). Opheliid genera are defined according to whether the body is divided in distinct regions or not, the extension of the ventral groove, as well as the presence of branchiae and lateral eyes. Species are instead diagnosed based on several parapodial features (e.g., shape of prechaetal lobe, ventral cirrus and presence of “dorsal cirrus”, relative length of chaetae across body), the number of lateral eyes (if present), the length of the branchiae, as well as the number of branchiate segments and pygidial cirri. Features of the anal tube are mainly relevant to identify species of Ophelininae, and include its shape, length relative to last chaetigers, number and shape of marginal anal cirri/papillae, as well as presence, shape, and position of the unpaired ventral cirrus and the paired basal cirri [58]. Unfortunately, the fact that branchiae and anal tube are easily detached has generated much confusion regarding the taxonomic status and identifications of some opheliid taxa (e.g., [2]). The many species described based on single/damaged specimens have contributed to worsen the situation [58], together with the lack of information on the intraspecific variation exhibited by some characters, such as number and presence of lateral eyes and anal tube papillae, which may change through different ontogenetic stages in the same species [66]. Examination of a sufficient number of specimens of several sizes is therefore crucial to alleviate this situation in the future [2,58,66].

Parapar et al. [15] suggested that features of nuchal and lateral organs might represent useful characters to diagnose species in the future, in spite that the latter, for instance, can be easily overlooked or is difficult to examine due to state of preservation [2]. In this context, the use of SEM for examination of properly fixed specimens seems mandatory to fully assess features of parapodia, as well as nuchal and lateral organs (e.g., [2,58,60,62,63,68]).

3.1.4. Internal Morphology

The internal anatomy of opheliids has been studied mostly in several intertidal species [16,17,69], including later detailed accounts on the structure of the proboscis [64], body musculature [20,21], respiratory system [50], and sensory organs (see below).

Opheliids lack circular muscle fibers, but they possess bands of longitudinal muscles protruding along the body surface [20], as well as oblique muscles that insert into the midventral line thereby contributing to shape the typical opheliid ventral groove. The structure of the proboscis varies greatly among taxa, corresponding to several of the types described by Tzetlin and Zhadan [64]: type 1, symmetrical, bubblelike, and ciliated as found in the Opheliinae; type 3, asymmetrical, dorsal-lobed (e.g., *Ophelina*, *Polyophthalmus*); type 4, formed instead by several retractable ciliated tentacles (some species of *Armandia*). Exceptionally, the proboscis of *Armandia amukusaensis* Saito, Tamaki and Imajima, 2000 has been reported as flanked by several “filaments” [66]. The digestive tract, and particularly the intestine, might be regionalized in certain species [70] (Figure 6).

The circulatory system is closed [17]. Gills appear as body wall protrusions containing coelom or vessels connected to blood sinuses [50]. Metanephridia are present in several species [71], although protonephridia have been reported in *Thoracophelia mucronata* (Treadwell, 1914) by McConnaughey and Fox [17]. The ultrastructure of sensory organs has been described thoroughly in several opheliids, including the nuchal organs in *Ophelia bicornis* [72] and *Ophelia rathkei* McIntosh, 1908 [65]), the subdermal eyes in *Armandia brevis* (Moore, 1906) [18] and the juveniles of *O. rathkei* [67], as well as the lateral eyes in *A. brevis* [73], *P. pictus*, and *Polyophthalmus qingdaoensis* Purschke, Ding and Müller, 1995 [19].

In this sense, the consistent differences in the ultrastructure of lateral eyes in *Polyophthalmus* (e.g., size and number of cells, number, and dimensions of cellular elements) seem also useful to distinguish species [19]. Thus, future ultrastructural studies might provide phylogenetically informative morphological characters, perhaps further illuminating the delineation of genera. In the same line, the use of micro-CT seems a promising source for phylogenetically informative characters insofar as it offers a comparatively easy overview of the internal anatomy and produces a minimum damage to the examined specimen (e.g., [74]) (Figure 6). It therefore represents a useful tool to compare, for instance, the

regionalization of the digestive tract as well as the organization of the circulatory system across genera and/or species.

3.1.5. Species Diversity and Distribution

The most speciose genera are *Ophelina* (about 59 species, excluding *Ammotrypanella*), *Armandia* (38) and *Ophelia* (37); *Thoracophelia* comprises 17 species. Depending on the sources, *Polyophthalmus* is composed of four [3] to nine [60] species, highlighting the need for further morphological and molecular work in order to assess its actual diversity as well as a fully review the synonyms and material attributed worldwide to *Polyophthalmus pictus* [4,60]. Finally, six species are classified into *Ammotrypanella* by those authors who consider the genus as valid [2,15,55].

Opheliids have been reported or described from the poles to the equator across all the 12 marine ecoregion realms defined by Spalding et al. [45] (Figure 2B). Similar distribution patterns are found in the genera *Armandia*, *Ophelia*, and *Ophelina*; whereas *Thoracophelia* is mostly restricted to the temperate realms (14 out of 17 species). Many opheliid species have been described from Temperate Northern Atlantic and Central Indo-Pacific (33 and 34, respectively) in comparison to other regions (ranging from 4 to 17). The type localities of half of the known species of *Ophelia* (16) are in the Temperate Northern Atlantic and about one third of each *Armandia* and *Ophelina* are found in the Central Indo-Pacific. These numbers, however, may be explained by the greater sampling effort historically performed in those areas and the subsequent more detailed knowledge that we have on their annelid faunas of the NW and NE Atlantic, California, and some areas of the Pacific Ocean [47,75]. Indeed, recent work done in unexplored Pacific areas has yielded many new taxa. For instance, Magalhães et al. [60] have described five new species from several western Pacific islands and Wiklund et al. [2] eight new species of *Ammotrypanella* and *Ophelina* plus other still formally undescribed taxa from the eastern Clarion-Clipperton Zone (central Pacific). Furthermore, Parapar and Moreira [62] and Moreira and Parapar [63] have described eleven new species of *Armandia* from Lizard Island (Great Barrier Reef) whereas only two valid species of this genus are present in the comparatively better-known Western Europe. These findings suggest that the actual diversity in other temperate and tropical regions may be greater, including other Pacific areas as well as Temperate Australia (only 13 species described so far) and Tropical Atlantic (nine species).

A wide geographic distribution has been reported for species such as *P. pictus*, *Armandia intermedia* Fauvel, 1902, *Ophelina acuminata* Örsted, 1843 and *O. abbranchiata* Støp-Bowitz, 1948. However, these taxa might represent complex of cryptic species as suggested by recent molecular analyses of several populations previously attributed to *O. abbranchiata* [2,76]. On the contrary, many taxa have not been reported after original description thus making it difficult to assess their distribution patterns. Finally, reports of species far away from their type locality should be considered with caution because of the lack of knowledge of local faunas (see [60]).

3.1.6. Biology and Ecology

Most *Ophelia* species inhabit clean sandy sediments from the intertidal fringe to the shallow subtidal down to depths of about 100 m [75]. The exception is *Ophelia profunda* Hartman, 1965 and *Ophelia pulchella* Tebble, 1953 that prefer, in turn, muddy bottoms; the former being reported down to 1700 m depth. Species of *Armandia*, *Polyophthalmus*, and *Thoracophelia* prefer coastal areas, the only remarkable exception being *Thoracophelia profunda* (Hartman, 1967) (4000 m). *Polyophthalmus translucens* Hartman, 1960 has been reported at depths of 900 m but Sene-Silva [53] suggested that this species may correspond to the genus *Ophelina*. Indeed, *Ophelina* shows a wider range of ecological preferences, with some species restricted to intertidal-shallow depths while others show wide bathymetric ranges (subtidal/shelf depths down to 2000–3000 m), or, alternatively, are limited to the deep-sea (at depths below 1000 m). *Ammotrypanella* species are distributed at depths below 400 m, more than reaching the abyssal realm.

The majority of opheliids burrow in coarse to fine sand or in muddy sediments. Ecology of several intertidal species of *Armandia*, *Ophelia*, and *Thoracophelia* have been extensively studied when compared to deep-sea species [13]. Some opheliids such as *Thoracophelia furcifera* Ehlers, 1897 and *T. mucronata* may reach high abundances in the intertidal of sandy beaches (2000–40,000 individuals per m² [8,17]). Spatial variations in abundance have been related to beach morphodynamics, granulometry, and organic content (e.g., [10]). Experimental work has suggested that the abundance of *A. brevis* is correlated negatively with proliferation of tube-building infaunal species [77]. In general, opheliids are found within well-oxygenated sediments but some *Ophelina* species thrive in muddy sediments with low oxygen content [50] or a high concentration of heavy metals [58]. On the other hand, *P. pictus* usually dwells among intertidal algae, reaching densities that surpass 5000 ind. per m² in *Cystoseira* mats where is also present all the year round [78]; *Polyophthalmus* is also found among fouling communities in artificial habitats [79].

Opheliids show two strategies to burrow into the sediment, i.e., peristalsis based on oblique muscular fibers acting in conjunction with cuticular fibers (e.g., *Thoracophelia*) resulting in a dual anchor burrowing mechanism [9,21] or, rather, by undulatory movements (e.g., *Armandia*). Regarding the latter, *A. brevis* lacks circular musculature and therefore relies on bands of oblique muscles that act antagonistically to longitudinal muscles. This muscular arrangement allows for lateral bending and undulating movements that rearrange the sediment grains around by creating a burrow [80]. *Armandia brevis* and other Ophelininae species display a similar pattern of movement when swimming in water; while there is no report of such behavior in Opheliinae.

These burrowing abilities facilitate the migration of intertidal species of *Thoracophelia* downwards or upwards into the sediment to cope with wave turbulence or avoid of low levels of oxygen in the interstitial water [81]. *Thoracophelia* is also capable to migrate horizontally seaward or landward into the sediment in response to changing beach morphodynamics in high-energy environments [7]. Vertical migration in *Ophelia* has also been related to the release of gametes/eggs near the sediment surface [82] or to the avoidance of interspecific competition [83]. Tamaki [84] reports that specimens of *Armandia* sp. migrate in offshore direction as they grow. Giangrande et al. [10] has suggested that the spatial migration in *Ophelia barquii* Fauvel, 1927, from the upper intertidal to upper infralittoral zones, may occur as a response to seasonal changes in hydrodynamics. Because of their burrowing activity, opheliids are important agents in sediment bioturbation [6].

Opheliids are nonselective deposit-feeders by swallowing sediment with the everted proboscis [85]. Feeding behavior has been studied in several species of *Ophelia*, *Ophelina*, and *Thoracophelia*; intertidal and shallow-water species show high ingestion rates [86]. On the contrary, *P. pictus* has been suggested to be a selective feeder [87].

In general, opheliids are mostly dioecious and synchronously release large amounts of gametes or eggs [88]. Life cycle and reproduction of several *Ophelia* species has been studied in North Atlantic and the Mediterranean. Life span extends from one to six years and reproduction occurs from spring to autumn. In general, species breed once a year. On the other hand, adults of *A. brevis* and *P. pictus* experience an epitokous planktonic phase in which they swimming into water to release their gametes [89,90]. Presence of similar epitokous phases has also been suggested for *A. polyophthalma* at least in aquarium conditions. Epitokous specimens show longer chaetae on the posterior five chaetigers that are in turn slightly compressed laterally [90].

Larvae might go through a short lecithotrophic planktonic stage of 4–12 days [5,10,82] or a longer planktonic life thus allowing for a greater dispersal ability (e.g., *A. brevis*; [89,91]). Larvae of *Ophelia*, *Thoracophelia*, *Armandia cirrhosa* Filippi, 1861, and *A. polyophthalma* consist only of two to five chaetigers right before settlement whereas those of *A. brevis* may have up to 20 segments [87,89,90,92,93]. Miner et al. [91] described the feeding mechanisms of the larvae of *A. brevis* that includes action by ciliary bands and direct ingestion with the mouth. After this pelagic phase, the larva settles on the substrate and the body enlarges to become a juvenile worm. Wilson [94] has demonstrated, after several experiments that the

settlement of *O. bicornis* larvae is conditioned by the presence of bacteria in the sand grains rather than by the grain size itself.

Polyopthalmus pictus is among the few polychaetes unable to regenerate body segments although it may show wound healing of posterior segments [95].

Deep-sea opheliids are known to be the hosts of two parasitic cyclopoid copepod species of the genus *Ophelicola* [96]. Opheliids are also consumed by several fishes and crabs; for example, *Ophelia limacina* (Rathke, 1843) has been found in the digestive tract of demersal fishes [97] and *P. pictus* in *Trachurus mediterraneus* (Steindachner, 1868) [98]. Kicklighter and Hay [99] also suggested that *A. agilis* may have some chemical deterrents that make it unpalatable for some fishes.

Some opheliids have been the subject of a number of ecotoxicological studies by exposing them in experimental conditions to contaminants (e.g., heavy metals) or antifouling compounds (e.g., tributyltin) in sediments. For instance, *O. bicornis* has been demonstrated to be sensitive to cadmium [12] whereas the exposition of *A. brevis* to TBT resulted in changes in body growth rates [11]. *Armandia agilis* (Andrews, 1891) has been suggested as an appropriate target species to discriminate between clean and contaminated sediments [100] and *Armandia cyprophilia* Neave and Glasby, 2013 is abundant in sediments with high concentrations of copper in otherwise depauperated polychaete assemblages [58]. Therefore, the use of opheliids as indicators of marine pollution seems a promising field of study.

3.2. Scalibregmatidae Malmgren, 1867

3.2.1. Systematics

The first described scalibregmatid was *Scalibregma inflatum* Rathke, 1843 [30], originally classified as an allied to the genus *Arenicola* Lamarck, 1801 [24], until Malmgren [101] established the family Scalibregmatidae in 1867. Later classifications considered Scalibregmatidae as part of the suborder Opheliida [97,102]. This placement was congruent with the results of subsequent morphological analyses, which nested Scalibregmatidae within the clade Scolecida as sister group of Opheliidae, although without any synapomorphy [44]. In contrast, molecular data have more frequently favored a sister-group relationship between Scalibregmatidae and Arenicolidae, often including the genus *Travisia* Johnston, 1840 [46,103], nowadays classified as a separated family [23]. However, the placement of Scalibregmatidae must be considered unresolved, as those analyses were limited to few molecular markers and did not include morphological information. Despite phylogenomic information is available for at least one species in the family [104], Scalibregmatidae has never been included in broad phylogenomic analyses [105].

Scalibregmatidae comprises about 68 described species and 14 valid genera [23]. However, there has been much confusion regarding the species composition of several of them, hampered by the fact that many scalibregmatid species have been described based on incomplete specimens or limited material [27,40]. Scalibregmatids have been traditionally categorized as arenicoliform or maggotlike depending on their overall body shape, although without assigning to these groups any systematic value. Arenicoliform species are typically elongated, inflated in the anterior end, and tapering towards the pygidium; whereas maggotlike species are shorter and stouter [31]. This distinction has been progressively abandoned partly because we know that these differences often rely on preservation artefacts and post mortem contraction; but mostly because intermediate forms also exist and this character even changes during the development of certain species [26,36].

There have been no attempts to resolve the internal relationships of Scalibregmatidae apart from few studies aiming at placing a few specific taxa [2,26,46,103], so the character evolution within the group remains unknown [43].

3.2.2. Taxonomic History

The study of Scalibregmatidae received a notable attention during the 19th century. By the beginning of the 20th century, many common European species were already de-

scribed [30,106–110] including also a few species from Australia [111], New Zealand [112], Cuba [113], and South Africa [111] (Table A2). This level of attention did not decline during the 20th century, when new species of Scalibregmatidae were described nearly every decade (Figures 7A and 8).

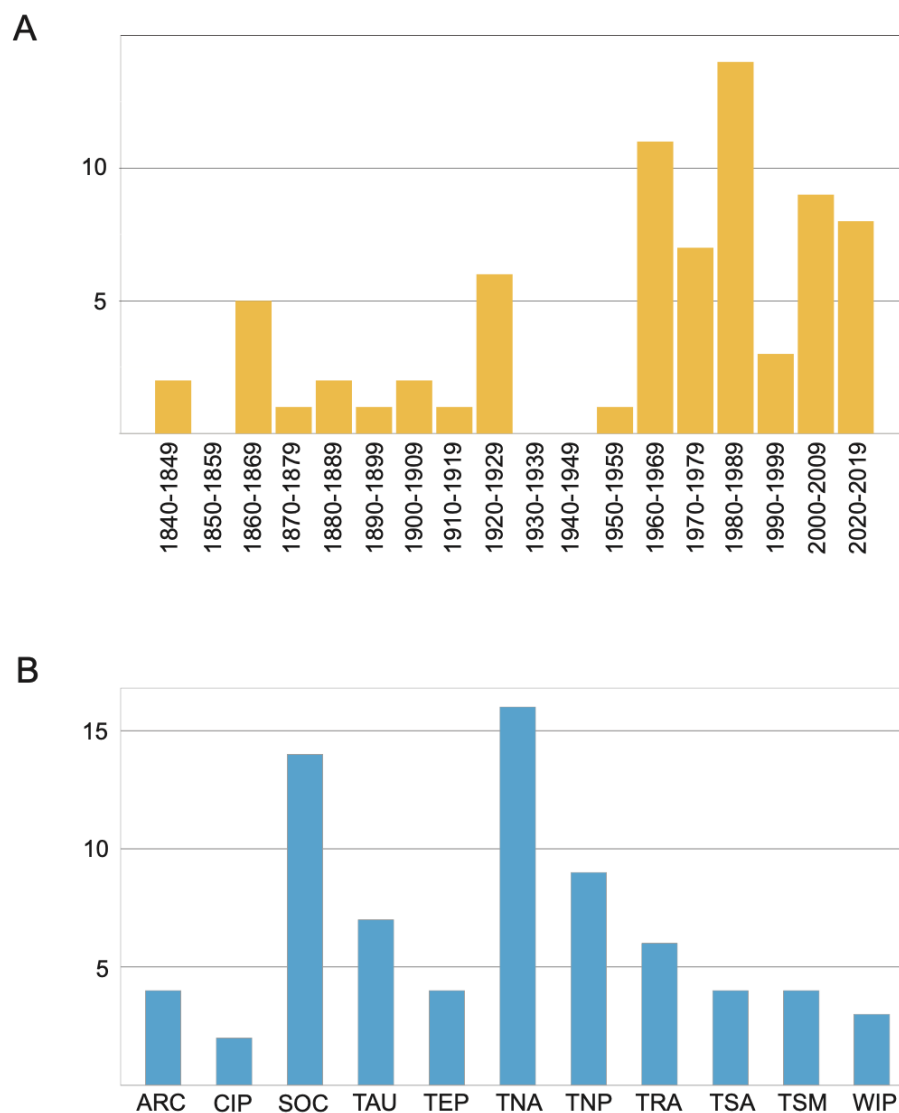


Figure 7. (A) number of scalibregmatid species described per decade; (B) number of valid scalibregmatid species listed under the bioregion (*sensu* Spalding et al. [45]) according to type locality. Abbreviations: ARC—Arctic; CIP—Central Indo-Pacific; SOC—Southern Ocean; TAU—Temperate Australasia; TEP—Tropical Eastern Pacific; TNA—Temperate Northern Atlantic; TNP—Temperate North Pacific; TRA—Tropical Atlantic; TSA—Temperate South Africa; TSM—Temperate South America; WIP—Western Indo-Pacific.

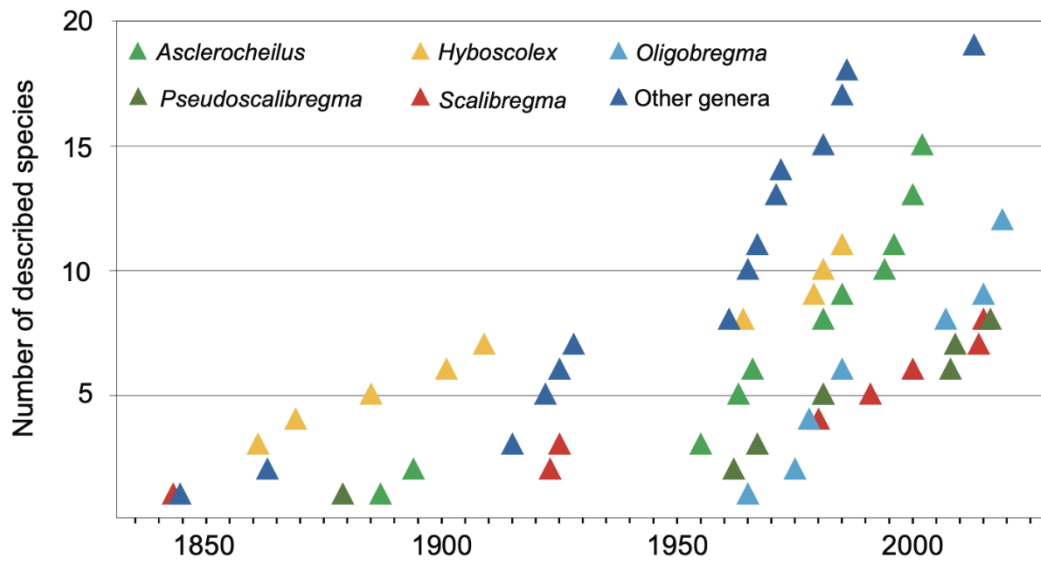


Figure 8. Number of described species (accumulated) of the main scalibregmatid genera from 1820 to 2020. Genera with less than five described species have been grouped under “Other genera”.

The first major revision for the family was published in 1925 [114], followed by the work by Kudenov and Blake [38], Kudenov [25] and Blake [31,36,47]. There have also been important works focused on individual genera, such as *Axiobregma* Pocklington and Fournier, 1987 [26,61], *Oligobregma* Kudenov and Blake, 1978 [37], and *Scalibregma* [35,36]. The status of the systematics of the family has been recently reviewed by Blake [23], who has summarized and amended the diagnoses of all the currently valid genera.

3.2.3. Taxonomic Characters and External Morphology

Members of Scalibregmatidae are relatively large annelids with few taxonomically informative characters. The prostomium is generally rounded or triangular, lacking antennae but often bearing a pair of lateral or frontal extensions, whose homology with palps remains unclear [43] (Figures 9 and 10B–E). Due to the presence of these structures, the prostomium has been often described as T-shaped [see 23]. Prostomial extensions are well developed in the species of *Axiobregma* and *Speleobregma* Bertelsen, 1983, where they are separated from the prostomium by a basal furrow and bear longitudinal bands of motile ciliary bands capable of producing water currents (Figure 10D,E) [26]. Prostomial appendages are also long in the enigmatic *Scalibregma antennata* Hartman and Fauchald, 1971, only known from its original collection off New England at 4800–5000 m depth [27], although the presence and arrangement of ciliary bands remain unknown (Figure 9G). In contrast, in the species of the genera *Asclerocheilus* Ashworth, 1901, *Oligobregma*, *Scalibregma*, and *Sclerobregma* Hartman, 1965 prostomial appendages consist of stiff hornlike prolongations, lacking ciliation and a basal furrow (Figure 9A,B) [31]. Despite these morphological differences, the fact that prostomial appendages follow a similar development in all investigated scalibregmatids suggests their homology across the family [26,36]. Epidermal eyes are sometimes present as simple ocelli (Figure 9F) or more complex structures composed of multiple ocelli (Figure 9B). Nuchal organs are usually small and often found retracted into grooves that extend transversally between the prostomium and the peristomium (Figure 10B,E). When they are everted, they resemble expanded bulbous vesicles [23]. Nuchal organs are associated with additional transverse bands of motile cilia in *Axiobregma cavernicola* Martínez, Di Domenico and Worsaae, 2013 and *Speleobregma lanzaroteum* Bertelsen, 1983 [26] (Figure 9G, Figure 10D,E and Figure 11D).

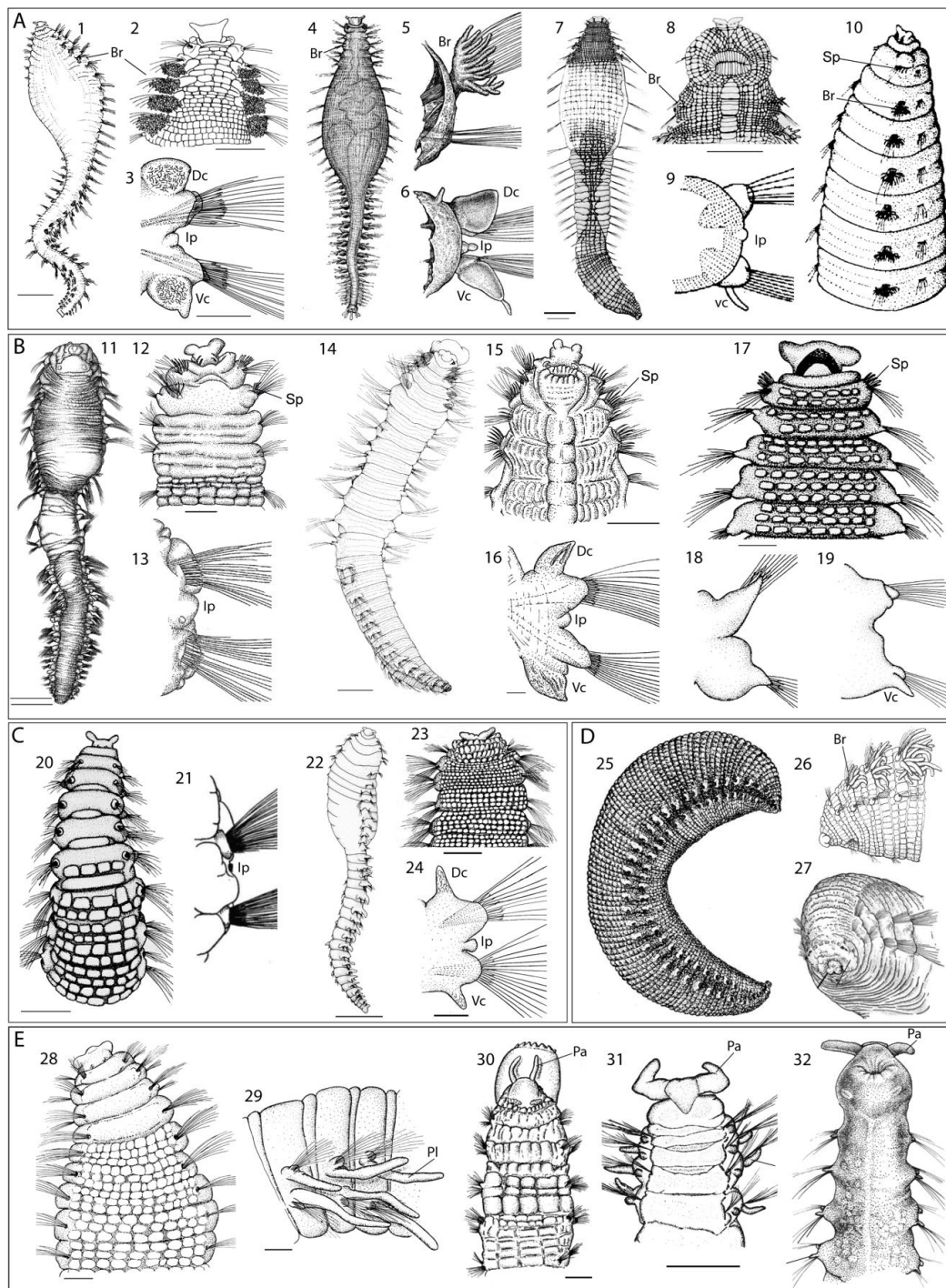


Figure 9. Stylized drawings showing the main taxonomic characters of different genera in Scalibregmatidae, artificially grouped according to the most conspicuous external traits. (A) Arenicoliform scalibregmatid genera with branchiae; genus *Scalibregma*, (1) *S. hanseni*, dorsal view, (2) *S. inflatum*, anterior end in dorsal view, (3) *S. hanseni*, left parapodium of chaetiger 21 in posterior view; genus *Sclerobregma*, (4) *S. branchiatum*, dorsal view, (5) chaetiger 3 in posterior view and (6) abdominal parapodium in anterior view; genus *Cryptosclerocheilus*, (7) *C. baffinensis*, dorsal view, (8) anterior end in ventral view; genus *Parasclerocheilus*, (9) *P. capensis*, chaetiger 40 and (10) anterior end in lateral view. (B) Arenicoliform scalibregmatids genera without branchiae and with spines; genus *Asclerocheilus*, (11) *A. tasmaniensis*, dorsal view, (12) *A. kudenovi*, anterior end dorsal view, (13) *A. beringianus*, chaetiger 15 in anterior view; genus *Oligobregma* (14) *O. quadrispinosa*, anterior view, (15) *O. mucronata*, anterior end in ventral view, (16) and posterior parapodium in anterior view; genus *Sclerocheilus*, (17) *S. unoculus*, anterior end in dorsal view, (18) chaetiger 16 in posterior view, and (19) chaetiger 29 in posterior view. (C) Arenicoliform scalibregmatid genera without branchiae and spines; genus *Hyboscolex*, (20) *H. quadricincta*, anterior end in dorsal view, (21) chaetiger 29 in posterior view. (D) *Hyboscolex*, (25) *H. quadricincta*, anterior end in dorsal view, (26) *H. quadricincta*, anterior end in ventral view, (27) *H. quadricincta*, anterior end in lateral view. (E) *Hyboscolex*, (28) *H. quadricincta*, anterior end in dorsal view, (29) *H. quadricincta*, anterior end in ventral view, (30) *H. quadricincta*, anterior end in lateral view, (31) *H. quadricincta*, anterior end in ventral view, (32) *H. quadricincta*, anterior end in lateral view.

H. pacificus, median parapodium in anterior view; genus *Pseudoscalibregma*, (22) *P. papilia*, dorsal view, (23) *P. usarpium*, anterior end in dorsal view, (24) *P. hartmanae*, posterior chaetigers in anterior view. (D) Maggotlike scalibregmatids genera; genus *Polyphysia*, (25) *P. crassa*, lateral view and (26) anterior end in anterior view; genus *Lipobranchius*, (27), *L. jeffreysi*, frontal view. (E) Morphologically divergent genera; genus *Scalibregmides*, (28) *S. peruanus*, anterior end in dorsal view, (29) *S. chilensis*; genus *Scalibregmella*, (30) *S. antennata*, anterior end in dorsal view; genus *Speleobregma*, (31) *S. lanzaroteum*, anterior end in dorsal view; genus *Axiokebuita*, (32) *A. minuta*, anterior end in ventral view. Abbreviations: Br—branchiae; Dc—dorsal cirri; Ip—interramal papillae or ciliation; Pa—prostomial appendages; Pl—parapodial lobe; Sp—spines; Vc—ventral cirri. Modified from (1,3) Bakken et al. [35]; (2) Mackie [34], (4–6) Hartman [115], (7–8) Blake [116], (9–10) Day, [117], (11) Kirkegaard [118], (12) Blake [119], (13) Imajima [120], (14) Schüller and Hilbig [37], (15–16) Blake [36], (17–20) Kudenov [25], (21) Imajima [121], (22) Schüller [55], (23–24, 28–29) Blake [31], (25) Støp-Bowitz, [122], (26) Hartmann-Schröder [97], (27) Wesenberg-Lund [123], (30) Blake [23], (31) Bertelsen [124], (32) Parapar et al. [61].

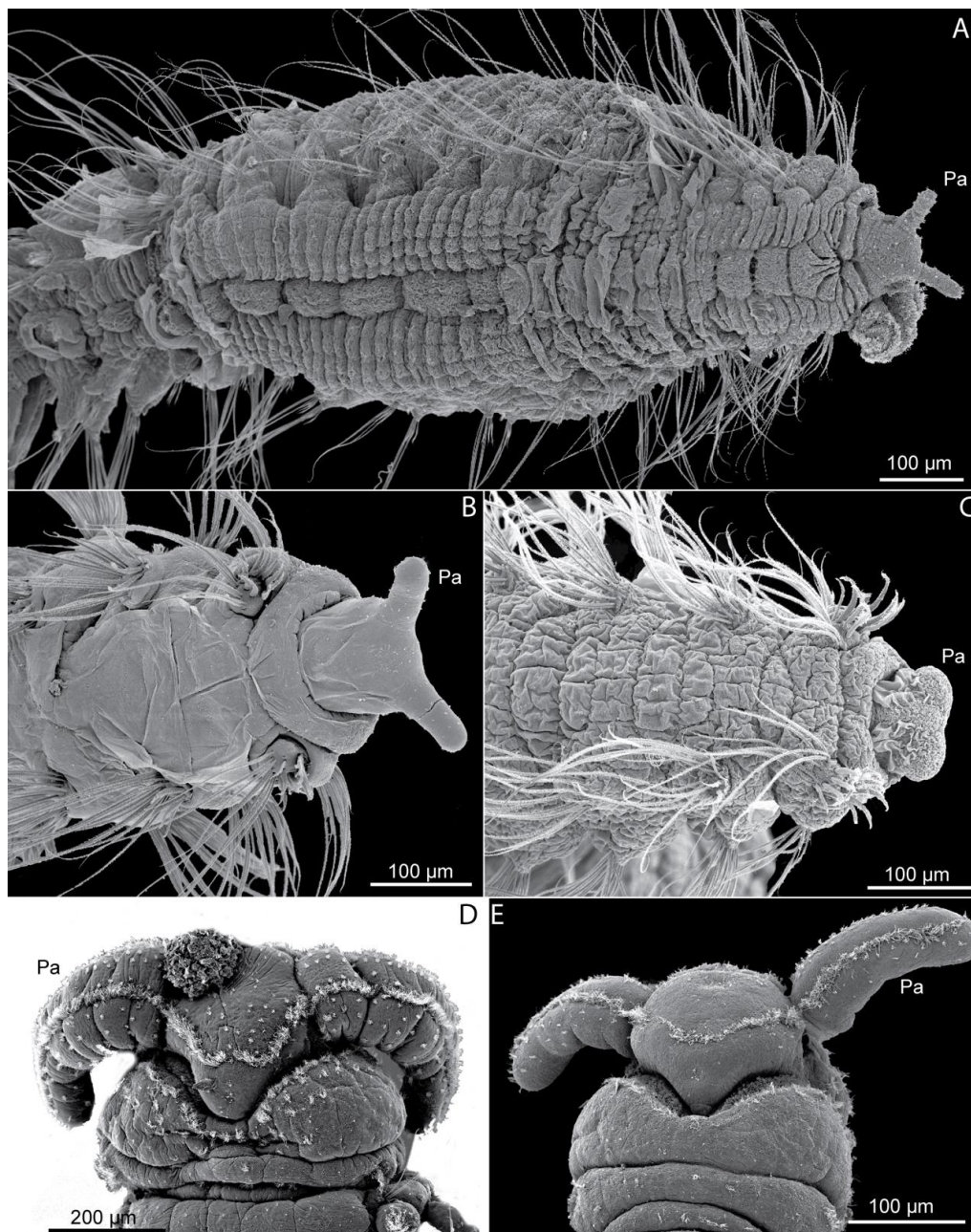


Figure 10. SEM micrographs of several Scalibregmatidae showing main prostomial diagnostic characters. (A) *Pseudoscalibregma* sp., Canary Islands, anterior end in ventral view, showing the pattern formed by the pads as well as the structure of the parapodia; (B) *Asclerocheilus* sp., Canary Islands, anterior end in dorsal view; (C) *Asclerocheilus* sp., northwestern Spain,

anterior end in dorsal view; (D) *S. lanzaroteum*, anterior end in dorsal view; (E) *A. cavernicola*, anterior end in dorsal view. Notice the difference in the prostomial shape and appendages amongst (B–E), as well the presence of different development of the peristomium, and the presence of different types of chaetae. Abbreviation: Pa—prostomial appendages.

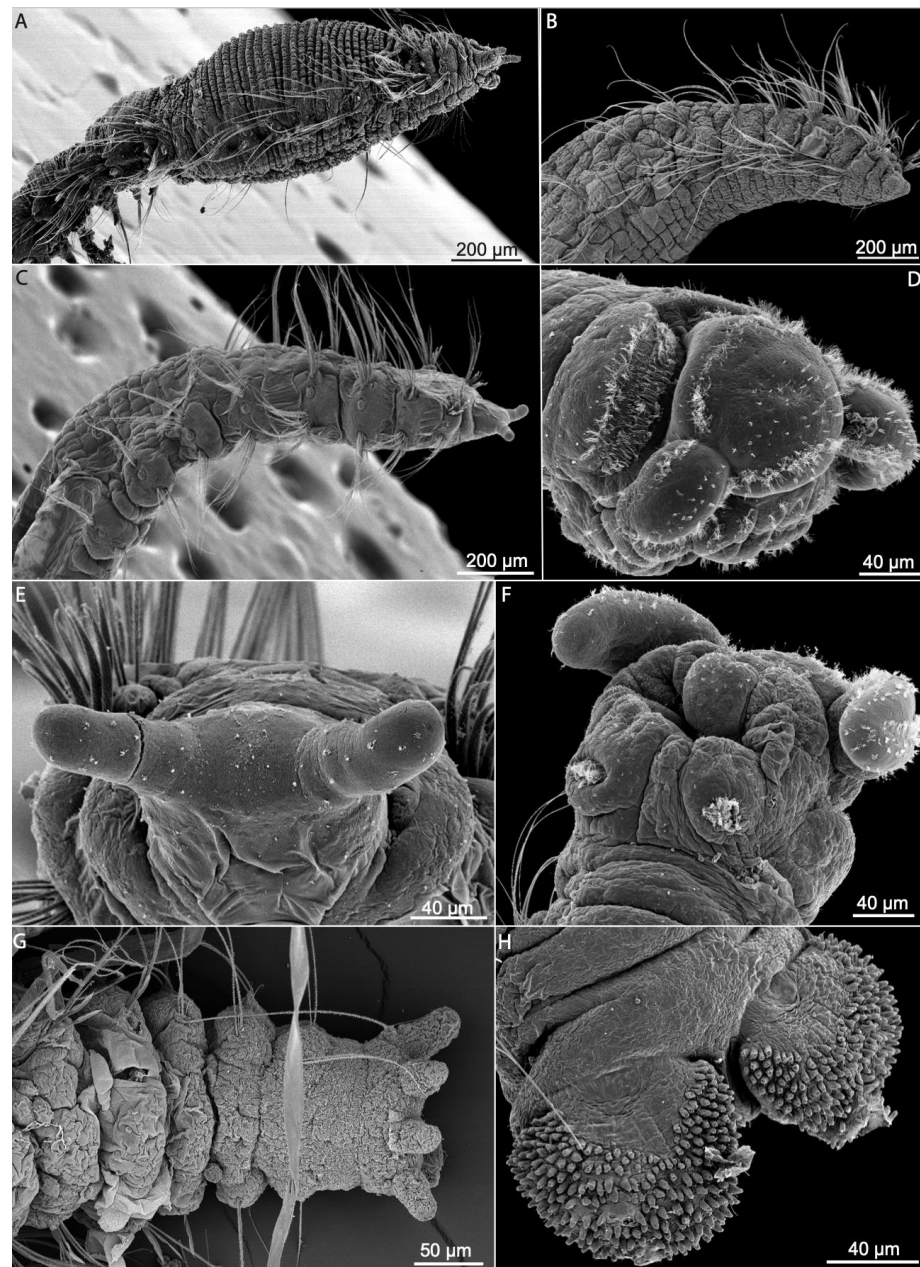


Figure 11. SEM micrographs of several Scalibregmatidae showing main diagnostic characters. (A) *Pseudoscalibregma* sp., Canary Islands, anterior end in lateral view; (B) *Asclerocheilus* sp., northwestern Spain, anterior end in lateral view; (C) *Asclerocheilus* sp., Canary Islands, anterior end in lateral view; notice the different morphology and epidermal pattern found on the anterior end on (A–C). (D) *A. cavernicola*, anterior end in lateral view; (E) *Asclerocheilus* sp., Canary Islands, anterior end in frontal view, compare the arrangement of the ciliary patterns between (D,E); (F) *A. cavernicola*, anterior end in ventral view, showing the ventral ciliary pads on the peristomium; (G) *Asclerocheilus* sp., northwestern Spain, posterior end in dorsal view, showing a typical shape and arrangement of the pygidium in Scalibregmatidae; (H) *A. cavernicola*, posterior end in dorsal view, showing the adhesive pygidium typical of the genera *Axiobebuita* and *Speleobregma*.

The peristomium typically consist of one dorsal and one to three ventral rings, merging into the upper and lower lips of the mouth. Unfortunately, detailed morphological descriptions of the peristomium have only been provided for a few species [23,36] (Figure 10C–E). The ventral mouth is connected to an axial proboscis, which is multilobed when everted and divided into proximal unciliated and distal ciliated zones [64]. The posterior part of peristomium possesses a pair of rounded ciliated areas of unknown function in *Axiokebuita* and *Speleobregma*, with potential taxonomic value (Figure 11F) [26].

The trunk includes up to 60 segments, each of them typically bearing one to six rows of elevated pads giving the worms an areolate appearance (Figures 9C and 10A–C). The number of these rows, as well as the number and size of the pads that form each of them, varies across different species and body regions. The pattern formed by the pads has been used to diagnose certain species, suggesting that these patterns might be species-specific in some genera [36]. Epidermal papillae are absent in Scalibregmatidae. A midventral groove is present in most genera, extending from the mouth towards the pygidium along the longitudinal body axis (Figure 10A). It is not clear, though, whether this structure bears systematic information or if its appearance depends on the post mortem contraction of the trunk musculature [23]. Transverse bands of presumably motile cilia have been described on *S. lanzaroteum* and *A. cavernicola* [26] (Figure 10D,E).

Branchiae have been considered as an important taxonomic character. The presence of branchiae in the anterior segment characterizes the genera *Scalibregma*, *Sclerobregma*, *Cryptosclerocheilus* Blake, 1972, and *Parasclerocheilus* Fauvel, 1928 (Figure 9A), in which they are attached to the notopodium from segment 2 up to segment 5–7. Branchiae are arborescent in most species, branching dichotomously a variable number of times; but can also be pectinate, with individual branchial filaments arising from an elongate flattened lamella, as in *Sclerobregma branchiatum* Hartman, 1965 (Figure 9A) [23]. However, recent studies suggest that their number and arrangement might vary ontogenetically within the same species [23,36]. This has raised concerns about the validity of certain species identification, particularly when few small individuals have been studied, and growth series are not incorporated into species descriptions. More information on the ontogeny of other species of Scalibregmatidae can be found elsewhere [23,26,36].

Parapodia are biramous in all scalibregmatids. The development of each ramus largely varies across species and body regions, but they are typically smaller anteriorly and more elongated towards the posterior body end. Parapodial structures, such as interramal papillae and parapodial cirri have been described in some species, holding useful taxonomic information. Interramal papillae are retractile and ciliated in *S. inflatum* [28] and *Asclerocheilus* (Figure 12B); whereas species of *Oligobregma* present interramal ciliated areas (Figure 12C). Interramal papillae in *A. cavernicola* and *S. lanzaroteum* project from the body wall and bear terminal ciliation [26,61] (Figure 12A,D). Nonciliated glandular papillae have been observed in *S. minutus* Grube, 1863 [41], and *P. palmeri* Blake, 2015 [36]. Parapodial dorsal and ventral cirri may help discriminating amongst species. Cirri are filiform in *Axiokebuita* and *Speleobregma* (Figure 9G), and leaf-shaped in *Oligobregma*, *Pseudoscalibregma* Ashworth, 1901, *Scalibregma*, and *Sclerobregma*. Cirri often exhibit glands, which are tubular in some species of *Scalibregma*, *Oligobregma*, and *Pseudoscalibregma*; but circular in *Axiokebuita* and *Speleobregma*. Parapodial lobes or lamellae are described in *Asclerocheilus californicum* and in the two species of the genus *Scalibregmidis* (Figure 9F) [31,40].

The arrangement of chaetae is a very important taxonomic characteristic in Scalibregmatidae. Chaetae are always simple and might include long capillaries (Figure 10A), geniculated (Figure 12I), lyrate (Figure 12E,G), short spinous (Figure 12H), and acicular (Figure 12F,H). Simple capillary chaetae are present in all described species, while the presence or absence of other types of chaetae is an important character to diagnose genera. The absence of lyrate chaetae characterizes the genera *Speleobregma* and *Axiokebuita*, whereas the morphology of these chaetae is useful to diagnose species in genera such as *Hyboscolex* and *Asclerocheilus*, amongst others. Spinous chaetae are small and typically

arranged as a single row restricted to the anterior most body segments. Since they occupy similar position to the lyrate chaetae, they are presumed as homologous to the former and rarely used in taxonomy. The presence of acicular chaetae, in contrast, is very useful and characterizes the genera *Sclerobregma*, *Parasclerocheilus*, *Asclerocheilus*, *Sclerocheilus*, and *Oligobregma*. Acicular chaetae are large and conspicuous, typically sickle-shaped or curved, and covered with fibrils visible in the scanning electron microscope. They are restricted to the anterior most segments and their arrangement is useful for species diagnoses. They can extend through a variable number of segments either on the notopodia or in both rami. Finally, geniculate chaetae are only found in *S. lanzaroteum* [124].

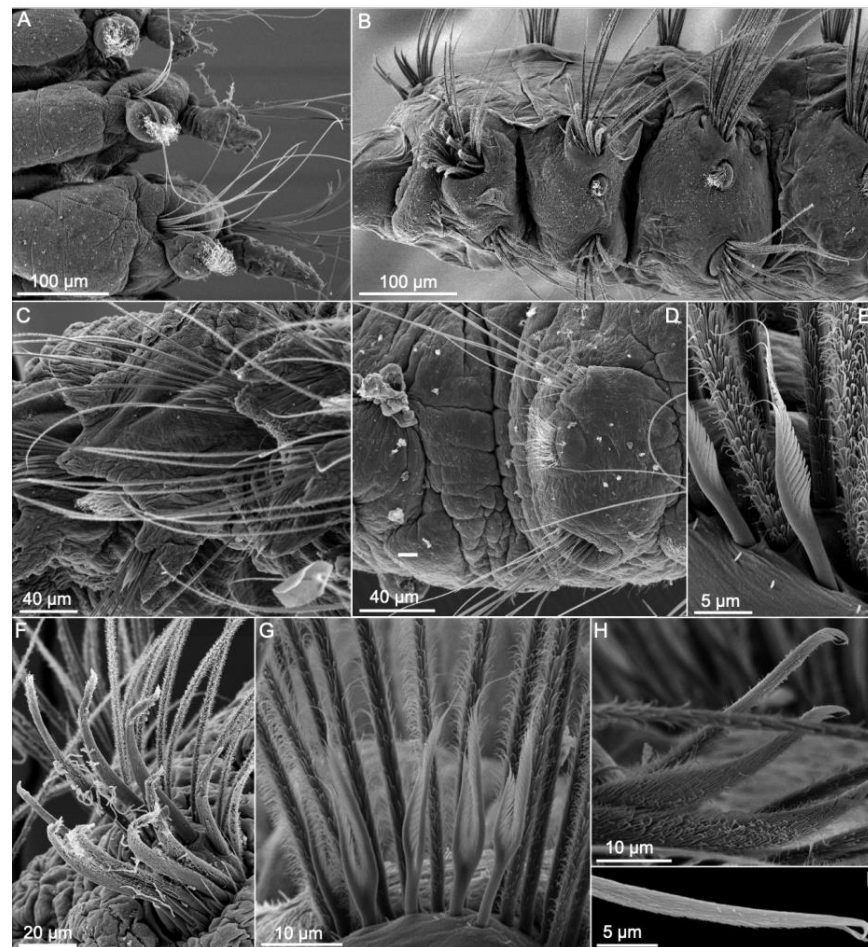


Figure 12. SEM micrographs of several Scalibregmatidae showing main diagnostic characters. (A) *Speleobregma lanzaroteum*, parapodia on the anterior segments in dorsal view, showing the presence of cirri; (B) *Asclerocheilus* sp., Canary Islands, parapodia on the anterior segments in lateral view; (C) *Asclerocheilus* sp., northwestern Spain, mid-body parapodium in frontal view; (D) *Axiokebuitta cavernicola*, mid-body parapodium in frontal view; (E), *Asclerocheilus* sp., Canary Islands, lyrate chaetae on anterior segments in lateral view; (F) *Asclerocheilus* sp., northwestern Spain, spines on segment 1; (G) *Asclerocheilus* sp., Canary Islands, lyrate chaetae on mid-body segment; (H) *Asclerocheilus* sp., Canary Islands, spines; (I) *S. lanzaroteum*, geniculate chaetae.

The pygidium is quite variable across different scalibregmatids. However, since scalibregmatids are found lacking the posterior end in most samples, the usefulness of this character is limited. In most species, the pygidium is simple and bears a typically terminal anus and surrounded by a variable number of cirri (Figure 11G) whose arrangement, length, and number are potentially useful to identify species. Species of *Axiokebuitta* and *Speleobregma* possess two enlarged rounded pygidial lobes covered with adhesive papillae (Figure 11H).

3.2.4. Internal Morphology

The internal morphology of Scalibregmatidae was thoroughly investigated during the early 20th century, particularly in the species *S. inflatum* [28] and *S. minutus* [41] mostly based on histological sections. Unfortunately, after these early works, very few studies have been undertaken using more modern microscopical techniques.

The body wall consists of the epidermis, which comprises elongated columnar cells and mucous secreting cells, as well as a muscular layer of circular muscles surrounding dorsal and ventral longitudinal muscular bundles [28]. Narrow oblique muscles are also present, arising ventrally from each side of the nerve cord and inserting into the body wall near the notopodial chaetal sacs. Parapodial musculature is limited to the chaetal sacs as well as the parapodial retractor muscles [28]. There is also a relatively strong mouth and pharyngeal musculature, with retractor muscles attached to the proboscis and two short muscles supplying the nuchal organs [28].

A thin epithelium delineates the coelomic cavity, which is well developed and spacious. As an adaptation for burrowing, septa are reduced along most of the body [28,41]. The gut is linear and attaches to the body cavity by few strands of muscular tissue in *S. inflatum*. The esophagus is straight and covered with secretory glands; whereas the midgut is wider and curled, and the hindgut is short, linear, and opens directly into the anus. Several blood sinuses are associated with the stomach in *S. inflatum* and *S. minutus* [28,41].

There is also a well-developed vascular system [28,41], consisting of dorsal and ventral vessels and their derivatives. The dorsal vessel extends along the alimentary canal supplying it with capillary vessels. It forms a blood reservoir near the anterior end of the stomach and a conical heart-like bulb before branching off to supply the pharynx, the peristomium, and the brain. The ventral blood vessel originates near the mouth and continues posteriorly, extending dorsally along the nerve cord. In *S. inflatum*, it supplies the branchiae, the stomach, and nephridia, as well as the chaetal sacs and their adjacent tissues.

A pair of metanephridia occurs in each chaetigerous segments, except for those most anterior. Gonads are associated with each metanephridium and are formed by the proliferation of cells covering the septum by which the nephrostome is attached to the body wall [28]. The gametes are released from the gonad at an early stage and complete their maturation in the coelom. Male gonads form sperm platelets bearing spermatids in *S. australis* and *O. mucronata*, and they mature into ect-aquasperm [36].

The brain has an anterior lobe associated with the prostomium and two posterior lobes associated with the nuchal organs. The prostomial appendages are innervated by a pair of nerves originating from the anterior lobe of the brain, whereas the esophageal connectives and the nerves innervating the nuchal organs arise from the middle and posterior lobes, respectively. The palps are innervated by one ventral and one dorsal nerve, corresponding to the fourth and ninth pairs respectively [42].

3.2.5. Species Diversity and Distribution

The most species rich scalibregmatid genus is *Asclerocheilus*, with 14 described species, followed by *Oligobregma* (12 species), *Hyboscolex* Schmarda, 1861 (10 species), *Pseudoscalibregma* (eight species), *Scalibregma* (eight species) and *Sclerocheilus* (four species). The remaining genera are less diverse, including *Polyphysia* Quatrefages, 1866 (three species), *Axiokebuita* (two or three species depending on the sources), *Parasclerocheilus* (two species), *Scalibregmidis* Hartmann-Schröder, 1965 (two species), and the monotypic *Cryptosclerocheilus*, *Lipobranchius* Cunningham and Ramage, 1888, *Sclerobregma*, and *Speleobregma*.

From a geographical point of view, scalibregmatids have been reported throughout the world and are present in all marine ecoregions [45] (Figure 7B). Most of the species have been described from the Temperate Northern Atlantic (17 species) and the Southern Ocean ecoregions (14 species), which together host nearly the half of the scalibregmatid type localities (Figure 7B). However, while the abundance of described species in the Temperate Northern Atlantic might just reflect the higher attention that historically has been paid to

the fauna of this region, the presence of so many scalibregmatids in Antarctica is somehow unusual and might respond to unidentified ecological or historical processes. This is particularly remarkable given that nearly all Antarctic species seem to be endemic from that area, although this endemism might be exacerbated by the lack of studies in surrounding deep-sea areas. The remaining type localities are distributed across the Temperate Northern Pacific (nine species), Temperate Australasia (seven species), Tropical Atlantic (six species), Tropical Eastern Pacific, Temperate South America, Arctic, and Temperate Southern Africa (all with four species), Western Indo-Pacific (three species), and Central Indo-Pacific (two species). However, given the fragmentary information available on the family, this pattern most likely reflects the different attention that the group has received across the world than any other biological meaningful factors.

Many scalibregmatids seem to have relatively broad distribution ranges. A remarkable example is *A. minuta*, which has been recorded both in Arctic and Antarctic latitudes, as well as hydrothermal vents in the Pacific Ocean and in the Galician Bank, off Northwest Spain (but see [23]); or *S. inflatum*, recorded from Northern Europe as well as from South Africa [117], Australia [38], Chile [40], and Japan [121]. However, many of these records are exclusively based on morphological data often evaluated from few specimens, generally preserved in suboptimal conditions. Therefore, one might expect that more detailed morphological examinations and the inclusion of molecular data will reveal that these records actually correspond to complex of species with narrower distributions and better-defined ecological preferences. For example, the re-examination of material originally attributed to *S. inflatum* has already revealed several different species with more restricted distribution. This includes the recent description of *S. australis* Blake, 2015 based on the detailed examination of growth series of Antarctic material [36], *S. californicum* Blake, 2000 from California [119], as well as *S. celticum* Mackie, 1991 and *S. hanseni* Bakken, Oug and Kongrud, 2014 from Europe [34,35]. Remarkably, these last species show sympatric occurrence with *S. inflatum*. Such discoveries, even in the relatively well explored waters of Europe, highlight once again that our knowledge on the diversity of the Scalibregmatidae is still very limited. Therefore, most discussions on the distribution patterns of the scalibregmatid species remain speculative.

In contrast to those species with large distribution areas, other species are exclusively known from a few localities. This is the case of the species *Scalibregmatides chilensis* Hartmann-Schröder, 1965, recorded only once from Puerto Aguirre (Chile) [40] and *S. peruanus* Blake, 1981 from Callao (Peru) [31]; a few species of the genus *Oligobregma*, such as *O. whaleyi* Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019 from a single deep-sea locality in the Pacific [2], or *O. oculata* Kudenov and Blake, 1978 and *O. simplex* Kudenov and Blake, 1978 each known from a single locality around Victoria (Australia) [38]. However, once again, the actual endemic status of these species remains doubtful due to our limited knowledge.

The endemism of *S. lanzaroteum* and *A. cavernicola* deserves a separate comment since the species are restricted to two different volcanic lava tubes in the Canary Islands [26]. *Speleobregma lanzaroteum* is an elusive species exclusively known from La Corona lava tube, in Lanzarote, an anchialine cave penetrating the saline aquifer of the island and characterised by the presence of a highly distinct fauna [125]. The species was described based on a single specimen collected in 1981 and only observed again after 27 years, when two more individuals were recovered in two successive dives [26,125]. The fact that these are the only three records of the species is remarkable because the cave has been regularly sampled over the last 40 years by well-trained cave divers who were explicitly sampling the fauna [126–129]. Therefore, the scarcity of records for *Speleobregma lanzaroteum* is more likely attributed to the low population densities described for many other cave species, than to an actual lack of sampling efforts [130]. *Axiobregma cavernicola* is, in contrast, limited to a specific gravelly patch found in Los Cerebros cave in Tenerife [26], while it is absent in the muddy or sandy sediments found elsewhere in the cave [131]. The fact that

both species are found in specific areas inside caves supports the idea that they may be actually endemic from these cave localities [132].

3.2.6. Biology and Ecology

Most scalibregmatids prefer muddy sediments at depths greater than 100 m. This seems to be the case, at least, for species in the genus *Scalibregma*, *Oligobregma*, *Polyphysia*, *Lipobranchius*, and *Pseudoscalibregma*, which are considered subsurface deposit feeders capturing food particles with their eversible multilobulated proboscis [85]. In particular, *S. inflatum* and *S. californicum* burrow by pushing the sediment to the sides of the body by lateral movements of the prostomium and afterwards moving forward by producing peristaltic waves [133]. The presence of the prostomial appendages probably increases the efficiency of this so-called shoveling process, while the absence of septa makes the production of waves more efficient. *Polyphysia crassa* (Örsted, 1843) burrows in a similar way, lacking prostomial horn, but also possessing reduced septa and a glandular epidermis to increase the efficiency of the peristaltic movements [85,134,135]. Because of the burrowing behavior, scalibregmatids play an important ecological role in soft bottoms bringing burrowed particles near to the surface, as it has been showed in the Cape Hatteras area [136] where they can be present quite deep in the sediment column [137]. These burrowing species can become very abundant or even dominate the benthic communities, as it has been shown for *S. australis* at the east side of the Antarctic Peninsula [36], and *S. inflatum* in Cape Hatteras between 550–1500 m depth [138]. Indirect evidence from various sources suggests that these are not isolated cases, but rather that species of these scalibregmatid genera might dominate soft bottom assemblages in many areas in high latitudes [23,35].

However, there are other species of scalibregmatids that seem to exhibit different habitat preferences. For example, *Oligobregma brasirae* Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019, *O. whaleyi*, and *O. tanyi* Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019, are exclusively known from the polymetallic nodule exploration areas in the eastern Clarion-Clipperton Zone [2], and there are many records of species of *Axiokebuita* from gravel, deep *Desmophyllum* Ehrenberg, 1834 coral reefs [26,61,103], or even rock crevices near hydrothermal vents at the Pacific Antarctic Ridge [139]. In shallow waters scalibregmatids are not uncommon in hard substrates. For example, *Scalibregmidia chilensis* has been recorded from a mytilid bank [40], *Hyboscolex quadricincta* Kudenov, 1985, *Asclerocheilus tropicus* Blake, 1981, and *A. mexicanus* Kudenov, 1985 have been collected from dead corals and sponges [25,39]; *Asclerocheilus acirratus* (Hartman, 1966) and *Hyboscolex verrucosa* Hartmann-Schröder, 1979 are known from algae in hard substrates [140,141], and *Asclerocheilus kudenovi* Blake, 2000 and *H. oculatus* (Ehlers, 1901) are recorded from unspecified hard, rocky substrates [119,142]. *Axiokebuita cavernicola* has only been reported from gravel sediments in the middle section of Los Cerebros lava tube in Tenerife, where there is an active water movement produced by waves driving a notable input of organic matter into the gravelly bed [26]. Adults of this species attach to the gravel particles using the adhesive papillae of the pygidium, while they collect suspended food particles using the water currents produced by the ciliation on their palps. Upon perturbation, they can also swim short distances using undulatory movements of the trunk. In contrast, juveniles of *A. cavernicola* lack palps and adhesive pygidium, and usually are found actively crawling and ciliary swimming in the petri dishes [26]. In contrast, *S. lanzaroteum* lives in La Corona lava tube, an anchialine cave system where food is limited to the organic matter carried by tidal currents [143]. Remarkably, *S. lanzaroteum* has only been found swimming in the water column using undulatory body movements and gentle movement of the parapodia. Similar life strategies have been discovered in other annelids exclusively reported in their isolated cave systems [126,144,145], suggesting that drifting in the water column might be the optimal life strategy in these type of cave environments. The capability of swimming is not unique in this cave-adapted scalibregmatid, since adults of several typically benthic species, such as *S.*

inflatum and *L. jeffreysii* (McIntosh, 1869) have been occasionally reported swarming in the plankton [146–148], although in all these cases, individuals possess specialized swimming chaetae.

The reproduction of scalibregmatids is largely unknown, and detailed studies are only available for a few selected species [23,149]. Fertilization is unknown but spawning might take place in the water column. This is presumed given the presence of ect-sperm and large oocytes in many species, as well as the observation of adult individuals of *S. inflatum*, *L. jeffreysii* and possibly *S. celticum*, swimming in the water column of the ocean, sometimes provided with long natatory chaetae [34,146–148]. Finally, despite nothing is known about the embryonic development, we know the postembryonic development of *S. australis*, *O. mucronata* and *A. cavernicola* [26,36] from the description of series of individuals of different size.

4. Conclusions and Future Perspectives

The Opheliidae are well known in some parts of the world such as the northern Atlantic; some areas (e.g., Pacific, Atlantic Africa), however, remain clearly understudied. The status of cosmopolitan species and several species not reported after original description should be reassessed. Furthermore, proper evaluation of some taxonomic characters needs to consider ontogenetic variability and preservation artefacts. Regarding Scalibregmatidae, the knowledge of the species richness and distribution is often fragmentary and strongly biased by the unbalanced sampling effort across the world. Indeed, except for the Antarctic and the northwestern Atlantic, the remaining marine areas have been poorly studied when it comes to Scalibregmatidae. Furthermore, both the position of this family within Annelida as well as its internal evolutionary relationships and systematics remain unresolved, warranting further assessment combining different sources of data; this also applies to Opheliidae because a full phylogenetic analysis of this family is still lacking as well.

Finally, as it still happens with other annelid families, current knowledge on the internal anatomy, life cycles, ecology, and behavior of opheliids and scalibregmatids has been obtained from a few studies on some common species. In this sense, traditional taxonomic approaches coupled with modern microscopy imaging techniques (e.g., micro-CT, SEM) and molecular methods (e.g., molecular phylogenies and species delimitation analyses) are needed; this will be paramount to assess properly intraspecific diversity issues that have hampered the taxonomy of these families in the past. This may be especially useful in finding appropriate, robust characters with systematic value in these morphologically homogenous taxa, aiding in an effective assessment of their current species diversity, and, ultimately, their distribution patterns and ecological preferences.

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Appendix A

Table A1. List of valid species of Opheliidae (after Blake and Maciolek [1,3]) with their type locality, realms *sensu* Spalding et al. [45] and depth ranges of type locality. N.d. = no data.

Species	Type Locality	Realms	Depth (m)
<i>Ammotrypanella arctica</i> (McIntosh, 1879)	North Atlantic Ocean	Temperate Northern Atlantic	2014–5023
<i>Ammotrypanella cirrosa</i> Schüller, 2008	Antarctic Peninsula; Weddell Sea	Southern Ocean	2014–4817
<i>Ammotrypanella keenani</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	404–4302
<i>Ammotrypanella kersteni</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4128
<i>Ammotrypanella mcintoshii</i> Schüller, 2008	off South Africa	Southern Ocean	1047–4720
<i>Ammotrypanella princessa</i> Schüller, 2008	Antarctic Peninsula, Weddell Sea	Southern Ocean	2014–4720
<i>Armandia agilis</i> (Andrews, 1891)	North Carolina, USA	Temperate Northern Atlantic	N.d.
<i>Armandia amakusaensis</i> Saito, Tamaki and Imajima, 2000	Western Kyushu, Japan	Temperate Northern Pacific	Intertidal
<i>Armandia andamana</i> Eibye-Jacobsen, 2002	Andaman Sea	Central Indo-Pacific	42–63
<i>Armandia bifida</i> Parapar and Moreira, 2015	Lizard Island, Australia	Central Indo-Pacific	Intertidal
<i>Armandia bilobata</i> Hartmann-Schröder, 1986	South Australia	Temperate Australasia	Intertidal
<i>Armandia bipapillata</i> Hartmann-Schröder, 1974	Inhambane, Mozambique	Western Indo-Pacific	Intertidal
<i>Armandia brevis</i> (Moore, 1906)	Icy Cape, Alaska, USA	Arctic	Intertidal to shallow subtidal
<i>Armandia broomensis</i> Hartmann-Schröder, 1979	Broome, Australia	Central Indo-Pacific	Intertidal
<i>Armandia buccina</i> Moreira and Parapar, 2017	Lizard Island, Australia	Central Indo-Pacific	0–12
<i>Armandia casuarina</i> Moreira and Parapar, 2017	Lizard Island, Australia	Central Indo-Pacific	Intertidal
<i>Armandia circumpapillata</i> Magalhães, Rizzo and Bailey-Brock, 2019	Oahu, Hawaii	Eastern Indo-Pacific	Shallow subtidal to 82 m
<i>Armandia cirrhosa</i> Filippi, 1861	Cagliari, Sardinia, Mediterranean	Temperate Northern Atlantic	Shallow subtidal
<i>Armandia dolio</i> Parapar and Moreira, 2015	Lizard Island, Australia	Central Indo-Pacific	5–14
<i>Armandia exigua</i> Kükenthal, 1887	China	Central Indo-Pacific	15
<i>Armandia filibranchia</i> Parapar and Moreira, 2015	Lizard Island, Australia	Central Indo-Pacific	9
<i>Armandia garretti</i> Magalhães, Rizzo and Bailey-Brock, 2019	Pearl Harbor, Hawaii	Eastern Indo-Pacific	0–20
<i>Armandia hossfeldii</i> Hartmann-Schröder, 1956	Brazil	Temperate South America	9.5–14
<i>Armandia ilhabelae</i> Hartmann-Schröder, 1956	Santos, Brazil	Temperate South America	Intertidal
<i>Armandia intermedia</i> Fauvel, 1902	River Casamance estuary, Senegal	Tropical Atlantic	Intertidal to subtidal
<i>Armandia laminosa</i> Parapar and Moreira, 2015	Lizard Island, Australia	Central Indo-Pacific	0–15
<i>Armandia lanceolata</i> Willey, 1905	South of Manaar Island, Sri Lanka	Western Indo-Pacific	15–16
<i>Armandia leptocirris</i> (Grube, 1878)	Philippines	Central Indo-Pacific	0–18
<i>Armandia loboii</i> Elias and Bremec, 2003	off Mar del Plata, Argentina	Temperate South America	5–13
<i>Armandia maculata</i> (Webster, 1884)	Bermuda	Tropical Atlantic	9–38
<i>Armandia mariacapae</i> Moreira and Parapar, 2017	Lizard Island, Australia	Central Indo-Pacific	0–12
<i>Armandia melanura</i> Gravier, 1905	Djibouti, Gulf of Aden	Western Indo-Pacific	Intertidal
<i>Armandia nonpapillata</i> Jones, 1962	Kingston Harbour, Jamaica	Tropical Atlantic	N.d.
<i>Armandia opisthocolata</i> Moreira and Parapar, 2017	Lizard Island, Australia	Central Indo-Pacific	5–15
<i>Armandia paraintermedia</i> Parapar and Moreira, 2015	Lizard Island, Australia	Central Indo-Pacific	0–24
<i>Armandia parva</i> Moreira and Parapar, 2017	Lizard Island, Australia	Central Indo-Pacific	0–15
<i>Armandia polyophtalma</i> Kükenthal, 1887	Gulf of Naples, Italy	Temperate Northern Atlantic	0–20
<i>Armandia salvadoriana</i> Hartmann-Schröder, 1956	El Salvador	Tropical Eastern Pacific	Intertidal
<i>Armandia sampadae</i> Gopal, Jaleel, Parameswaran and Vijayan, 2016	Andaman Islands	Western Indo-Pacific	52–57
<i>Armandia secundariopapillata</i> Hartmann-Schröder, 1984	SW Australia	Temperate Australasia	Intertidal
<i>Armandia sinaitica</i> Amoureux, 1983	Gulf of Akaba, Red Sea	Western Indo-Pacific	Intertidal
<i>Armandia simodaensis</i> Takahashi, 1938	Japan	Temperate Northern Pacific	N.d.
<i>Armandia tubulata</i> Parapar and Moreira, 2015	Lizard Island, Australia	Central Indo-Pacific	1–10
<i>Armandia weissenbornii</i> Kükenthal, 1887	Perim Island, Red Sea	Western Indo-Pacific	N.d.
<i>Ophelia africana</i> Tebble, 1953	Table Bay, South Africa	Temperate Southern Africa	Intertidal to shallow subtidal
<i>Ophelia agulhana</i> Day, 1961	False Bay, South Africa	Temperate Southern Africa	Intertidal to shallow subtidal

Table A1. Cont.

Species	Type Locality	Realms	Depth (m)
<i>Ophelia algida</i> Maciolek and Blake, 2006	Off Macquarie Island, Southern Ocean	Southern Ocean	112–124
<i>Ophelia amoureuxi</i> Bellan and Costa, 1988	Côte d'Azur	Temperate Northern Atlantic	90–95
<i>Ophelia anomala</i> Day, 1961	False Bay, South Africa	Temperate Southern Africa	15–80
<i>Ophelia ashworthi</i> Fauvel, 1917	Gulf of St Vincent and Spencer	Temperate Australasia	Subtidal
<i>Ophelia assimilis</i> Tebble, 1953	Central California	Temperate Northern Pacific	Intertidal to shallow subtidal
<i>Ophelia barquii</i> Fauvel, 1927	Agay, Var, France	Temperate Northern Atlantic	Intertidal
<i>Ophelia bicornis</i> Savigny, 1822	La Rochelle, France	Temperate Northern Atlantic	Intertidal to subtidal
<i>Ophelia bipartita</i> Monro, 1936	S Chile	Temperate South America	35
<i>Ophelia borealis</i> Quatrefages, 1866	Greenland	Arctic	N.d.
<i>Ophelia bulbibranchiata</i> Hartmann-Schröder and Parker, 1995	Pearson Island, Australia	Temperate Australasia	not recorded
<i>Ophelia capensis</i> Kirkegaard, 1959	Table Bay, South Africa	Temperate Southern Africa	50–80
<i>Ophelia celtica</i> Amoureuux and Dauvin, 1981	Atlantic France	Temperate Northern Atlantic	<100
<i>Ophelia dannevigii</i> Benham, 1916	St. Francis Island, Australia	Temperate Australasia	~60
<i>Ophelia denticulata</i> Verrill, 1875	Maine, USA	Temperate Northern Atlantic	N.d.
<i>Ophelia elongata</i> Hutchings and Murray, 1984	Burwood Beach, Australia	Temperate Australasia	Subtidal
<i>Ophelia formosa</i> (Kinberg, 1866)	La Plata, Argentina (?)	Temperate South America	N.d.
<i>Ophelia glabra</i> Stimpson, 1853	East Canada	Temperate Northern Atlantic	N.d.
<i>Ophelia kirkegaardii</i> Intes and Le Loeuff, 1977	Off Abidjan, Ivory Coast	Tropical Atlantic	20–40
<i>Ophelia koloana</i> Gibbs, 1971	Solomon Islands	Central Indo-Pacific	2
<i>Ophelia laubieri</i> Bellan and Costa, 1988	Estuário do Sado, Portugal	Temperate Northern Atlantic	Low intertidal to subtidal
<i>Ophelia limacina</i> (Rathke, 1843)	Norway	Temperate Northern Atlantic	0–500
<i>Ophelia magna</i> (Treadwell, 1914)	California, USA	Temperate Northern Pacific	N.d.
<i>Ophelia multibranchia</i> Hutchings and Murray, 1984	Botany Bay, Australia	Temperate Australasia	3–4
<i>Ophelia neglecta</i> Schneider, 1892	France	Temperate Northern Atlantic	Intertidal to subtidal
<i>Ophelia peresi</i> Bellan and Picard, 1965	Tuléar, Madagascar	Western Indo-Pacific	15–20
<i>Ophelia praetiosa</i> (Kinberg, 1866)	Cabo Virgenes, Argentina	Temperate South America	13–95
<i>Ophelia profunda</i> Hartman, 1965	Off New England, USA	Temperate Northern Atlantic	1000–1700
<i>Ophelia pulchella</i> Tebble, 1953	Southern California, USA	Temperate Northern Pacific	Subtidal
<i>Ophelia radiata</i> (Delle Chiaje, 1828)	Gulf of Naples, Italy	Temperate Northern Atlantic	Intertidal to subtidal
<i>Ophelia rathkei</i> McIntosh, 1908	UK	Temperate Northern Atlantic	Intertidal to subtidal
<i>Ophelia roscoffensis</i> Augener, 1910	Roscoff, France	Temperate Northern Atlantic	Subtidal
<i>Ophelia rullieri</i> Bellan, 1975	Gaspésie, Quebec	Temperate Northern Atlantic	Intertidal to shallow subtidal
<i>Ophelia simplex</i> Leidy, 1855	Rhode Island, USA	Temperate Northern Atlantic	N.d.
<i>Ophelia translucens</i> (Katzmann, 1973)	Zlarin, Croatia	Temperate Northern Atlantic	20–40
<i>Ophelia verrilli</i> Riser, 1987	New England, USA	Temperate Northern Atlantic	Intertidal to shallow subtidal
<i>Ophelina abranchiata</i> Støp-Bowitz, 1948	Greenland	Arctic	90–4500
<i>Ophelina acuminata</i> Örsted, 1843	Øresund Strait, Hveen Island, Sweden	Temperate Northern Atlantic	Shelf and slope
<i>Ophelina adamantea</i> (Kinberg, 1866)	Rio de Janeiro, Brazil	Temperate South America	N.d.
<i>Ophelina alata</i> Elias, Bremec, Lana and Orensanz, 2003	SE Brazil	Temperate South America	Subtidal
<i>Ophelina ammotrypanella</i> Schüller, 2008	Antarctic peninsula, Weddell Sea	Southern Ocean	1970–3050
<i>Ophelina aulogastrella</i> (Hartman and Fauchald, 1971)	off New England, USA	Temperate Northern Atlantic	196–5023
<i>Ophelina basicirra</i> Parapar, Moreira and Helgason, 2011	NW Iceland	Temperate Northern Atlantic	23–2298
<i>Ophelina bimensis</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina bowitzi</i> Parapar, Moreira and Helgason, 2011	Southern Iceland	Temperate Northern Atlantic	1897–2709
<i>Ophelina brasiliensis</i> Hansen, 1882	Brazil	Temperate South America	Subtidal
<i>Ophelina brattegardii</i> Kongsrud, Bakken and Oug, 2011	off East Greenland	Arctic	1600
<i>Ophelina breviata</i> (Ehlers, 1913)	Wilhelm II Coast, Antarctic Ocean	Southern Ocean	20–3000
<i>Ophelina brevibranchiata</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina buitendijki</i> (Horst, 1919)	Java Sea	Central Indo-Pacific	N.d.
<i>Ophelina chaetifera</i> (Hartman, 1965)	off New England, USA	Temperate Northern Atlantic	1330–5007
<i>Ophelina cordiformis</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	N.d.

Table A1. Cont.

Species	Type Locality	Realms	Depth (m)
<i>Ophelina curli</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4026
<i>Ophelina cylindricaudata</i> (Hansen, 1879)	off West Norway	Temperate Northern Atlantic	7–4663
<i>Ophelina cyprophilia</i> Neave and Glasby, 2013	Darwin Harbour, Australia	Central Indo-Pacific	0–10
<i>Ophelina delapidans</i> (Kinberg, 1866)	Valparaiso, Chile	Temperate South America	Shallow subtidal
<i>Ophelina dubia</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina ehlersi</i> (Horst, 1919)	Jedan, Aroe Isles, Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina fauveli</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	10–21
<i>Ophelina ganae</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4076–4302
<i>Ophelina gaucha</i> Elias, Bremec, Lana and Orensanz, 2003	SE Brazil	Temperate South America	0–18
<i>Ophelina hachaensis</i> Augener, 1934	Riohacha, Colombia	Tropical Atlantic	6
<i>Ophelina helgolandiae</i> Augener, 1912	Spitsbergen, Norway	Arctic	562–2710
<i>Ophelina gigantea</i> (Rullier, 1965)	Moreton Bay, Australia	Temperate Australasia	N.d.
<i>Ophelina grandis</i> (Pillai, 1961)	Tambalagam Bay, Sri Lanka	Western Indo-Pacific	1.8–7.3
<i>Ophelina groenlandica</i> Støp-Bowitz, 1948	East Greenland	Arctic	Shelf and slope
<i>Ophelina gymnopyge</i> (Ehlers, 1908)	Kerguelen Islands	Southern Ocean	13–199
<i>Ophelina jeffreysi</i> (McIntosh in Jeffreys, 1876)	Labrador Sea, North Atlantic Ocean	Arctic	1066–3200
<i>Ophelina juhazi</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4100
<i>Ophelina kampanii</i> (Horst, 1919)	Jedan, Aroe Isles, Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina kinbergii</i> Hansen, 1882	Río de Janeiro, Brazil	Temperate South America	Subtidal
<i>Ophelina kohmi</i> Magalhães, Rizzo and Bailey-Brock, 2019	Guam	Central Indo-Pacific	Shallow subtidal
<i>Ophelina kuekenthali</i> (McIntosh, 1908)	North Atlantic Ocean	Temperate Northern Atlantic	~1400
<i>Ophelina langii</i> (Kükenthal, 1887)	Philippines	Central Indo-Pacific	20
<i>Ophelina longicaudata</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina longicephala</i> Hartmann-Schröder, 1977	Off Portugal	Temperate Northern Atlantic	77
<i>Ophelina longicirrata</i> Hartmann-Schröder and Parker, 1995	South Australia	Temperate Australasia	N.d.
<i>Ophelina manana</i> Magalhães, Rizzo and Bailey-Brock, 2019	Oahu, Hawaii	Eastern Indo-Pacific	400–500
<i>Ophelina martinezarbizui</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4026–4425
<i>Ophelina meyeræ</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4302
<i>Ophelina minima</i> Hartmann-Schröder, 1974	Skagerrak	Temperate Northern Atlantic	230–645
<i>Ophelina modesta</i> Støp-Bowitz, 1958	Oslo, Norway	Temperate Northern Atlantic	100–200
<i>Ophelina nematoides</i> (Ehlers, 1913)	Antarctic Ocean	Southern Ocean	246–2725
<i>Ophelina norvegica</i> Støp-Bowitz, 1945	East Norway	Temperate Northern Atlantic	Subtidal
<i>Ophelina nunnallyi</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4425–4302
<i>Ophelina nybelini</i> (Eliason, 1951)	Azores Islands	Temperate Northern Atlantic	4540–4600
<i>Ophelina opisthobranchiata</i> Wirén, 1901	Spitsbergen, Norway	Arctic	800–3900
<i>Ophelina profunda</i> (Caullery, 1944)	Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina pygocirrata</i> (Ehlers, 1920)	Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina remigera</i> (Ehlers, 1918)	Aru Islands, Sungai Manumbai, Indonesia	Central Indo-Pacific	N.d.
<i>Ophelina robusta</i> Schüller, 2008	Antarctic Peninsula, Weddell Sea	Southern Ocean	2668–3050
<i>Ophelina scaphigera</i> (Ehlers, 1900)	Magellan Strait	Temperate South America	18–3382
<i>Ophelina setigera</i> (Hartman, 1978)	Weddell Sea	Southern Ocean	3111
<i>Ophelina sibogae</i> (Caullery, 1944)	Java	Central Indo-Pacific	79–81
<i>Ophelina syringopyge</i> (Ehlers, 1901)	South Georgia	Southern Ocean	9–876
<i>Ophelina tessellata</i> Neave and Glasby, 2013	Melville Bay, Australia	Central Indo-Pacific	0–10
<i>Polyophthalmus australis</i> Grube, 1869	Cape York, Australia	Central Indo-Pacific	N.d.
<i>Polyophthalmus ceylonensis</i> Kükenthal, 1887	Sri Lanka	Western Indo-Pacific	N.d.
<i>Polyophthalmus collaris</i> Michaelsen, 1892	Sri Lanka	Western Indo-Pacific	N.d.
<i>Polyophthalmus longisetosus</i> Michaelsen, 1892	Sri Lanka	Western Indo-Pacific	N.d.
<i>Polyophthalmus mauiola</i> Magalhães, Rizzo and Bailey-Brock, 2019	Mamala Bay, Hawaii	Eastern Indo-Pacific	27–56
<i>Polyophthalmus pictus</i> (Dujardin, 1839)	France	Temperate Northern Atlantic	Intertidal
<i>Polyophthalmus qingdaoensis</i> Purschke, Ding and Müller, 1995	Qingdao, Yellow Sea	Temperate Northern Pacific	N.d.

Table A1. Cont.

Species	Type Locality	Realms	Depth (m)
<i>Polyophthalmus striatus</i> Kükenthal, 1887	Hong Kong	Central Indo-Pacific	N.d.
<i>Polyophthalmus translucens</i> Hartman, 1960	Southern California, USA	Temperate Northern Pacific	914
<i>Thoracophelia arctica</i> (Grube, 1866)	Arctic Ocean	Arctic	N.d.
<i>Thoracophelia bibranchia</i> (Hutchings and Murray, 1984)	Merimbula, Australia	Temperate Australasia	Intertidal
<i>Thoracophelia dillonensis</i> (Hartman, 1938)	Dillon Beach, California, USA	Temperate Northern Pacific	Intertidal
<i>Thoracophelia ezoensis</i> Okuda, 1936	Hokkaido, Japan	Temperate Northern Pacific	N.d.
<i>Thoracophelia flabellifera</i> Ziegelmeier, 1955	German Bight, North Sea	Temperate Northern Atlantic	13
<i>Thoracophelia furcifera</i> Ehlers, 1897	Punta Arenas, Magellan Strait	Temperate South America	Intertidal
<i>Thoracophelia heterocirra</i> (Rozbaczylo and Zamorano, 1970)	El Tabo, Chile	Temperate South America	Intertidal
<i>Thoracophelia japonica</i> (Misaka and Sato, 2003)	Oura Bay, Japan	Temperate Northern Pacific	0–16
<i>Thoracophelia longiseta</i> (Hutchings and Murray, 1984)	Ocean Beach, Australia	Temperate Australasia	Intertidal
<i>Thoracophelia mammillata</i> (Santos, Nonato and Petersen, 2004)	Rio de Janeiro, Brazil	Temperate South America	22–45
<i>Thoracophelia mucronata</i> (Treadwell, 1914)	La Jolla, Southern California	Temperate Northern Pacific	Intertidal
<i>Thoracophelia otagoensis</i> (Probert, 1976)	Otago Peninsula, New Zealand	Temperate Australasia	Intertidal
<i>Thoracophelia papillata</i> (Santos, Nonato and Petersen, 2004)	Abais beach, Brazil	Tropical Atlantic	Intertidal
<i>Thoracophelia profunda</i> (Hartman, 1967)	Cape Horn, Chile	Temperate South America	4008
<i>Thoracophelia yasudai</i> Okuda, 1934	Kainawa, Japan	Temperate Northern Pacific	Intertidal
<i>Thoracophelia williamsi</i> (Hartman, 1938)	Dillon Beach, California, USA	Temperate Northern Pacific	Intertidal
<i>Thoracophelia zeidlereri</i> (Hartmann-Schröder and Parker, 1995)	Haystack Beach, Australia	Temperate Australasia	Intertidal

Table A2. List of valid species of Scalibregmatidae (after Blake [3,23]) with their type locality, realms *sensu* Spalding et al. [45] and depth ranges of type locality. N.d. = no data.

Species	Type Locality	Realms	Depth (m)
<i>Asclerocheilus acirratu</i> (Hartman, 1966)	White Cove, Southern California, USA	Temperate Northern Pacific	0–3
<i>Asclerocheilus ashworthi</i> Blake, 1981	Elephant Island, Antarctica	Southern Ocean	223–397
<i>Asclerocheilus beringianus</i> Uschakov, 1955	Bering Sea	Arctic	986–2005
<i>Asclerocheilus californicus</i> Hartman, 1963	Santa Monica, Redondo and San Pedro valley, California, USA	Temperate Northern Pacific	542–890
<i>Asclerocheilus capensis</i> Day, 1963	South Africa	Temperate Southern Africa	9–26
<i>Asclerocheilus elisabethae</i> Eibye-Jacobsen, 2002	Thailand, Andaman Sea	Western Indo-Pacific	70–76
<i>Asclerocheilus glabrus</i> (Ehlers, 1887)	Cuba	Tropical Atlantic	320
<i>Asclerocheilus intermedius</i> (Saint-Joseph, 1894)	Dinard, France	Temperate Northern Atlantic	96–1830
<i>Asclerocheilus kudenovi</i> Blake, 2000	Point Arguello, California, USA	Temperate Northern Pacific	91.5–123
<i>Asclerocheilus mexicanus</i> Kudenov, 1985	Florida, Gulf of Mexico	Tropical Atlantic	2.4–76.2
<i>Asclerocheilus shanei</i> Hartmann-Schröder, 1994	Scamander, Tasmania	Temperate Australia	122
<i>Asclerocheilus shananae</i> Eibye-Jacobsen, 2002	Thailand, Andaman Sea	Western Indo-Pacific	70–76
<i>Asclerocheilus tasmanicus</i> Kirkegaard, 1996	Tasman Sea, W of New Zealand	Temperate Australia	3710–3830
<i>Asclerocheilus tropicus</i> Blake, 1981	NW off Guayaquil, Ecuador	Tropical Eastern Pacific	3–10
<i>Asclerocheilus victoriensis</i> Blake, 2000	Victoria, Australia	Temperate Australia	6–22
<i>Axiokebuita cavernicola</i> Martínez, Di Domenico and Worsaae, 2013	Los Cerebros cave, Tenerife, Canary Islands	Temperate Northern Atlantic	8–15
<i>Axiokebuita minuta</i> (Hartman, 1967)	Antarctica	Southern Ocean	180–3685
<i>Cryptosclerocheilus baffinensis</i> Blake, 1972	Southern Baffin Bay	Arctic	1830
<i>Hyboscolex dicranochaetus</i> (Schmarda, 1861)	Table Bay, Cape New Hope, South Africa	Temperate Southern Africa	0.5–19.8
<i>Hyboscolex equatorialis</i> Blake, 1981	NW of Guayaquil, Ecuador	Temperate Southern America	8–9
<i>Hyboscolex homochaetus</i> (Schmarda, 1861)	New Zealand	Temperate Southern Africa	N.d.
<i>Hyboscolex longisetus</i> Schmarda, 1861	Table Bay, Cape New Hope, South Africa	Temperate Southern Africa	9–110

Table A2. Cont.

Species	Type Locality	Realms	Depth (m)
<i>Hyboscolex oculatus</i> (Ehlers, 1901)	Tumbes Peninsula, near Talcahuano, Chile	Temperate Southern America	ca. 0.5–10
<i>Hyboscolex pacificus</i> (Moore, 1909)	Santa Monica, California, USA	Temperate Northern Pacific	200
<i>Hyboscolex quadricincta</i> Kudenov, 1985	Florida, Gulf of Mexico	Tropical Atlantic	0.6–31
<i>Hyboscolex reticulatus</i> (McIntosh, 1885)	Queen Charlotte Sound, New Zealand	Temperate Australia	2011
<i>Hyboscolex verrucosus</i> Hartmann-Schröder, 1979	Port Hedland, Western Australia	Central Indo-Pacific	0–5
<i>Lipobranchius jeffreysii</i> McIntosh, 1869	Hebrides and Shetland Islands	Temperate Northern Atlantic	22–1194
<i>Oligobregma aciculatum</i> (Hartman, 1965)	New England, abyssal	Temperate Northern Atlantic	1925–4825
<i>Oligobregma brasierae</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4425
<i>Oligobregma collare</i> (Levenstein, 1975)	Drake Passage, Antarctica	Southern Ocean	3733–3806
<i>Oligobregma lonchochaeta</i> Detinova, 1985	Reykjanes Ridge, off Iceland	Temperate Northern Atlantic	2930–2951
<i>Oligobregma mucronata</i> Blake, 2015	Greenpeace Trough, East Antarctic Peninsula	Southern Ocean	323–912
<i>Oligobregma notiale</i> Blake, 1981	Palmer Archipelago, Antarctic Peninsula	Southern Ocean	18–923
<i>Oligobregma oculata</i> Kudenov and Blake, 1978	East of Saint Maurice island, New Caledonia	Central Indo-Pacific	57
<i>Oligobregma pseudocollare</i> Schüller and Hilbig, 2007	Scotia Sea, Antarctica	Southern Ocean	2889–2892
<i>Oligobregma quadrispinosa</i> Schüller and Hilbig, 2007	Scotia Sea, Antarctica	Southern Ocean	2258–2313
<i>Oligobregma simplex</i> Kudenov and Blake, 1978	Western Port, Victoria, Australia	Temperate Australia	11
<i>Oligobregma tani</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4137
<i>Oligobregma whaleyi</i> Wiklund, Neal, Glover, Drennan, Rabone and Dahlgren, 2019	Clarion-Clipperton Zone, Pacific Ocean	Tropical Eastern Pacific	4425
<i>Parasclerocheilus branchiatus</i> Fauvel, 1928	Shingle Island, Gulf of Manaar, India	Western Indo-Pacific	N.d.
<i>Parasclerocheilus capensis</i> Day, 1961	Langebaan Lagoon, South Africa	Temperate Southern Africa	26
<i>Polyphysia caulleryi</i> (McIntosh, 1922)	Inland Sea of Japan	Temperate Northern Pacific	47
<i>Polyphysia crassa</i> (Ørsted, 1843)	Denmark	Temperate Northern Atlantic	0–1755
<i>Polyphysia hystrix</i> (McIntosh, 1922)	Channel slope, Antarctica	Temperate Northern Atlantic	4701261
<i>Pseudoscalibregma bransfieldium</i> (Hartman, 1967)	E. Bransfield Strait, Antarctica	Southern Ocean	323–916
<i>Pseudoscalibregma hartmanae</i> Blake, 1981	Weddell Sea, Antarctica	Southern Ocean	585
<i>Pseudoscalibregma orientalis</i> Imajima, 2009	Japan	Temperate Northern Pacific	373–1005
<i>Pseudoscalibregma pallens</i> Levenstein, 1962	Kermadec Trench	Temperate Australia	8928–9174
<i>Pseudoscalibregma palmeri</i> Blake, 2015	Weddell Sea, Off Lindenberg Island, Antarctica	Southern Ocean	385–768
<i>Pseudoscalibregma papilia</i> Schüller, 2008	South Sandwich Islands, Antarctica	Southern Ocean	2258–2313
<i>Pseudoscalibregma parvum</i> (Hansen, 1878)	North Sea	Temperate Northern Atlantic	53–1802
<i>Pseudoscalibregma usarpium</i> Blake, 1981	Ross Sea, Antarctica	Southern Ocean	2143
<i>Scalibregma australis</i> Blake, 2015	Greenpeace Trough, East Antarctic Peninsula	Southern Ocean	12–978
<i>Scalibregma californicum</i> Blake, 2000	Santa Maria Basin, off Point Sal, California	Temperate Northern Pacific	90–2710
<i>Scalibregma celticum</i> Mackie, 1991	Milford Haven, Dyfed, Wales	Temperate Northern Atlantic	6–21
<i>Scalibregma hansenii</i> Bakken, Oug and Kongsrud, 2014	Egga, west of Nordland County, Norway	Temperate Northern Atlantic	765
<i>Scalibregma inflatum</i> Rathke, 1843	Norway	Temperate Northern Atlantic	1–3690
<i>Scalibregma robustum</i> Zachs, 1925	White Sea, Russia	Arctic	N.d.
<i>Scalibregma stenocerum</i> (Bertelsen and Weston, 1980)	Daytona Beach, Florida	Tropical Atlantic	17–65
<i>Scalibregma wireni</i> Furrer, 1925	Kaiser Joseph Fjord, East Greenland	Arctic	3–9
<i>Scalibregmella antennata</i> Hartman and Fauchald, 1971	Bermuda, abyssal	Temperate Northern Atlantic	4833–5023
<i>Scalibregmidés chilensis</i> Hartmann-Schröder, 1965	Puerto Aguirre, Chile	Temperate Southern America	10
<i>Scalibregmidés peruanus</i> Blake, 1981	island near Pucusana, south of Callao, Peru	Temperate Southern America	0–5
<i>Sclerobregma branchiatum</i> Hartman, 1965	New England	Temperate Northern Atlantic	1330–2022
<i>Sclerocheilus antarcticus</i> Ashworth, 1915	Petermann Island, Antarctica	Southern Ocean	45–311
<i>Sclerocheilus deriugini</i> Zachs, 1925	Kola Fjord, Northern Russia	Temperate Northern Atlantic	N.d.
<i>Sclerocheilus minutus</i> Grube, 1863	Nerizine, Mali Losinj, Croatia	Temperate Northern Pacific	N.d.
<i>Sclerocheilus unoculus</i> Kudenov, 1985	Florida, Gulf of Mexico	Tropical Atlantic	18–37
<i>Speleobregma lanzaroteum</i> Bertelsen, 1986	La Corona lava tube, Lanzarote, Canary Islands	Temperate Northern Atlantic	5–25

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