

Review

The Early Branching Group of Orbiniida Sensu Struck et al., 2015: Parergodrilidae and Orbiniidae

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Abstract: This review addresses the state of the art of the systematics and the improvements in the biology, ecology and species diversity of the two annelid taxa Parergodrilidae and Orbiniidae, the early branching group of Orbiniida sensu Struck et al., 2015 according to molecular studies. An effort to identify gaps of knowledge is given to understand the distribution, dispersal and the diversity Parergodrilidae and Orbiniidae hold, as well as to give several directions for future research. Parergodrilidae is a taxon of interstitial annelids constituted by the terrestrial *Parergodrilus heideri* (monotypic genus up to date), reported throughout Europe but also in Korea and North America, and the genus *Stygocapitella*, which includes eleven species from the upper shore of sandy beaches distributed along Europe and other regions of the world. Orbiniidae contains more than 200 described species spread over 20 valid genera, varying in size from a few millimeters up to 30 cm, distributed globally and living in a wide variety of soft bottoms. Improving the knowledge on these two sister-taxa is crucial for the understanding of the evolution to interstitial forms by progenesis in Annelida.

Keywords: biodiversity; biology; distribution; diversity; ecology; phylogeny; taxonomy



Citation: Meca, M.A.; Zhadan, A.; Struck, T.H. The Early Branching Group of Orbiniida Sensu Struck et al., 2015: Parergodrilidae and Orbiniidae. *Diversity* **2021**, *13*, 29. <https://doi.org/10.3390/d13010029>

Received: 17 November 2020

Accepted: 21 December 2020

Published: 13 January 2021

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1. Introduction

While abounding the concepts of Sedentaria and Errantia, Fauchald [1] erected Orbiniida comprising Orbiniidae, Paraonidae and Questidae due to the lack of antennae and palps and possession of an eversible pharynx and biramous parapodia with simple chaetae. All three taxa had before been regarded as part of Sedentaria, e.g., [2–4]. Based on their morphological-cladistic analyses, Rouse and Fauchald [5] regarded all three taxa also as a monophyletic group within Scolecida. Molecular data placed Questidae within Orbiniidae but Paraonidae as probably more closely related to Cirratulida see [6,7]. Struck et al. [8] re-erected the groups Sedentaria and Errantia but with changes in their taxon composition; Orbiniidae was in this study part of Errantia. However, a following study showed that this was caused by a single erroneously assigned paralogous gene and instead Orbiniidae had to be placed in Sedentaria [9]. Subsequent phylogenomic studies generally found Orbiniidae as sister to or being part of the sistergroup to the remaining Sedentaria [7,10,11].

As part of this placement within Sedentaria, Orbiniida has been recognized again, but with a different taxon composition [12]. Besides Orbiniidae (including Questidae), it now comprises several interstitial annelid groups, each of which were at one point assigned to the polyphyletic Archannelida (see [7,13] and the article on interstitial annelids in this issue for a more detailed discussion). Namely, these taxa belonging to Orbiniida are Parergodrilidae, Dinophilidae, *Diurodrilus*, *Apharyngtus* and Nerillidae [12]. According to the authors, the evolution of these groups is best explained by recurrent independent events of

progenesis, which most likely happened in an orbiniid-like ancestor. However, depending on the analytical strategy applied some recent analyses showed that Dinophilidae are placed outside Orbiniida and together with *Lobatocerebrum* as sister to Pleistoannelida, while independent of the strategy Parergodrilidae, *Apharyngtus* and *Diurodrilus* remained closely related to Orbiniidae [11]. Nerillidae were not included in the analyses and, hence, no data have been provided yet excluding them from Orbiniida. Of all interstitial taxa possibly placed within Orbiniida, the close relationship of Parergodrilidae and Orbiniidae is the best supported by molecular data [12,14–21].

In conclusion, Orbiniida as of today consists of Orbiniidae, Parergodrilidae, Nerillidae, *Apharyngtus* and *Diurodrilus* as well as possibly Dinophilidae [7,10–12]. However, for reasons of consistency all interstitial taxa except Parergodrilidae are treated in the article on interstitial annelids in this issue. Here, we will review the recent advances of our knowledge about the biology, ecology, taxonomy and species diversity as well as identify relevant gaps of knowledge to understand the species diversity, distribution and dispersal of Orbiniidae and Parergodrilidae.

2. Parergodrilidae Reisinger, 1925

Parergodrilidae is a taxon of small-sized, stout annelids of 0.8 to 2.8 mm body length to 0.1 to 0.25 mm body width, which until very recently consisted of only two species in two genera, namely *Stygocapitella subterranea* Knöllner, 1934 and *Parergodrilus heideri* Reisinger, 1925. The latter is a terrestrial polychaete, while the former lives in the transition zone from the marine environment to the terrestrial habitat. Parergodrilidae was in its first description placed within Archiannelida [22], while others regarded them as clitellates [23]. Moreover, before Karling [24] it was not recognized that *S. subterranea* and *P. heideri* constitute one taxon and *S. subterranea* was regarded as closely related to Capitellidae [25]. After Karling [24] Parergodrilidae was often considered as closely related to Ctenodrilidae but without the indication of morphological autapomorphies, e.g., [1,26]. Alternatively, a closer relationship to *Hrabeiella periglandulata*, another terrestrial polychaete species, has been suggested [27]. However, none of the relationships was strongly supported by morphological data, e.g., [28–30]. Accordingly, the morphological-cladistic analyses by Rouse and Fauchald [5] found Parergodrilidae as *in certae sedis* within polychaetes. Nowadays, however, as mentioned above molecular data unequivocally support a sistergroup relationship to Orbiniidae.

2.1. *Parergodrilus heideri* Reisinger, 1925

Parergodrilus heideri was first described from leaf litter samples in Austrian beech forests by Reisinger [22] (Figure 1D). It had been assumed for some time that the species is restricted to this kind of habitat, specifically the leaf-litter, organic soil layer of montane beech forests, which is humid, but not water-logged, and slightly alkaline to moderately acid, e.g., [30–35]. However, the species has now been recorded from different habitats including different forest types like spruce and maple forests, low-land, wetter and more acidic ones, e.g., [31,36–40]. Hence, the original restricted distribution could reflect more biases in sampling than restriction of the species. Nonetheless, the species seems to occur only in the humus-rich upper layer of soil, often within the first three to six centimeters.

Interestingly, there is a strong difference in the sex ratio favoring females with ratios of 1:8 to 1:170 [28–30,33,41]. Accordingly, in the beginning only female specimens were found and considered to be hermaphrodites [22]. However, later these were recognized as females and *P. heideri* is generally regarded as being gonochoristic, while some doubts remain about the latter conclusion [24,33,42–45]. Different reasons for this pronounced sex ratio imbalance have been suggested, which include differences in behavior, longevity and size [33]. In Austria, males have only been found during the summer months, while in a German beech forest, mature females with vitellogenic oocytes and spermatozoa in the receptacula seminis have been found throughout the year [33,45]. Hence, it is uncertain if reproduction occurs throughout the year, only during the summer period

or only insemination occurs during the summer months with spermatozoa stored in the receptacula seminis throughout the year. Eggs are deposited in cocoons, which are attached to the substrate. The eight to ten day-long development is direct and four-chaetiger stages of 60–80 μm body length hatch from the cocoon. Early cleavage resembles an unequal spirale cleavage [33].

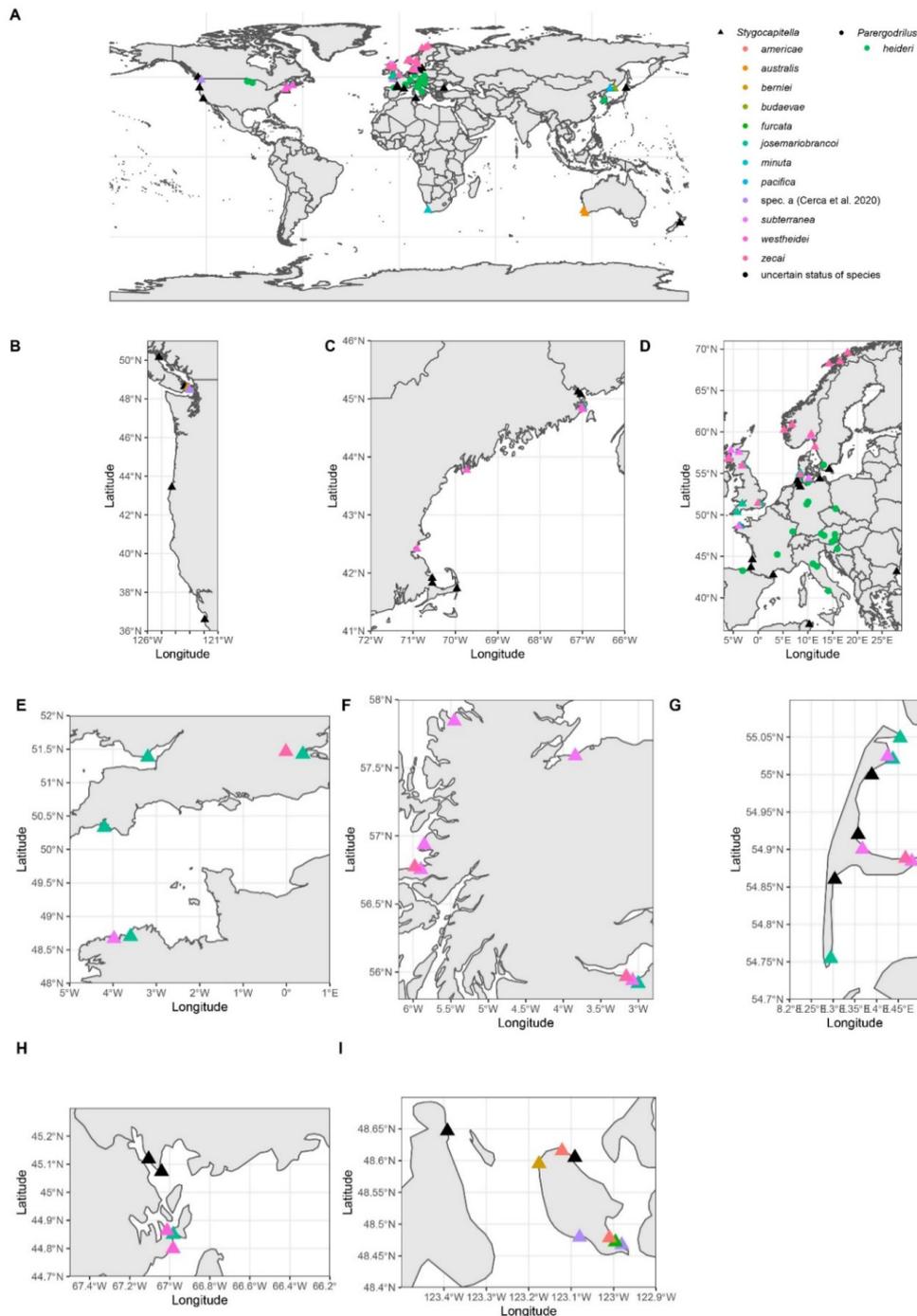


Figure 1. Map of known records for both *Stygocapitella* (triangles) and *Parergodrilus* (circles). Color codes for the different species are shown in the upper right legend. Records of *Stygocapitella* with known species affiliation (see text) are shown as black triangles. (A) Whole world; (B) North America Pacific coast; (C) North America Atlantic coast; (D) Europe; (E) The Channel; (F) Scottish coast; (G) North Sea island Sylt; (H) Passamaquoddy Bay and adjacent waters; (I) San Juan Island. Maps were generated using the R packages tidyverse, ggplot2, sf, rnaturalearth, rnaturalearthdata, rnaturalearthhires, ggmap and ggpubr.

In *P. heideri*, males possess ten chaetigers (Figure 2), while females have only eight. Both also have an additional achaetigerous segment after the peristomium [33]. Each chaetigerous segment has a pair of bundles, which contain two very simple, oligochaete-like chaetae (Figure 2). For a more detailed description of the morphology and internal anatomy please see Purschke [45]. As there is at present only a single species recognized in the genus *Parergodrillus*, no morphological diagnostic features for species identification are known. However, the possible presence of cryptic species has been suggested. *Parergodrillus* can be differentiated from *Stygocapitella*, based on several characters, which among others include the presence of simple chaetae, the lack of bilimbate and whipped chaetae as well as of two praepygidial achaetigerous segments (Figure 2).

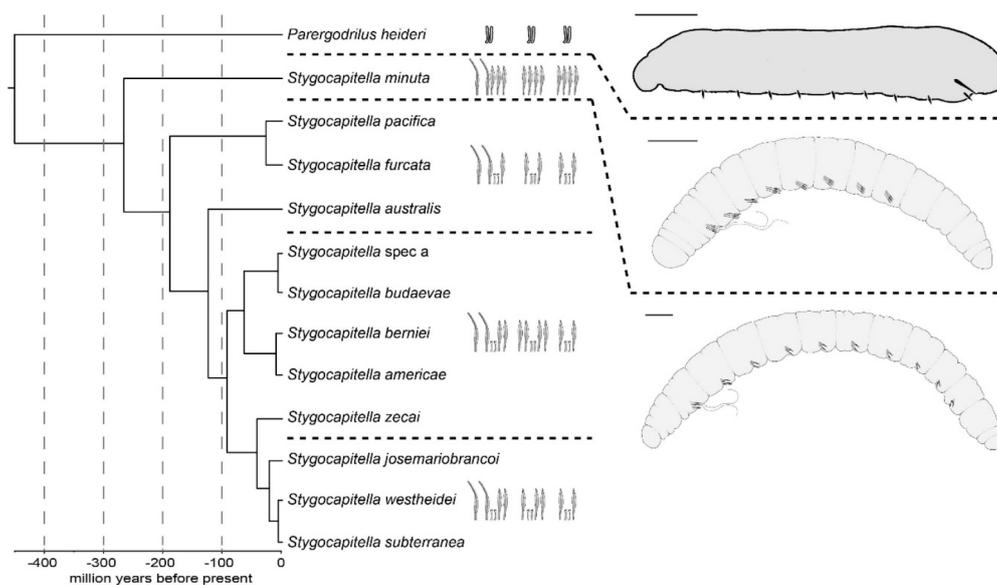


Figure 2. Parergodrilidae based on different sources (Cerca et al. [46]; Cerca et al. [47]; Struck et al. [48]). Besides the species names the different chaetal patterns are shown for the 1st, 2nd and 3rd chaetiger. All following chaetigers have the same pattern as shown for the 3rd. Schematic drawings of the general morphology of *Parergodrillus* and the two different ones for *Stygocapitella* are based on Reisinger [33] and Struck et al. [48]. The scale bars equal 125 μm .

Distribution

Besides the first records from Austria, *P. heideri* has been found throughout Europe including records from Spain, Italy and Croatia in the South to Sweden in the North (Figure 1D), e.g., [28,30–32,34,36,38–41,49,50]. Recently, also first findings outside Europe have been reported, specifically in Korea and North America (Figure 1A) [37,51]. Hence, the known distribution of *P. heideri* has been strongly expanded in recent years. Even though *P. heideri* is very well studied with respect to morphology, anatomy, and early development by comparison to other meiofaunal species for more details see [45] and is relatively well documented from Europe, many questions concerning the genus' species composition and diversity still remain uncertain or unanswered. The increasing records from atypical habitats indicate that the habitat restrictions are less rigorous than originally considered. Hence, what are the habitat requirements for this species? How sensitive is it truly to desiccation and flooding, different forest types and soil conditions? The center of distribution thus far seems to be Europe and the distribution is seemingly restricted to the Northern hemisphere. Is the lack of *Parergodrillus* species from the Southern hemisphere and the sparse distribution outside Europe true or does it just reflect a sampling bias with stronger efforts having taken place in Europe? Finally, a thorough taxonomic revision of the species including also molecular data from all records around the world and from different habitats has not been conducted yet. Hence, it is uncertain if cryptic species are present within this species and if such cryptic species could be associated with different habitat

preferences and/or different regions. For example, do the records outside Europe truly represent the same species? In the same vein, the molecular data will also allow one to assess if the records outside Europe could indicate recent invasions, for example, alongside earthworm introductions or if the species are native species in these areas. Schlaghamerský and Frelich [37] regard the species as native as they regard transport of such small annelids as part of commercial fish bait of anglers (i.e., earthworms) as not very likely. However, they also state, “an initial introduction to North America with soil from Europe cannot be fully excluded”.

2.2. *Stygocapitella Knöllner, 1934*

Stygocapitella was first described by Knöllner [25] from a wide sandy beach with medium coarse sediments at the German Baltic coast (Figure 1D). Following records also found *Stygocapitella* at similar sandy beaches with medium coarse sediments (Figure 3A–C), e.g., [24,52–56]. However, more extensive sampling also at beaches, which are not wide with only medium coarse sediments, revealed that *Stygocapitella* also occurred at them [30,43,52,57], sometimes in high abundance (personal observations). These beaches could be wide or narrow, with or without stones and pebbles on top of or intermixed with medium-coarse sediment (Figure 3D–G). Usually the specimens can be found around or up to 18 m above high tide level, but at some beaches of the Thames (i.e., Cutty Sark, UK) and the Nærøfjord (Bakka, Norway) they are found substantially below high tide level or even at low tide level (personal observations). In the beaches, they occur usually in the first 20 cm of depth but can also be found as deep as 1 m [30,58,59]. Throughout the year the abundance is around 10–20 specimens/100 cm³ in most beaches investigated in more detail thus far, but it can occasionally be three to four times higher [30,58,59]. During winter months, the specimens migrate to deeper layers to avoid freezing and the same migration pattern can be observed to avoid desiccation in the uppermost layers [30,58,59]. Generally, *Stygocapitella* seems to prefer the zone of damp sand in the beach with 3% water content in relation to the dry weight of the sediment, but they seem to sustain also water content up to 21.5% [30]. The latter point is further supported by records closer to low tide level, which means that for at least a few hours each day these animals experience complete water saturation. In summary, *Stygocapitella* is usually found in medium coarse sediments in the damp zone of the upper shore of sandy beaches but occasionally also in sediments with higher water content. These beaches can be differently exposed to tides, small or wide, with or without stones and pebbles.

In contrast to *P. heideri*, the sex ratio in *Stygocapitella* is 1:1 and no dimorphism is visible. Reproduction seems to take place throughout the year as all juvenile stages can be observed in all months. The direct development resembles the one of *P. heideri* with eggs being deposited in cocoons and hatching at the four-chaetiger stage. However, the hatchlings are larger with a body length of about 0.75 mm and do not possess the full complement of chaetae in the first two segments, which develop in the later juvenile stages. Cleavage pattern and duration of development are unknown. In general, 70–90% of the populations are immature adults [45].

The first described species of *Stygocapitella* was *S. subterranea* by Knöllner [25]. *Stygocapitella subterranea* possesses ten chaetigers plus one achaetigerous segment after the peristomium and two achaetigerous before the pygidium. Three different types of chaetae are present: whipped-like chaetae, bilimbate chaetae and forked chaetae (Figure 2). The chaetal composition at the chaetigers shows a specific pattern in each pair of bundles. At the first chaetiger, each bundle possesses two whipped-like, two forked and two bilimbate chaetae. The second one has one bilimbate, two forked and two bilimbate chaetae. Finally, the third and all following ones have one bilimbate, two forked and one bilimbate chaetae (Figure 2). For a more detailed description of the morphology and internal anatomy please see Purschke [45].

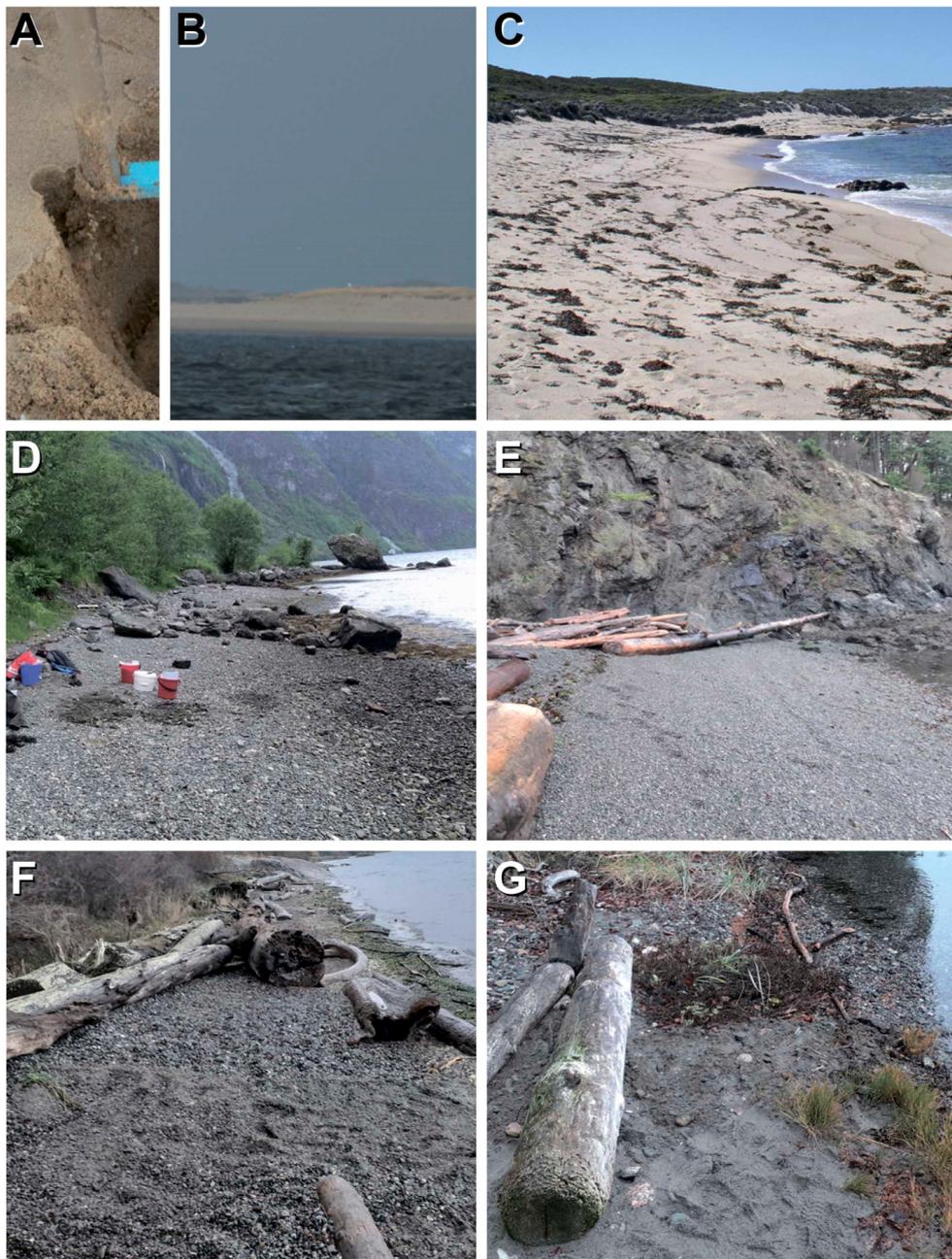


Figure 3. Pictures of the different beaches with known records of *Stygocapitella*. (A) Medium coarse sediment from Hausstrand, North Sea island Sylt; (B) Ellenbogen, North Sea island Sylt; (C) Sarge Bay, Australia; (D) Bakka, Norway; (E) Reid State Park, San Juan Island; (F) 4th of July beach, San Juan Island; (G) Roche Harbor, San Juan Island.

2.2.1. Distribution

After the first description of *S. subterranea* from the German Baltic Sea [25], this species has also been found at numerous additional beaches in Europe including the North, Baltic, Mediterranean, and Black Sea and the European Atlantic coast (Figure 1D) [24,30,44,50,53,55,58–67]. It has also been found at several beaches outside Europe, in specific North America, Australia, New Zealand and Japan (Figure 1A–C) [30,52,54,56,57,68]. Interestingly, all records in both hemispheres are so far restricted to the boreal and temperate zones barely reaching into the subtropical zone (Figure 1A). As there have been several attempts focusing on this species, the distribution gap in the tropics and subtropics seem not to be a sampling effect [45]. All of these records

were assigned to *S. subterranea*. Therefore, *Stygocapitella* was often considered a typical example of the Meiofauna paradox as it had a cosmopolitan distribution but seemingly no active or passive long-distance dispersal stage [57,60,69,70]. However, a first molecular study with one population each from the US Pacific, US Atlantic and European Atlantic coast indicated that no gene flow between these three populations occurs [57], but no taxonomic action was taken. Additionally, analyses of sperm ultrastructure revealed no differences between the same three populations (Purschke personal communication).

2.2.2. Taxonomy

The first record of *Stygocapitella*, which was not assigned to *S. subterranea*, was *S. minuta* Struck et al., 2017, which was found in South Africa (Figure 1A) [48]. The specimens are clearly different from *S. subterranea* as *S. minuta* has only eight chaetigers but four achaetigerous segments in front of the pygidium (Figure 2). Moreover, mature adults are only about 1.5 mm long and hence much smaller than *S. subterranea*. Forked chaetae are lacking altogether and two additional bilimbate chaetae are present instead. As part of this study specimens from the Australian localities were investigated anew and it could be shown that even though they were overall similar to specimens from the type locality they differed in the chaetal composition. They have one bilimbate chaeta less in the first and second chaetiger (Figure 2). Therefore, these specimens were described as *S. australis* Struck et al., 2017 (Figures 1A and 2). The morphological results were supported by molecular data showing that there were deep divergences between the three species dating back about 260 and 80 million years, respectively.

This study was followed by a more thorough revision of the genus *Stygocapitella* by Cerca et al. [46] including several populations from both North American coastlines, Europe and a new record from the Russian Pacific coast. This study found that besides the *S. minuta*-, *S. australis*- and *S. subterranea*-morphotypes a fourth morphotype can be observed, which is very similar to the *S. subterranea*-morphotype but differs in the chaetal composition of the second chaetiger by possessing one more bilimbate chaeta (Figure 2). In addition, a few species are smaller than others. However, species delimitation in this study had to mostly rely on molecular data using two mitochondrial and two nuclear markers. In total, twelve different species could be differentiated of which eight were described anew. One species could not be described as no holotype could be assigned. Two of these eight species, *S. pacifica* and *S. budaeva*, were completely new to science as they were collected from the Russian Pacific coast, which has not been sampled previously (Figure 1A). Along the North American Pacific coast, three species, *S. furcata*, *S. berniei* and *S. americanae*, were described (Figure 1A,B). Hence, including the undescribed species four species previously assigned to *S. subterranea* occur on San Juan island alone (Figure 1I). At the Northern European coastlines, two additional species, *S. josemariobrancoi* and *S. zecai*, are now recognized besides *S. subterranea* (Figure 1A,D,E–G). The European species *S. josemariobrancoi* also has a record from the North American Atlantic coast (Figure 1H), where *S. westheidei* has also been found (Figure 1H). Additional support for these delimitations is gained from the fact that species occur in sympatry at each of these coastlines, which in this case means that they occur within the same beach, often within the same 50 cm³ of sediment (Figure 1A,F–H). Hence, the number of formally described species has increased from one to eleven in recent days and only three of them are due to new records, while the remaining ones have been recorded as *S. subterranea* before. All species are cryptic species except for *S. minuta*, as it is the only one, which can unambiguously be distinguished from all other species based on its morphology [71]. Accordingly, the previously assumed cosmopolitan distribution of *S. subterranea* is no longer given. While several species still show a relatively broad distribution along European, American or Australian coastlines, other species (i.e., *S. pacifica*, *S. budaeva*, *S. furcata*, *S. berniei*, *S. americanae* and *S. minuta*) seem to have a very restricted distribution. However, in these latter cases only one population (*S. pacifica*, *S. budaeva*, and *S. minuta*) or very few populations in close vicinity to each other (*S. furcata*, *S. berniei*, and *S. americanae*) have been studied. Finally, all previous records, which have

been assigned to *S. subterranea* (black triangles in Figure 1), need to be investigated again to assign them to one of these species or even identify a new one. As the morphological characters to differentiate the species from each other are very limited and except for *S. minuta* restricted to the chaetal pattern at the first two chaetigers and to some degree body size, these new analyses need to include molecular data to be more reliable. As long as this has not been done these records should be treated as *Stygocapitella* sp.

Besides the geographic distribution, the temporal distribution has also been studied in this complex of cryptic species [47]. It was confirmed that the radiation of *Stygocapitella* took place about 260 million years ago (Figure 2). More interestingly, the three morphotypes each represented by several species have not changed for at least 18 million (*S. subterranea*-morphotype) to 140 million years (*S. australis*-morphotype). [47]. This can also be shown when the morphological disparity is compared to genetic distance. The morphological disparity in this group is about five to eight times lower than, for example, in its sistergroup Orbiniidae or another interstitial group, Nerillidae (Figure 4) [47]. Even at very high genetic distance, it is only half the disparity of these two groups. Hence, these species are clearly affected by morphological stasis and include species with the longest known period of stasis namely *S. pacifica*, *S. furcata* and *S. australis* [46,47].

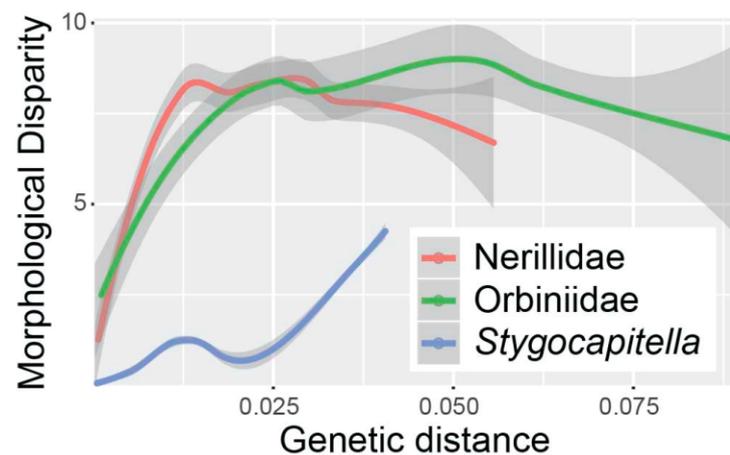


Figure 4. A simplified re-drawing of Figure 5C of Cerca et al. [47]. The plot shows the relationship of morphological disparity measured by pairwise MMD indices in relation to genetic distance measured by pairwise genetic distances of the nuclear 18S rRNA marker. The values for *Stygocapitella* are compared to the sistergroup of Parergodrilidae, Orbiniidae, and another interstitial annelid group, Nerillidae. The grey area indicates the 95% confidence interval of the fit (line) to the data points (not shown).

2.2.3. Conclusions

Besides large-scale differences in the distribution along different oceanic coastlines, no other differences, for example in macroecological factors like annual average temperature, could be detected so far between the species [46,47]. Hence, it is not certain yet, which factors drive distribution, speciation and stasis in these species. However, detailed studies of their different interstitial environments are lacking. The first studies in Europe in this respect [30,58,59,61,62] can only be starting points to investigate these relationships and dependencies and in the light of the new taxonomy the sampling is not sufficient, because what was thought before to be the result of one species is now representing populations from three different species and also includes some sympatric populations. For example, the beaches on the North Sea Island sampled in these studies contain only very rarely *S. subterranea*, but *S. josemariobrancoi* or species of uncertain status (Figure 1G) [30,58,59].

The dates listed above for divergence of morphotypes or species are too young to be able to explain the recent day distribution of *Stygocapitella* species by vicariance [46,48]. Hence, this distribution must have been established by occasional long-distance dispersal

events across oceans including at least two times dispersal across the equator leading to the present-day distribution gap [46]. However, how this was accomplished is still uncertain. Moreover, the colonization of *S. josemariobrancoi* of the North American Atlantic coast must have happened very recently as these specimens share identical haplotypes with European specimens across all molecular markers [46]. This could have possibly been human-mediated distribution, maybe by ballast sand. However, this scenario seems not to occur otherwise in *Stygocapitella* [72].

In summary, this whole group is very well suited to study the factors causing morphological stasis as well as the drivers of speciation in cryptic species as it allows studying change and stasis at different time scales using morphological, ecological, biogeographic, reproductive biological, developmental, physiological, population dynamic and genomic data. These kinds of data will also help to understand if the different species occupy different microniches allowing to survive in sympatry. However, these kinds of data are also lacking to a very large degree and research in this direction is only just beginning. Moreover, given the recent results there is a high probability that the number of species in this genus will still substantially increase. Finally, due to strong sampling efforts many records are known from Europe and North America, but this is not the case on the other continents. Given the recent findings in South Africa and Russia it is very likely that they also occur in the temperate zones of the Southern hemisphere and along the Western Pacific coastlines is East Asia.

3. Orbiniidae Hartman, 1942

Orbiniidae are sedentary annelids which can be distinguished generally from the rest of Annelida by a rounded or pointed prostomium without appendages, one or two achaetous rings of the peristomium (Figure 5A), body separated into thorax and abdomen bearing biramous parapodia (Figure 5B) and branchia disposed dorsally in the abdomen (Figure 5C). This general scheme fits with the medium- to large-sized genera like *Scoloplos*, *Leitoscoloplos*, *Leodamas*, *Naineris*, *Orbinia* and *Phylo* (Figure 5D–F), being at the same time the most frequently reported genera and also the most species-rich genera. The adults of most of the species of these genera measure between 3.5 and 20 cm in length, though others can be up to 30 cm long (e.g., some *Orbinia*). On the other hand, in the small-sized taxa (with adults measuring few mm) like in *Orbiniella* or *Pettibonella* (Figure 5G), the distinction of the body regions is weak or lacking and some species do not possess branchia (Figure 5H). Moreover, *Orbiniella branchiata* Hartman, 1967 [73] bears three achaetous rings in the peristomium. The presence of crenulations in the capillary chaetae, the autapomorphy of the family, is characteristic to all genera independent of their size and defines the attribution of a species to Orbiniidae [6,74] (see the part on chaetae typology in the discussion on taxonomical characters from this subchapter for details).

The most relevant regional identification keys for orbiniids are those of Day [3] for South Africa, Day [75] for North Carolina (USA), Day [76] and Zhadan [77] for Australia and New Zealand, Kirkegaard [78] for the North Sea, Blake [79] for Southern California (USA), Lopez [80] for the Western Mediterranean and Diaz-Diaz et al. [81] for the Caribbean Sea. A number of keys for the different orbiniid groups are available, such as Gillet [82] and Parapar et al. [83] for *Orbiniella*, Solis-Weiss and Fauchald [84] for Protoaricinae, Sun and Li [85] for 22 species of *Orbinia*, Sun et al. [86] for 30 species of *Leodamas* and Blake [87] for the seven deep-water species of *Leitoscoloplos* from the Eastern Pacific.

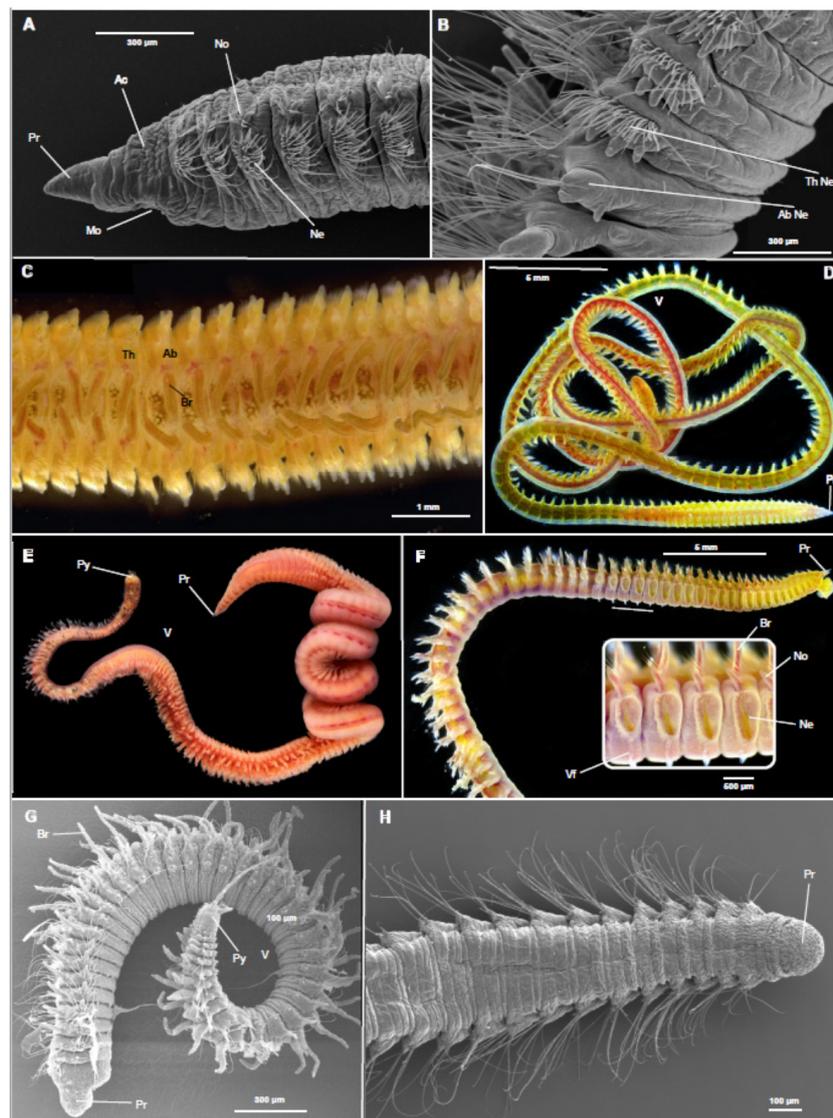


Figure 5. Scanning electron microscopy (SEM) and light microscopy images of different orbiniiids. (A). *Scoloplos armiger*, anterior end. (B). *Orbinia* cf. *armandi*, transition thorax-abdomen. (C). *Naineris laevigata*, detail of the dorsum with branchiae. (D). *Leodamas chevalieri*, general view of a living specimen. (E). *Scoloplos armiger*, general view of a living specimen. (F). *Phylo kuwaitica*, anterior-mid body view of a living specimen and detail of posterior thoracic chaetigers. (G). *Pettibonella multiuncinata*, general view. (H). *Orbinella* sp., dorsum of the anterior end. Ab. Abdomen; Ab Ne. Abdominal Neuropodium; Ac. Achaetous ring; Br. Branchiae; Mo. Mouth; Ne. Neuropodium; No. Notopodium; Pr. Prostomium; Py. Pygidium; V. 1478 Ventrum; Vf. Ventral fringe. Photo E is not scaled.

3.1. Systematics

3.1.1. Morphological Era

Originally orbiniiids carried the name Ariciidae Malmgren, 1867 [88] which has been subsequently changed by Hartman [89] to Orbinidae, as the type genus of the family, *Aricia* Savigny 1822 [90], was preoccupied in Lepidoptera. *Orbinia* Quatrefages 1866 [91] had been designated as the type genus few years earlier [92]. The first important taxonomic work on Orbinidae systematics belongs to Eisig [93], who reviewed previous works and suggested most of the currently accepted terminology. Later, Hartman [94] performed the revision of orbiniid systematics, in which she redefined all genera, reviewed most of the common species and divided the family into two subfamilies based on the number of the peristomial rings: Orbininae (one peristomial ring) and Protoariciinae (two peristomial rings). In the same year, Pettibone [95] reviewed several genera and species based on the material from

the east coast of North America, describing three new species. The system of Orbiniidae suggested by Hartman [94] was largely accepted until the end of the 20th century and it is still the most comprehensive and detailed work on orbiniids. Nonetheless, there were important contributions to the orbiniid systematics. Day [75] reviewed the generic system for the subfamily Orbiniinae and Solis-Weiss and Fauchald [84] did the same for the subfamily Protoariciinae. Day [76] erected the genus *Leitoscoloplos* and Mackie [96] revised the genus, transferring some species to the genus *Scoloplos*. Gillet [82], Parapar et al. [83], and Blake [87] reviewed *Orbiniella* and Badalamenti and Castelli [97] *Schroederella*. Blake [98] described *Methanoaricia dendrobranchiata*, a new species and genus (monotypic up to date) reported from the seeps of the Gulf of Mexico. The discovery of this genus led to the new revision of the whole family. This resulted in the division of Orbiniidae into three subfamilies: Orbiniinae, Microrbiniinae and Methanoariciinae, established for the unusual *M. dendrobranchiata*. Blake [98] demonstrated that the number of rings in peristomium can vary during the ontogeny in several genera and excluded it from orbiniid taxonomy. Following Blake [79,98], many protoariciins represent the juveniles of other orbiniid genera suggesting synonymization of *Pararicia* with *Protoariciella* or *Naineris* in Blake [79].

3.1.2. Genetics Era

The first molecular phylogenetic study of Orbiniidae was conducted by Bleidorn et al. [99]. It included eight orbiniid species among other annelid genera and received strong support for a close relationship between orbiniids and Questidae Hartman, 1966 [100]. Currently, questids are considered part of Orbiniidae [6,101], constituting the genus *Questa*. Three molecular phylogenetic reconstructions focusing on relationships between orbiniid genera reported several genera as paraphyletic [19,101,102] without support for Hartman's [94] or Blake's [98] classifications. Bleidorn [19] confirmed the placement of *Methanoaricia dendrobranchiata* within Orbiniidae based on two genes (16S and 18S). Twenty species belonging to 11 different genera were included in the analyses, in which *Scoloplos*, *Leitoscoloplos*, *Orbinia* and *Phylo* were recovered as paraphyletic. An extension of this phylogenetic reconstruction was made by Bleidorn et al. [101] (Figure 6A) adding to the analyses four more genes (cox1, cox3, nad1 and nad4), six more species and a morphological character matrix. Similar results (i.e., paraphyly of the former genera except for *Naineris*, which was monophyletic) were obtained even with the expanded dataset, and most of the traditional characters revealed to be useless for phylogeny. The authors suggested that repeated loss of characters and progenesis were the main processes in the evolution of orbiniids. In addition, some of the small-sized species with two peristomial rings (i.e., belonging to Protoariciinae sensu Hartman, 1957) included in the analyses showed significant genetic divergence and, thus, good evidence of being valid species. However, one specimen identified as *Protoariciella uncinata* Hartmann-Schröder, 1962 [103] was found to be genetically identical with the individuals of *Leodamas tribulosus* (Ehlers, 1897) [104]. This has partly corroborated the hypothesis by Blake [79,98] that species/genera of Protoariciinae might be misidentified juvenile stages of Orbiniidae. The latest phylogeny focused on Orbiniidae by Zhadan et al. [102] included 53 specimens belonging to 33 species from 12 genera. Three NJ analyses performed independently for COI, 16S and 18S (Figure 6B–D) recovered all genera tested by Bleidorn et al. [101] as paraphyletic; however, the tree topologies were different in the two studies, with *Naineris* being paraphyletic in Zhadan et al. [102].

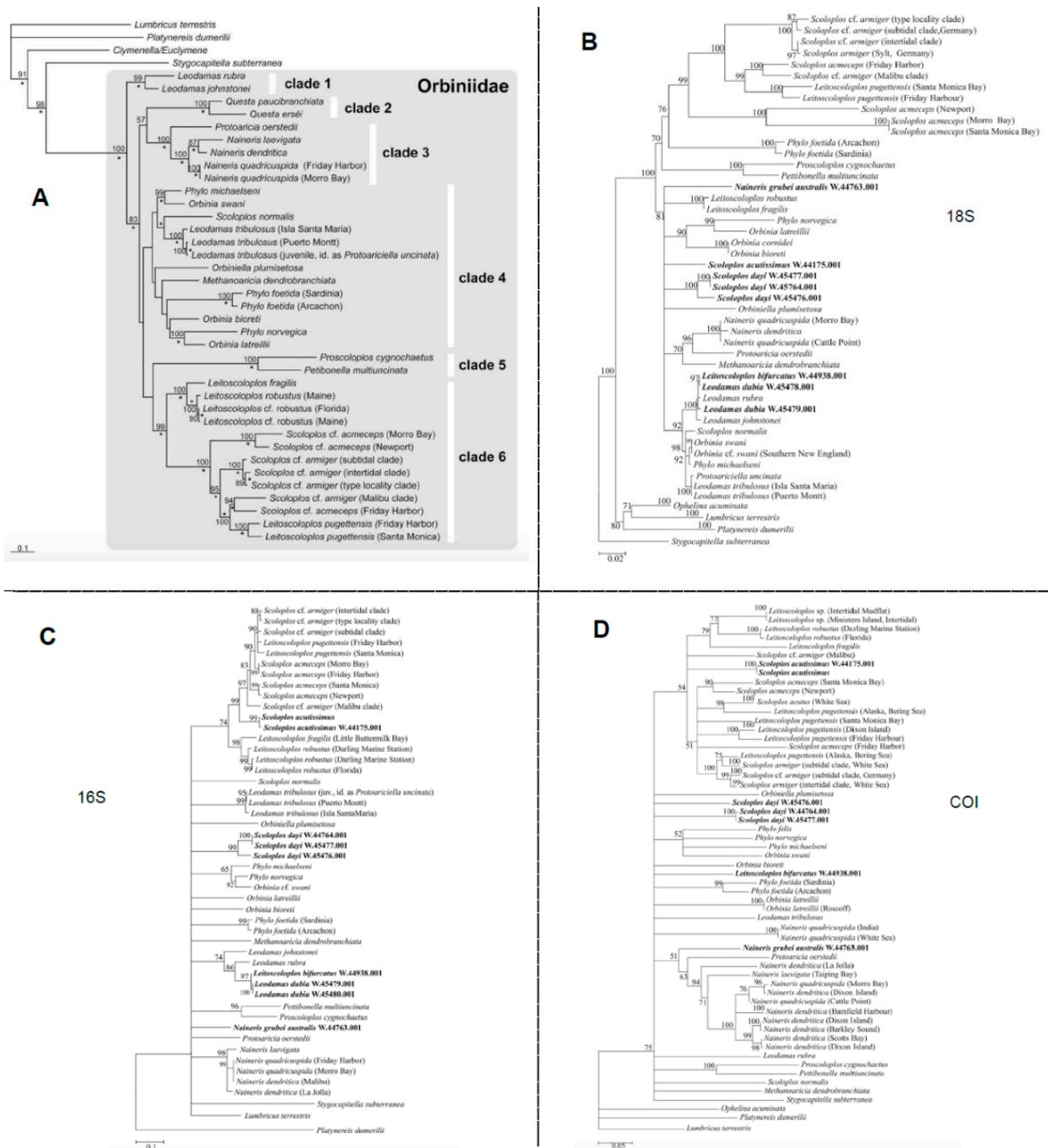


Figure 6. The four phylogenetic inferences performed for Orbiiniidae in Bleidorn et al. [101] (A) and Zhadan et al. [102] (B–D). A. Maximum likelihood analyses based on six concatenated gene fragments (18S, 16S, cox1, cox3, nad1 and nad4), resulting in six orbiiniid clades. Numbers at the nodes show bootstrap values from 1000 replicates and asterisks (*) indicate nodes with a posterior probability of >0.95 in the Bayesian analysis. (B–D). Three Neighbor Joining analyses based on individual genes (18S, 16S and COI) marked in each tree. The bootstrap values were obtained from 1000 replicates. Most of the clades from A changed in adding species in (B–D).

3.1.3. Current State: Traditional Taxonomy vs. Genetics

Currently, Orbiiniidae comprise more than 200 accepted species within 20 valid genera (see the Tables S1 and S2 in Supplementary Materials). Following Bleidorn and Helm [6] these numbers should be taken “with a grain of salt” given the high number of upcoming papers describing new orbiiniid fauna [87] and the paraphyly of most of the genera as shown by the molecular analyses. We consider the monotypic genus *Scolopella* as

nonvalid following Bleidorn and Helm [6], as it is undistinguishable from the juveniles of *Leitoscoloplos* and consequently synonymized. With his monographs of 2017 [74] and 2020 [87], Blake has updated the previously accepted system for Orbiniidae [98], emending the two subfamilies Orbiniinae (*Berkeleyia*, *Califia*, *Leitoscoloplos*, *Leodamas*, *Naineris*, *Orbinia*, *Phylo*, *Protoaricia*, *Schroederella*, *Scoloplella*, *Scoloplos* and *Uncorbinia*) and Microrbiniinae (*Microrbinia*, *Orbiniella*, *Proscoloplos* and *Pettibonella*), and reviewing the definition of ten genera. *Protoariciella* was included in Orbiniinae in Blake [74] as problematic and not considered in Blake [87] since only the type species *Protoariciella uncinata* bore thickened notopodial chaetae in the posteriormost segments, the diagnostic character for the genus. Furthermore, one individual identified as *P. uncinata* was shown to be genetically identical to *Leodamas tribulosus* in Bleidorn et al. [101]. The genera *Pararicia*, *Paraorbiniella* and *Questa* were not considered by Blake [74,87] in his redefinition of the orbiniid subfamilies, whilst *Scoloplella* was included into Orbiniinae.

The morphological characters used in the Blake's generic system generally were the same that Hartman used in her revision from 1957, namely: the shape of the prostomium, the number of thoracic segments, the position of the first pair of branchiae, the shape of the parapodia, the presence/absence of subpodial papillae and their number, and the chaetal characteristics. The characters show high degree of variation among orbiniid species and genera with some species having ambiguous generic placement. This makes the orbiniid system unresolved which has been suggested by Mackie [96] in his revision of *Leitoscoloplos* even before the molecular analyses emerged. *Leitoscoloplos multipapillatus* Alcántara and Solís-Weiss, 2014 [105] is an example of a species that combines diagnostic characters of two genera. The species does not have hooks in the thoracic neuropodia characteristic to *Leitoscoloplos* but bears subpodial and stomach papillae, which, together with the absence of the spear-like spines, suggests its placing within *Orbinia*. Another example of ambiguous attribution of a species to a genus is *Naineris setosa* (Verrill, 1900) [106], a large orbiniid with a *Naineris*-like rounded prostomium bearing only camerated capillaries in the thoracic neuropodia, the diagnostic character of *Leitoscoloplos*. Furthermore, *Orbinia sagitta* Leão and Santos, 2016 [107] was erroneously placed into *Orbinia* lacking subpodal lobes and having *Leodamas*-like uncini, being similar to *Leodamas sinensis* Sun, Sui and Li, 2018 [86] (authors' observations).

A phylogeny with sufficient taxon coverage and amount of genetic data is required as a first step for the revision of the orbiniid system. Once the robust phylogeny of the family is constructed, the morphological revision of the well-supported monophyletic clades, in search of synapomorphies, is necessary in order to provide supported system of orbiniids. It is worth saying that none of the known orbiniid species was originally described, both traditionally and currently, incorporating molecular analyses and the only available genetic data in public databases (as GenBank and BOLD) comes from the commented phylogeny papers of Bleidorn, Zhadan and collaborators [19,101,102], other few works as Kruse et al. [108], Meyer et al. [109] or Carr et al. [110] or from unpublished data.

3.2. Discussion on Taxonomical Characters

Naineris and *Protoaricia* are sister groups forming well supported clade on most phylogenetic trees [101,102]. This is the rare case in orbiniid phylogeny when morphological characters are congruent with molecular data. Besides the presence of statocysts mentioned in Bleidorn et al. [101], these two genera also share the dorsal ciliated ridges between branchial bases in abdominal segments and special chaetae in thoracic—subuluncini and cauduncini [93] (p. 216, Figure XIV); [94] (p. 219–221). Progenetic evolution is the best explanation for the similarities between *Protoaricia* and *Naineris* [19,101]. Phylogenetic studies with bigger taxon coverage of both genera are needed to confirm this statement. In the following, we discuss some taxonomical characters which are often overlooked or not described well but can be useful for phylogenetic analysis of Orbiniidae.

Dorsal organs are paired ciliated patches usually with a nonciliated mound between them, situated on all abdominal and sometimes on posterior thoracic segments. They are

serially homologous to nuchal organs [6,94]. In living and sometimes in preserved worms, dorsal organs are marked with pigmentation; however, often the shape of the pigmented spots differs from the shape of ciliated dorsal organs seen with SEM. The dorsal organs are rarely illustrated and described but potentially can serve as genus- or species-specific character. For example, *Scoloplos* and *Leitoscoloplos* species have dorsal organs as straight or curved ciliated stripes, whereas *Naineris* bear five pairs of round ciliated spots [102].

The most promising source of characters useful for phylogenetic analysis of Orbiniidae are shape, number and distribution of chaetae, especially in thoracic neuropodia. Thoracic neurochaetae are organized in several transverse rows in most orbiniids. Hoffmann and Hausen [111] investigated the chaetal arrangement of three species of Orbiniidae belonging to different clades both in morphology-based and sequence-based phylogenies: *Scoloplos armiger*, *Orbinia latreillii* and *Pettibonella multiuncinata*. SEM and 3D reconstructions based on series of histological sections were used to reveal the position of different chaetae, their organizations in rows, the depth of their bases inside the parapodial tissue and the locations of formative sites of the chaetal rows. All three investigated species showed very similar patterns in the thoracic neuropodia: they had anterior main and posterior secondary transverse rows; main rows had a dorsally located formative site, which indicates homology with the transverse rows of other sedentary polychaete taxa. The number of chaetae and the depth of the chaetal bases decreased from frontal to caudal rows. Two additional secondary rows had their own formative site in the dorsoventral middle of the chaetal patch, and they were located along the caudoventral edge of the posteriormost main row and bent frontally. Interestingly, only capillary chaetae were present in the posterior main row and the posterior secondary row in all three investigated species whereas other rows could contain uncini as well as capillaries. The author supposed the described design of the thoracic neuropodia with main and secondary transverse rows represents the ancestral pattern for Orbiniidae [111]. This parapodial pattern is illustrated here on example of juvenile *Scoloplos armiger* (Figure 7A).

This approach suggested for the study and description of chaetal arrangement seems to be very promising. There were no such detailed investigations of other orbiniid genera, so it is hard to confirm or refuse that the general scheme works for all Orbiniidae; but good quality SEM photos sometimes are enough to reveal the chaetal position in other orbiniid taxa. The species of the genus *Leodamas* are the most convenient for SEM investigations of the thoracic neuropodia, as their chaetae usually are short and oriented more or less perpendicularly to a body wall. Unfortunately, in most orbiniids SEM images do not allow recording the chaetal arrangement in details, when anterior chaetae are long, oriented in caudal direction and cover the bases of posterior chaetae; also, chaetal rows can be not obvious, like in many *Scoloplos* and *Leitoscoloplos* species. In this situation special efforts are necessary to illustrate the chaetal position in neuropodia; it can be parapodia, mounted with different angles, parapodia with broken chaetae to show only their bases, serial histological sections with 3D reconstructions or confocal laser scanning microscopy (cLSM), which allows one to see chaetae themselves by autofluorescence as well as formative and degenerative zones with specific markers.

Here we present the attempt to analyze chaetal arrangement in thoracic neuropodia of different orbiniid taxa and compare them with Hoffmann and Hausen's [111] scheme using published SEM photos. *Leodamas acutissimus* (Hartmann-Schröder, 1991) [112] has thoracic neuropodia which are in good agreement with the orbiniid general pattern, including the presence of capillaries only in posterior main row and posterior secondary row. It has three of four main rows consisting of uncini, then a short main row consisting of capillaries which is located only in upper half of the neuropodia; and two secondary rows, anterior consisting of uncini and posterior row of capillaries, both located only in lower part of the neuropodia. The length of uncini increases from anterior to posterior rows. Unlike other orbiniids discussed here the last row is situated behind the papilla of postchaetal lamellae (Figure 7B). A similar pattern is found in thoracic neuropodia of *Orbinia camposiense* Leão and Santos, 2016 [107]. It differs by a longer first secondary row which is bent frontally

under the main rows and a reduced posterior secondary row with two capillaries only (Figure 7C). *Leodamas verax* Kinberg, 1866 [113] (the type species of the genus *Leodamas*) was redescribed with designation of the holotype by Blake [74]. Its thoracic neuropodia bear three main rows of uncini and one short secondary row, consisting of longer uncini; it is curved down frontally under the main rows; capillary chaetae are totally absent. Unlike general pattern of orbiniids sensu Hoffmann and Hausen [111], the length of the chaetae in the main rows decrease from anterior to posterior (Figure 7D). The same neuropodial arrangement was found in *Leodamas cirratus* (Ehlers, 1897) [104] (Figure 7E). Unlike *L. acutissimus* and *L. verax*, *Leodamas dubia* (Tebble, 1955) [114] from Australia had four main rows containing uncini and a tuft of two capillaries in the uppermost position of the third row. Uncini of the posterior row were the longest, which correspond with Hoffmann and Hausen's [111] description but no sign of secondary rows was seen; also, capillaries were located in the third, and not in the posterior row (Figure 7F). *Califia bilamellata* Blake, 2017 [74] has three main rows of uncini and no secondary rows (Figure 3G). The given examples show that the scheme suggested by Hoffmann and Hausen [111] has many modifications among Orbiniidae. When the phylogenetic tree of Orbiniidae is obtained, tracing of various states of this character will help one to understand the evolution of chaetal arrangement in this group. Especially interesting to investigate are the spear-shape chaetae in the genus *Phylo*. According to Hartman [94] (p. 222), the oldest chaetae in the row is the uppermost one. It means the formative site should be ventral, so these specialized chaetae supposedly grow in the opposite direction to uncini of other studied genera.

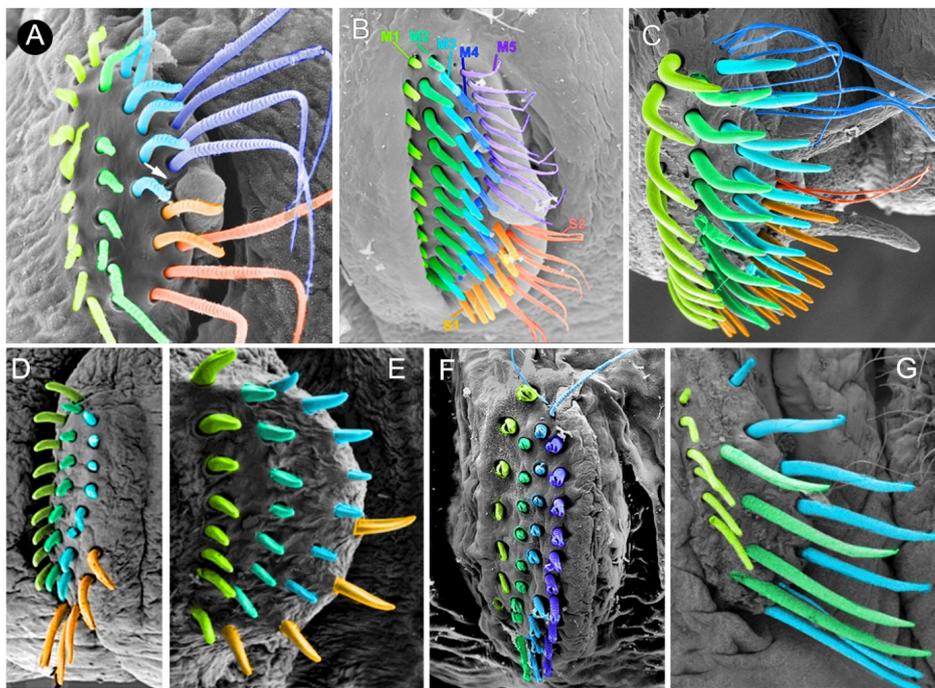


Figure 7. Thoracic neuropodia of Orbiniidae with colored rows of chaetae, SEM. (A). *Scoloplos armiger*, juvenile, Ch 1; (B). *Scoloplos acutissimus*, Ch 11; (C). *Orbinia camposiensis*, Ch 18; (D). *Leodamas verax*; (E). *Leodamas cirratus*; (F). *Leodamas dubia*, Ch 15; (G). *Califia bilamellata*, Ch 3. Rows designations are given according to Hoffmann and Hausen [111]: green, blue and purple colors indicate main rows (M1–M5), orange and red—secondary rows (S1, S2; white arrow points formative site). The anterior end is on the left in all photos. A: after Hoffmann and Hausen [111]; (B,F): after Zhadan et al. [102]; (C): after Leão and Santos [107]; (D–G): after Blake [74]. Photos are not in scale.

In addition to the arrangement of chaetae in parapodia, the ratio of different types of chaetae is important for orbiniid taxonomy. For example, *Leitoscoloplos* bear capillaries only, different *Scoloplos* species—both uncini and capillaries in different proportions, and

some *Leodamas* species—uncini only. Cryptic species of *Scoloplos armiger* complex can be distinguished by the number of uncini in thoracic neuropodia (unpublished data).

The most common chaetal type for Orbiniidae is crenulated capillaries. They can be present in notopodia and neuropodia and in thorax and abdomen. The crenulations are formed by transverse rows of barbs (Figure 8A,B,I). On capillaries, these structures are also called camerations, which may be single, double or in a form of interlocking transverse ribs [74]. Similar crenulations are also present in other types of chaetae (Figure 8D,G–I,L,N–Q,S–V). Some more types of specialized chaetae are known in orbiniids. Acicular spines are present in neuropodia and sometimes in notopodia in *Orbiniella* (Figure 8C). Forked chaetae occur in abdominal notopodia in many orbiniid species [74] and they have two unequal tynes with blunt or tapered tips. Those with a blunt tip have a distinct hole in the tip. Flattened filaments arise from inner part of the tynes (Figure 8D,E). Swan-shape chaetae are present in both noto- and neuropodia in posterior body of *Proscoplos* and *Pettibonella* (Figure 8F) and most probably evolved convergently to uncini [111]. Flail chaetae are similar with capillaries but have abruptly tapering tips (Figure 8G); they occur in abdominal neuropodia (sometimes in notopodia) in many orbiniid genera. Subuncini are intermediate between uncini and capillaries having thick bases and pointed tips (Figure 8H). Abdominal parapodia bear thick protruding aciculae that can be smooth or serrated, straight or strongly hooked (Figure 8I–K). Other types of chaetae not illustrated here are brush-tipped uncini of *Califia*, bifid and trifid crochets of *Questa*, spear-shape chaetae of *Phylo*, and hirsute spines of *Orbiniella spinosa* Blake, 2017 [74] (pp. 112–113, Figure 54F,G).

Uncini (also called hooks, crochets, spines, blunt-tipped chaetae) differ by curvature, serration, comparative thickness and length, development of a hood, shape of tips and presence of grooves. They vary from notably (Figure 8L–N) to slightly bent (Figure 8O–R) or are straight (Figure 8S–V). They can be coarsely (Figure 8L), moderately (Figure 8O–Q,U) or slightly (Figure 8N,S,T) serrated or smooth (Figure 8R). The number of denticles varies from three (Figure 8L) to 10–15 (Figure 8O,P). Uncini can be long and have the same thickness as capillaries (Figure 8O,P) or be short and much thicker (Figure 8V). They can have a clearly visible hood (Figure 8N,Q,T), a thin, poorly visible hood (Figure 8L,O,S) or lack a hood (Figure 8R). Sometimes the hood is as thick as the chaeta itself, so the impression of bidentate tips arises (Figure 8P,V). The tips of uncini are always more or less rounded, but the exact shape varies from conical to obtuse (Figure 8O,Q,R–U). In some species, uncini bear a longitudinal groove on the distal end, which can be short and shallow (Figure 8S,Q) or long and deep, so the tip of the chaetae is deeply notched (Figure 8N). Often uncini have different shape and size in anterior and posterior thoracic segments (Figure 8L,M) or even in one parapodia in different rows (Figure 8V).

The functional role of different types of chaetae in Orbiniidae is not clear. Generally, capillaries are believed to be important in locomotion, stabilization during peristalsis and sensing the environment; they also help to irrigate borrows and tubes [116]. Most likely, capillaries in Orbiniidae perform all these functions. For large orbiniids with dorsally elevated abdominal parapodia, it can be that notopodia with notochaetae form a channel covering branchiae, which produce a water current inside it with cilia. Hooks (including spines and uncini) play a role in anchoring polychaetes [116]. As orbiniids are not tube dwellers, they possibly use uncini for preventing backward slipping during burrowing in sediment, but this statement needs to be proven in experiments and live observations. The function of forked, flail and other types of orbiniid chaetae is unknown.

A promising approach which can be used for species delimitation when the morphological differences between lineages are subtle is morphometrics. The characters more suitable for morphometry in orbiniids are from the cephalic regions (i.e., prostomium, achateous segments), parapodia (i.e., neuropodial and notopodial lobes, both thoracic and abdominal, and subpodal papillae), branchiae and the ventral side. Morphometrics has proven useful in annelid groups such as Hesionidae [117,118], Phyllodocidae [119], Syllidae [120] or Nereididae [121]. The only morphometric study performed in Orbiniidae was

implemented by Hernandez-Alcantara and Solis-Weiss [105] to distinguish *Leitoscoloplos multipapillatus* among its coexistent *Leitoscoloplos panamensis* (Monro, 1933) [122] and a third taxon, *Leitoscoloplos* sp., in the Gulf of California.

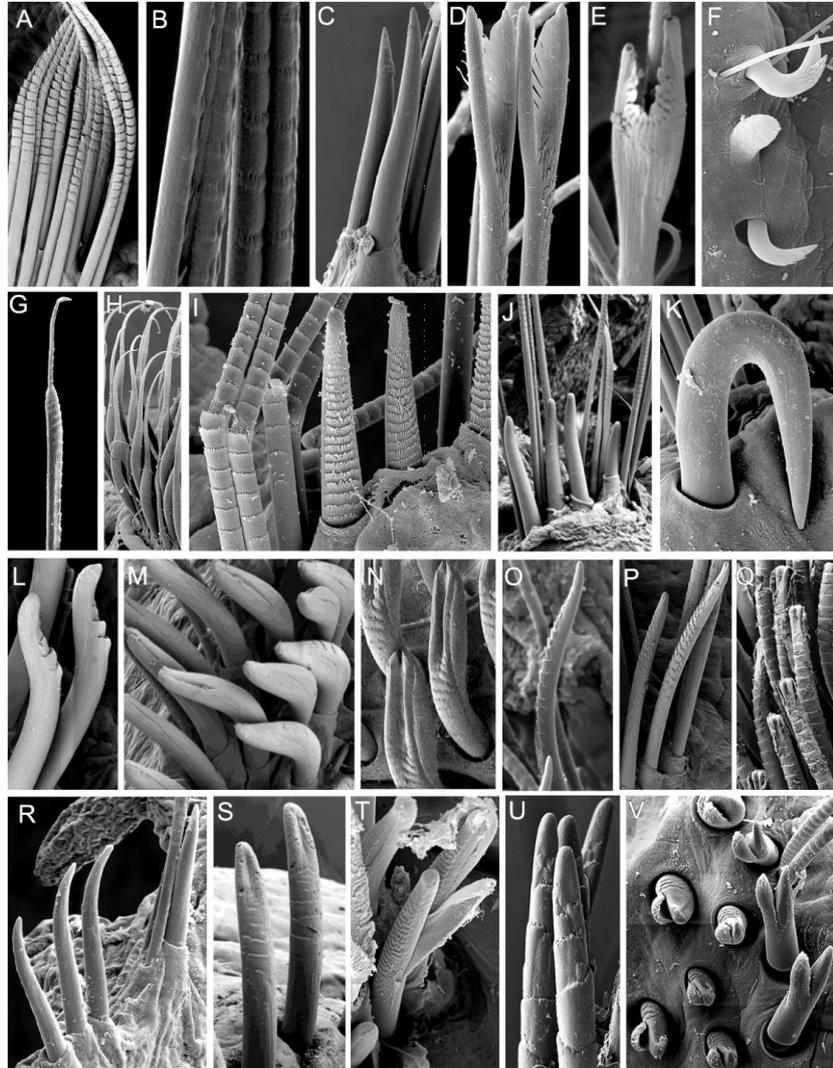


Figure 8. Chaetae of Orbiniidae. (A). *Orbinia orensanzi*, thoracic notopodial capillaries; (B,C). *Orbiniella andeepia*, anterior capillary notochoetae and notopodial spines respectively; (D). *Leodamas dubia*, forked chaetae of abdominal notopodia; (E). *Scoloplos bathytatus*, forked chaeta of abdominal notopodia; (F). *Proscoloplos cygnochaetus*, posterior parapodium; (G). *Orbinia camposiensis*, flail chaetae from abdominal neuropodium; (H–J). *Naineris grubei australis*, subuluncini of thoracic neuropodia and abdominal neuropodial capillaries and spines, respectively; (K). *Leodamas dubia*, abdominal neuropodial acicula, protruding and strongly hooked; (L–V): thoracic neuropodial uncini. (L,M). *Orbinia orensanzi*, from middle and posterior neuropodia respectively; (N). *Leodamas tribulosus*; (O). *Scoloplos bathytatus*; (P). *Scoloplos suroestense*; (Q). *Naineris grubei*; (R). *Scoloplos maranhensis*; (S). *Leodamas verax*; (T). *Scoloplos dayi*; (U). *Leodamas hyphalos*; (V). *Leodamas dubia*. (A–C,E,J,L–Q,S,U): after Blake [74]; (D,H,I,K,T,V): after Zhadan et al. [102], (F): after Meyer et al. [109]; (G): after Leão and Santos [107]; (R): after Oliveira et al. [115]. Photos are not in scale.

3.3. Diversity

3.3.1. Species Numbers

Since the first described orbiniid, *Scoloplos armiger* (Müller 1776) [123], the number of reported species was increasing slowly until Hartman's revision in 1957 [94] accepting 74 valid species (Figure 9). Several new orbiniids were described in different studies following Hartman's system [73,124–127] and, as a result, the species number reached around

120 [1]. During the following years, several local faunistic studies of Orbiniidae were performed [76,82,84,96,97,112,128–142]. Rouse [143] listed around 150 species of Orbiniidae; twice as much as Hartman [94] defined in her monograph less than 50 years earlier. The 21st century brought several important contributions to the knowledge about orbiniid diversity [83,85,86,98,107,144–151]. The two recent works by Blake [74,87] described 37 new orbiniids from which 23 were from the deep-sea (deeper than 500 m), and among them, 18 were from more than 1500 m depth. These studies aid a better understanding of the deep-sea orbiniid diversity, increasing the number of reported deep-sea species from 28 to 51. Bleidorn and Helm [6] listed 204 valid species belonging to 20 genera and Blake [87] reported 240 species of orbiniids; however, here we report 222 species including all described subspecies (commented below).

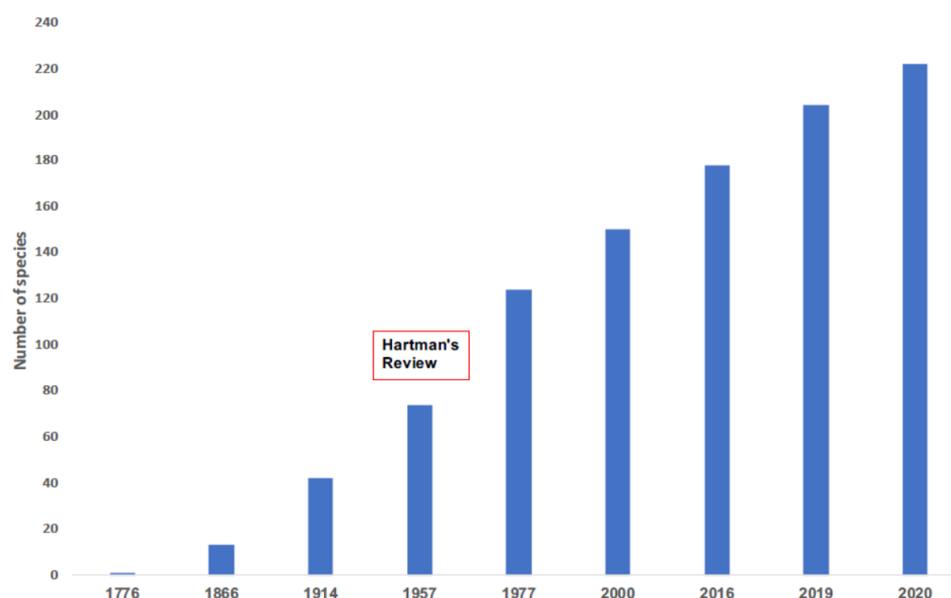


Figure 9. Bar diagram showing the evolution of the number of known orbiniid species from the first described species, *Scoloplos armiger*, in Müller [123] to this study. Note the exponential growth in species discoveries after Eisig [93] and, specially, during the subsequent decades to the Hartman’s review [94].

3.3.2. Species Distribution

Orbiniidae occur world-wide in all marine depths, being most common, sometimes forming dense aggregations, in intertidal and shallow waters down to 500 m. Their diversity, depending on the region, can vary from having a great number of species (e.g., 14 in Southern California) to few (e.g., three in the White Sea). The most diverse areas in terms of number of reported species are Asia (with 45 species and 10 genera), the Pacific North America (with 42 species and 10 genera), the Atlantic North America (with 33 species and 16 genera) and the Atlantic South America (with 33 species and 9 genera) (Figure 10). The variation on the orbiniid diversity in certain areas possibly reflects the systematic efforts done by different researchers (e.g., Hartman, Fauchald or Solis-Weiss in the North East Pacific, the Gulf of Mexico and the Caribbean Sea; Lana, Almeida or Pagliosa in the South West Atlantic; Day in South Africa; Hartmann-Schröder or Hutchings in Australia). The poorly studied areas (e.g., East Coast of USA and Canada, South Eastern Pacific, Western Africa or Indo-West Pacific) may have a great number of still undiscovered species.

The deep-sea orbiniids (below 500 m) are rarely encountered and poorly known [87]. The 51 species of Orbiniidae from the deep-sea habitats are from *Leitoscoloplos* (12), *Orbiniella* (11), *Leodamas* (6), *Scoloplos* (6), *Berkeleyia* (4), *Califia* (4), *Phylo* (4), *Naineris* (3) and *Microrbinia* (1). The genera *Orbiniella*, *Berkeleyia*, *Califia* and *Microrbinia* are composed mainly by deep-water species. From all these species, only *Microrbinia linea* Hartman, 1965 was reported as

dominant at 2000 m depth off North Carolina (Western North Atlantic) during a monitoring program conducted from 1983 to 1987 [152]. Relatively dense populations of two other species were reported by Blake [87]: *Leitoscoloplos gordaensis* Blake, 2020 (with 31 specimens in a single HOV Alvin core from the Gorda Ridge, Escanaba Trough, 3271m) and *Naineris uncinata* Hartman, 1957 (with 30 specimens from a multicore deployment at a gas hydrate site on the Cascadia Subduction zone off Oregon, 786 m). The deepest recorded orbiniid is *Berkeleyia hadala* Blake, 2017, which was found in 6143 m in the abyssal plain from the Peru-Chile Trench.

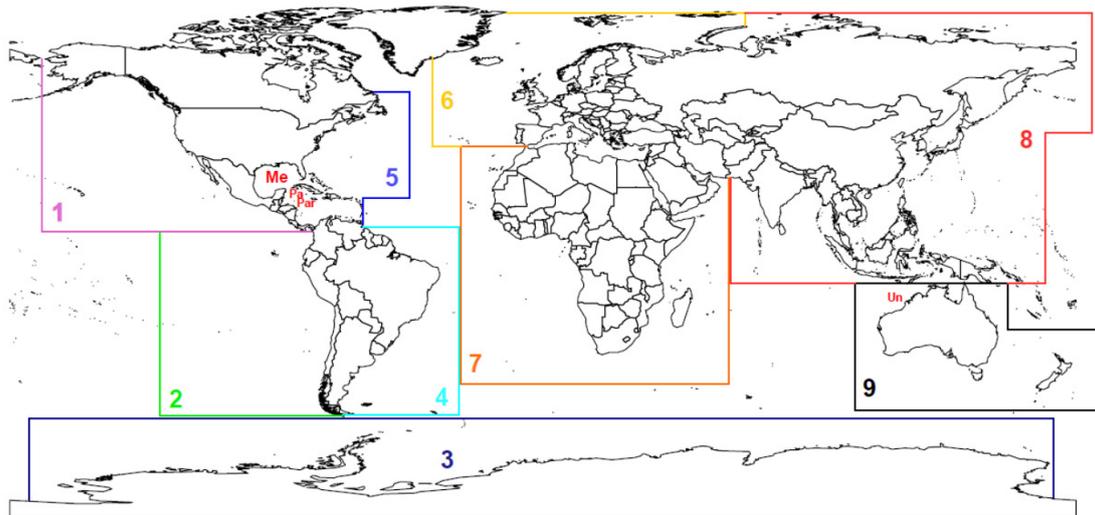


Figure 10. The nine biogeographic areas used for the review of the Orbiniidae diversity distribution with, first, the number of species records and, second, the genera reported for each area. (1). Pacific North America (42, 10); (2). Pacific South America (23, 10); (3). Antarctica (18, 7); (4). Atlantic South America (33, 9); (5). Atlantic North America (33, 16); (6). Europe (31, 11); (7). Africa (32, 13); (8). Asia (45, 10); (9). Australia and New Zealand (29, 7). The monotypic genera based on the original report are represented: Pa. *Paraorbiniella paucibranchiata*; Par. *Pararicia belizensis*; Un. *Uncorbiniella brevibranchiata*. The restricted distribution of the monotypic genus *Methanoaricia* is also marked: Me. *M. dendrobranchiata*. Map was generated using the R packages ggplot2 and sf.

The most widely distributed species are *Scoloplos armiger* and *Naineris laevigata*. The first revealed to be a complex of cryptic species (see details below), while the status of the second has not been confirmed yet with molecular data. *Naineris laevigata* was first described from Nice (France) and later reported from different localities around the Mediterranean Sea as well as in other distant locations in North and South America, South Africa and Asia. Other widely distributed orbiniids are *Naineris quadricuspida* (Fabricius, 1780) [153], *Phylo felix* Kinberg, 1866 [113], *Phylo norvegicus* (M. Sars in G. O. Sars, 1872) [154], and *Protoaricia oerstedii* (Claparède, 1864) [155], the status of the last three has not been tested yet. For the first, a significant genetic differentiation was reported in Zhadan et al. [102] between three genetically identical specimens from three locations (i.e., Friday Harbor, Morro Bay and Cattle Point) in the North East Pacific and two genetically identical specimens from two distant places (i.e., India and White Sea) (Figure 6D), but more data is required for confirming a nonworldwide distribution pattern. An interesting case of a confirmed nearly cosmopolitan distribution was reported in *Proscoloplos cygnochaetus* Day, 1954 [156]. Analysis of morphology and genetics of three different species of *Proscoloplos* from Australia, South Africa and France revealed a single species with a wide geographical range [109]. The authors suggested a possible human transport by vessels and, thus, an invasive nature of the species. A similar case is that of *Naineris setosa*, an alien orbiniid in the Mediterranean Sea. The species showed an American subtropical-tropical distribution (see Table S1 in Supplementary Materials for details) and was reported, first, from an aquaculture facility in the Adriatic Sea (Italy) by Blake and Giangrande [157] and, later, in Tunisia by

Khedhri et al. [158]. However, the status of the “alien” populations vs. the “native” ones in *N. setosa* has yet to be confirmed. *Scoloplos capensis* (Day, 1961) has been recorded as an alien species in the Bay of Bengal (India) with a South-African origin [159,160]. *Naineris quadraticeps* Day, 1965 [161] was described from the Red Sea and afterwards noticed in the Aegean Sea [162] based on two incomplete specimens in poor conditions. Harmelin [162] considered the specimens as juveniles of *N. quadraticeps*, with some minor differences attributed to their juvenile condition. As the record is based on two juveniles, it is considered doubtful [160]. *Leitoscoloplos kerguelensis* (McIntosh, 1885) [163] has been recorded globally but considered as an Antarctic and sub-Antarctic exclusive species by Blake [74] and as an alien species in the Thyrrenian Sea [164] based on an incomplete specimen. Mackie [96] compared this specimen with the type material and concluded that they have some differences, considering the record in the Mediterranean as doubtful.

3.3.3. Cryptic Diversity and Subspecies

Cryptic species have been reported for *Scoloplos armiger*, *Phylo foetida* (Claparède, 1868) [165], *Scoloplos acmeiceps* Chamberlin, 1919 [166], *Leitoscoloplos pugettensis* (Pettibone, 1957) [95] and *Naineris dendritica* (Kinberg, 1866) [101,110,167,168]. Another potential sibling species issue is known for *Leitoscoloplos acutus* (Verrill, 1873) [169] and *Leitoscoloplos mammosus* Mackie, 1987, two similar species with overlapping distributions (see below for details).

Scoloplos armiger was originally described from Kristiansand (Norway) and later reported in several ecological studies [79,170–175] being a dominant macrofaunal species and showing a cosmopolitan distribution with records at the Pacific North American coast, in Europe, including the Arctic and the White Seas, and Japan. It has been reported to be a complex of cryptic species based on, first, RAPD DNA markers [108] and, later, mitochondrial markers [168,174], with at least two clades in the Pacific region (designated as “Malibu clade” and “San Diego Clade”) and four clades in the North Sea (named “Type locality clade”, “Subtidal clade”, “Intertidal clade” and “Intertidal clade 2”). Recent morphological studies performed on the *Scoloplos* populations from Southern California revealed three morphotypes of *S. armiger*-like species and two of *S. acmeiceps*-like species (Haggin, pers. comm.). The study of the genetic clustering among these morphotypes and their relationships with the reported clades by Bleidorn et al. [168] is in process with the aim to describe the species recovered in phylogenetic analyses. Similarly, the species descriptions referred to the North Sea’s clades is in preparation [6]. In addition, the populations of *S. armiger* from the White Sea have been shown to constitute two clades (Zhadan, unpubl.). The eight documented clades of *S. armiger* are accompanied by subtle diagnostic morphological characters and, in the case of the European populations, along with separation by depth. In the North Sea, two clades are known from the intertidal and the other two from the subtidal and, in the White Sea, one is from the intertidal and the other from the subtidal and close to the “Type locality clade”. Moreover, two distinct reproductive modes occur in the North Sea’s populations [176]. Intertidal females produce egg cocoons, but no pelagic larvae, while subtidal females produce pelagic larvae, but no egg cocoons. Furthermore, the intertidal males have spermatozoa with heads twice as long as those in subtidal males and also a significantly shorter flagellum. The subtidal clades showed an additional autumn spawning [177]. The authors suggested that the difference in the sperm morphology could cause the reproductive isolation at the fertilization stage.

Leitoscoloplos pugettensis is a common macrofaunal component in the West Coast of North America, from Alaska to Costa Rica, being the most abundant orbiiniid in intertidal and subtidal bottoms in California [79]. In the phylogenetic works by Bleidorn and collaborators [101,168] two distinct clades of *L. pugettensis* were reported, one from Friday Harbor and another from Santa Monica, Northern and Southern California, respectively. Furthermore, Carr et al. [110] found five MOTUs among the Canadian populations of *L. pugettensis* using the DNA barcoding approach. More recently, Haggin (pers. comm.) detected at least six morphotypes showing a different pattern of depth distribution. Another

widespread species from Western North America (i.e., *Scoloplos acmeceps*) showed to have at least three clades (Morro Bay and Friday Harbor from Northern California, and Newport from Rhode Island) by means of the molecular analyses of Bleidorn et al. [101]. Similarly to *L. pugettensis*, Haggin (pers. comm.) detected at least two different morphotypes of *S. acmeceps* coexisting in the intertidal and the shelf (<200 m) areas in Southern California.

Naineris dendritica is frequently sampled in the intertidal sands and muds along the Californian coast [79,178] and is also recorded in the Pacific North America, the Arctic Canada and the Gulf of Mexico (see Table S1 in Supplementary Materials for details). Carr et al. [110] reported four MOTUs among the British Columbia and the Arctic Canada, with a high divergent clustering in the British Columbia. Additionally, Zhadan et al. [102], using some of the published sequences from Carr et al. [110] and previous works of Bleidorn and collaborators [19,101], found significant genetic dissimilarity between two Southern Californian specimens according to the 16S NJ tree (Figure 6C) and a high genetic distance between one Southern Californian specimen and the Canadian populations according to the COI NJ Tree (Figure 6D).

Leitoscoloplos mammosus, described from Loch Creran (Scotland) by Mackie [96], is morphologically very similar to *Leitoscoloplos acutus*, described from Massachusetts, USA, and was later recorded from North Carolina to Canadian Arctic and also in the White Sea, Russia [179,180]. In recent years, several records of both *L. mammosus*, from Iceland, The Channel and the North and the Norwegian Seas, and *L. acutus*, from the Barents and the Kara Seas, have been reported (pers. obs. by the authors; Andy Mackie, pers. comm.; OBIS, <https://obis.org/taxon/607421> and <https://obis.org/taxon/130514>; GBIF, <https://www.gbif.org/species/4289003> and <https://www.gbif.org/species/2319969>). Morphological comparison of materials from the type locality together with molecular studies should help to resolve the relationships and validity of the two species.

Several subspecies were recorded for Orbiniidae, but none of them has been verified by genetic analyses. *Phylo foetida* is the orbiniid with the most documented subspecies (seven, see Table S1 in Supplementary Materials). The species was initially described from the Gulf of Naples (Italy) and later reported, together with the distinct subspecies, from several localities around the Mediterranean Sea, Gulf of Biscay, English Channel as well as from Mozambique, Madagascar and Libia in Africa [181]. Bleidorn et al. [101] found significant genetic dissimilarity between two distinct specimens of *P. foetida* from Sardinia (Mediterranean) and Arcachon (Gulf of Biscay). The remaining reported subspecies are *Scoloplos acmeceps profundus* Hartman, 1960 [182], *Phylo felix asiaticus* Wu, 1962 [124] and *Leodamas chevalieri candensis* Harmelin, 1969 [162].

3.4. Ecology

3.4.1. Habitat

Orbiniids are burrowing deposit-feeding annelids which live in soft bottoms rich in organic matter. They are strictly known from marine waters though some taxa, such as *Naineris laevigata* (Grube, 1855) [183], *Scoloplos capensis* (Day, 1961) [184] or *Scoloplos marsupialis* (Southern, 1921) [185], are quite tolerant to low salinity [159,186,187]. Orbiniidae can be found in a wide variety of sediments, as in mud (Figure 11A,B), sand (Figure 11C,D), mud or sand with shell fragments, mixed bottoms with stones or annelid reefs (Figure 11E), bivalve beds or in algal meadows (Figure 11F,G). The large-sized genera (as *Scoloplos* and *Leitoscoloplos*) are usually recorded from intertidal and shallow muddy bottoms, except for *Orbinia*, which prefers sandy sediments, and *Califia*, mostly reported from deep waters. The small-sized genera (as *Protoariciella* and *Protoaricia*), together with *Naineris*, are often encountered among algal holdfasts, with the exception of *Questa* and the deep-sea genera *Berkeleyia* and *Microrbinia*, which have never been reported in algal congregations. Although *Orbinia* is mainly deep sea, some shallow species inhabits algal groupings, as *O. spinosa* or *O. plumisetosa* Buzhinskaya, 1993 [139]. The interstitial *Questa* live in coarse, fine and coralline sands from shallow waters. The monotypic genera *Paraorbiniella*, *Pararicia* and *Uncorbinia* were reported from littoral zones and have not been documented again since

their original description (see Table S1 in Supplementary Materials for details). The species inhabiting the intertidal are tolerant to hypoxic conditions through several adaptations. However, *S. cf. armiger* showed only moderate resistance to anoxia in the Wadden Sea, and individuals actively ascends to oxidative layers during low tides [188]. In contrast, the co-existent *Arenicola marina* (Linnaeus, 1758) [189] can inhabit deeper sediment layers by means of a more efficient anaerobic metabolism. *Leitoscoloplos mammosus* is a dominant macrofauna species in the anoxic mud of the Upper Basin of Loch Creran (Scotland), an area with strong accumulations of detritus (Andy Mackie, pers. comm.). The most hypoxic habitats inhabited by Orbiniidae are abyssal plains (with 16 recorded species), hydrothermal vents (i.e., *Leitoscoloplos sahlingi* Blake, 2020, *Orbiniella hobsonae* Blake and Hilbig, 1990 [138] and *Orbiniella grasslei* Blake, 2020) and hydrocarbon seeps (i.e., *Methanoaricia dendrobranchiata*). This last species lives in association with the bivalve *Gigantidas childressi* (Gustafson, R. D. Turner, Lutz and Vrijenhoek, 1998) [190] as an adaptation to the hydrocarbon enriched sediments on the Louisiana continental slope (Gulf of Mexico). Other adaptations of this orbiniid to this extreme habitat are described and compiled elsewhere [6,191–193].



Figure 11. Photographs of some common and special habitats in Orbiniidae. (A). Muddy intertidal. (B). Muddy subtidal. (C). Sandy intertidal. (D). Sandy subtidal. (E) Mixed muddy/rocky intertidal. (F). Intertidal algal meadow, with detail on the algal species *Ulva* sp. (G). Subtidal algal meadow (different filamentous algae). All photos were taken from the White Sea, Russia, except C which was taken from Oxwich Bay, Wales.

Traditionally, the description of a new orbiniid species is not accompanied by the description of its habitat, which are relevant data for species delimitation according to the Integrative Taxonomy concept [118,194–196]. Furthermore, it is crucial to resample certain areas, especially type localities. We encourage researchers to include data on the habitat of the species in ongoing work.

3.4.2. Relation to Pollution

Although orbiniids have not been traditionally used as bioindicators, some species (e.g., *Scoloplos* cf. *armiger* and *Scoloplos madagascarensis* Fauvel, 1919 [197] in Reunion Islands, Eastern Madagascar) increase in density under the presence of pollutants, showing the potential of their use as indicators of disturbance or nonpollution. These species were referred to ecological group III “Species tolerant to excess of organic matter” according to the AMBI biotic index [198], as their populations were stimulated by discharges of industrial wastes in their natural habitat [199]. Similarly, *Leitoscoloplos pugettensis* in Southern California marine bays was referred to group III by Teixeira et al. [200]. An interesting case is that of *Leitoscoloplos fragilis* (Verrill, 1873) [169], which showed tissue accumulation of the hydrocarbon Benzo(a)pyrene under high exposures without effects on mortality [201], making it tolerant to and indicator of Polycyclic Aromatic Hydrocarbons contamination.

Other orbiniids are sensitive to high concentrations of pollutants, decreasing their density or disappearing completely from the environment. For instance, *Leitoscoloplos foliosus* (Hartman, 1951) [202] revealed to be sensitive and an indicator of low metals and low/moderate organic pollution in Northern Gulf of Mexico estuaries [203]. *Scoloplos* cf. *armiger* and *Scoloplos typicus* (Eisig, 1914) [93] are referred to ecological group I “Species very sensitive to organic enrichment and present under unpolluted conditions” in the Cantabrian Sea (Northern Spain) [198]. In a domestic sewage impact study in the macrofaunal composition of several intertidal mussel beds of Mar de la Plata (Argentina) [204], *Protoariciella uncinata* was subdominant in a control unpolluted station and disappeared in the most impacted station.

3.5. Conclusions

Orbiniidae are common and often abundant in bottom communities. In spite of a long history of investigations, many aspects of their morphology, biology, systematics and phylogeny remain poorly known. We can suggest several directions of topical future research. The main approach should be integrative taxonomy combining morphological, molecular and biological data. For many species, re-examination of type specimens or designating of neotypes is required as well as thorough investigations of specimens from different geographical areas. Preferably these studies should include scanning electron microscopy for revealing fine details of chaetal and ciliation patterns. Other techniques, such as histological sections or confocal microscopy can be useful for examination of chaetal arrangement. The phylogenetic system of Orbiniidae requires advanced genetic studies, including new technologies such as next generation sequencing, in combination with morphological examinations of the well-supported clades in search of possible new informative characters. Taxon coverage of molecular based studies should be expanded considerably. Obtaining genetic information for type species of each genus is crucial; specimens for genetic analysis should be collected from the type localities. For species with wide geographical distribution, population genetic studies are necessary to reveal cryptic species. Studies of postlarval development will help researchers to understand the transformations of morphological structures during ontogenesis and the progenetic evolution of orbiniids. Morphofunctional observations and experimental research of burrowing will possibly shed light on the function of different types of chaetae and other parapodial structures.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/1/29/s1>, Table S1: Species table, Table S2: Summary table.

Author Contributions: The three authors contributed to the conceptualization, investigation and writing (both for the original draft and review and editing) in the following order: M.A.M., T.H.S. and A.Z. All authors have read and agreed to the published version of the manuscript.

Funding: A.Z. was funded by grants from the Russian Foundation of Basic Research no. 18-05-60158, 19-04-00501.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: We greatly acknowledge the text revision and comments made on previous versions of this Manuscript by Nataliya Budaeva. Christoph Bleidorn made inputs on orbiniid knowledge and provided Figure 5G. We also would like to thank the original photographs provided by Katrine Kongshavn (Figure 5H), Kate Mortimer and Andrew S. Y. Mackie (Figure 11C), the bibliography contributed by João Gil and Verônica Oliveira, and the shared knowledge on the Californian orbiniid morphotypes and on the orbiniid species distribution from NE Pacific by Brent Haggin and Leslie Harris.

Conflicts of Interest: The authors declare no conflict of interest.

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