

Review

The Current State of Eunicida (Annelida) Systematics and Biodiversity

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Abstract: In this study, we analyze the current state of knowledge on extant Eunicida systematics, morphology, feeding, life history, habitat, ecology, distribution patterns, local diversity and exploitation. Eunicida is an order of Errantia annelids characterized by the presence of ventral mandibles and dorsal maxillae in a ventral muscularized pharynx. The origin of Eunicida dates back to the late Cambrian, and the peaks of jaw morphology diversity and number of families are in the Ordovician. Species richness is heterogeneous among the seven recent families, with more than half of the valid species belonging to the Eunicidae + Onuphidae clade, one of the latest clades to diverge. Eunicidans inhabit soft and hard substrates from intertidal to deep waters in all oceans. The few freshwater species are restricted to Histriobdellidae, a family exclusively commensal/parasite of crustaceans. The reproductive biology, development and ecology of most families are poorly known and the information available suggests low dispersal ability. However, all families have records of widely distributed species. Scrutiny of these wide distributions has often revealed the presence of exotic species or more than one species. The exploration of the deep-sea and of new habitats has led to recent descriptions of new species. Furthermore, the revision of type specimens, the examination of new morphological features and the use of molecular data have revealed hidden biodiversity under unjustified synonyms, poor understanding of morphological features and incomplete descriptions. Molecular studies are still very few or nonexistent for the families Histriobdellidae, Hartmaniellidae, Lumbrineridae and Oeonidae. The integration of new methodologies for morphological and molecular study, along with information on biological and ecological traits appears to be the path to improve the knowledge on the diversity of Eunicida.

Keywords: marine invertebrate; diversity; distribution; jaw; maxillae; polychaete; Polychaeta; Dorvilleidae; Eunicidae; Hartmaniellidae; Histriobdellidae; Lumbrineridae; Oeonidae; Onuphidae



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1. Introduction

Eunicida was raised to order level relatively recently (Uschacov [1] as Eunicimorpha, Dales [2] as Eunicida) despite being recognized as a taxon much earlier (superfamily Eunicia [3] or family Eunicidae [4]). The taxon identity is supported by the presence of eversible jaws, which comprise dorsal maxillae and ventral mandibles, in a ventral muscularized pharynx. The composition of Eunicida has been relatively stable including

seven recent (Dorvilleidae Chamberlin, 1919; Eunicidae Berthold, 1827; Hartmaniellidae Imajima, 1977; Histiobdellidae Vaillant, 1890; Lumbrineridae Schmarda, 1861; Oeononidae Kinberg, 1865; and Onuphidae Kinberg, 1865) (Figure 1 and Figures 2–10) and 17 extinct families [5].

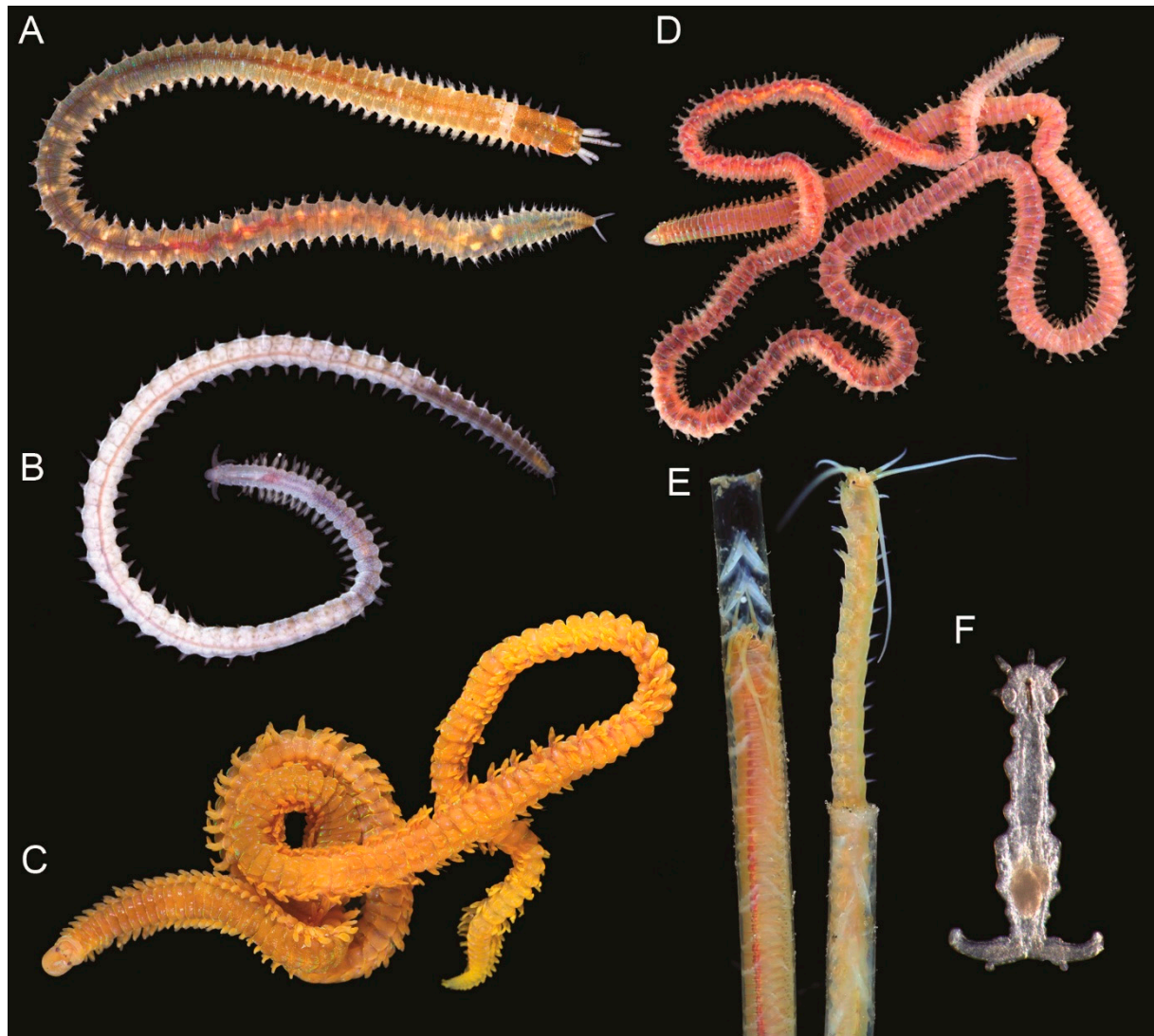


Figure 1. Live specimens representing eunicidan families: (A) *Nicidion* sp., Eunicidae, © A. Sememov; (B) Dorvilleidae gen. sp., © A. Sememov; (C) *Oenone fulgida* (Lamarck, 1818), Oeononidae, © A. Sememov; (D) Lumbrineridae gen. sp., © A. Sememov; (E) *Hyalinoecia tubicola* (O.F. Müller, 1776), Onuphidae, © N. Budaeva; (F) *Histiobdella homari* Van Beneden, 1858, Histiobdellidae, © C. Helm.

Eunicida is sister to Phyllococida within the Errantia clade [6,7]. Phylogenetic analyses using multiple genes or genomic data recover monophyletic Eunicida and families, with exception of Dorvilleidae in analyses including the genus *Pettibonea* [6,8–12]. Eunicidae and Onuphidae are consistently recovered as sister groups in analyses with only recent taxa and molecular data but formed a polytomy with the extinct genus *Esconites* Thompson and Johnson, 1977 in analyses with extant and extinct taxa based on morphological data [9]. The relationship among the other families is inconsistent. Oeononidae, Dorvilleidae, Oeononidae + Dorvilleidae or Oeononidae+Lumbrineridae have resulted as sister groups of the Eunicidae + Onuphidae clade. Lumbrineridae and Dorvilleidae have also been recovered as a sister family to all other Eunicida [6,8,9]. The relationships recovered with phylogenomic analyses [6] agree, at least in part, with hypotheses drawn from Orensanz's [13]

and Paxton's [14] comprehension of the evolution of jaws. All of them recover the clade Eunicidae + Onuphidae and have Dorvilleidae as the sister group to all other Eunicida. These hypotheses contrast in the placement of Lumbrineridae as a sister group to Oeononidae [6,13] or in a clade with Hartmaniellidae, sister group to (Dorvilleidae (Oeononidae (Eunicidae, Onuphidae))) [14]. Orensanz [13] suggests the clade Lumbrineridae+Oeononidae is the sister to (Hartmaniellidae, (Eunicidae, Onuphidae)). Hartmaniellidae and Histiobdellidae have not been included in any formal phylogenetic analyses. Their monophyletic status and placement within Eunicida remain to be tested.

Species richness is heterogeneous among families. Eunicidae (12 genera, 453 spp.) bears the highest number of species followed by Onuphidae (22 genera, 340 spp.), Lumbrineridae (19 genera, 279 spp.), Dorvilleidae (32 genera, 200 spp.), Oeononidae (12 genera, 109 spp.), Histiobdellidae (3 genera, 13 spp.) and Hartmaniellidae (1 genus, 3 spp.) [15]. Despite being among one of the latest clades to diverge, the Eunicidae + Onuphidae clade comprises more than half of the recent species within Eunicida (1397 spp.). This could indicate a higher diversification rate, a lower extinction rate or just an underestimation of species diversity in other families, such as Dorvilleidae, for which 73% of the valid species were described in the last 50 years (Figure 2). In the families Eunicidae and Onuphidae, the species described in the last 50 years correspond, respectively, to 30% and 53% of the total of valid species. Many descriptions of new species in Eunicida are due to the discovery of new habitats and increase in exploration of the deep-sea (e.g., [16–19]) as well as the study of meiofaunal polychaetes (e.g., [20–23]). However, the revision of type specimens, the examination of new morphological features and the use of molecular data are revealing a hidden biodiversity under unjustified synonyms, poor understanding of morphological features and incomplete descriptions [24–26]. The lack of correspondence between the number of genera and the number of species per family (e.g., Eunicidae) illustrates more homogeneity in the external morphology of some families or just more conservative taxonomic decisions.

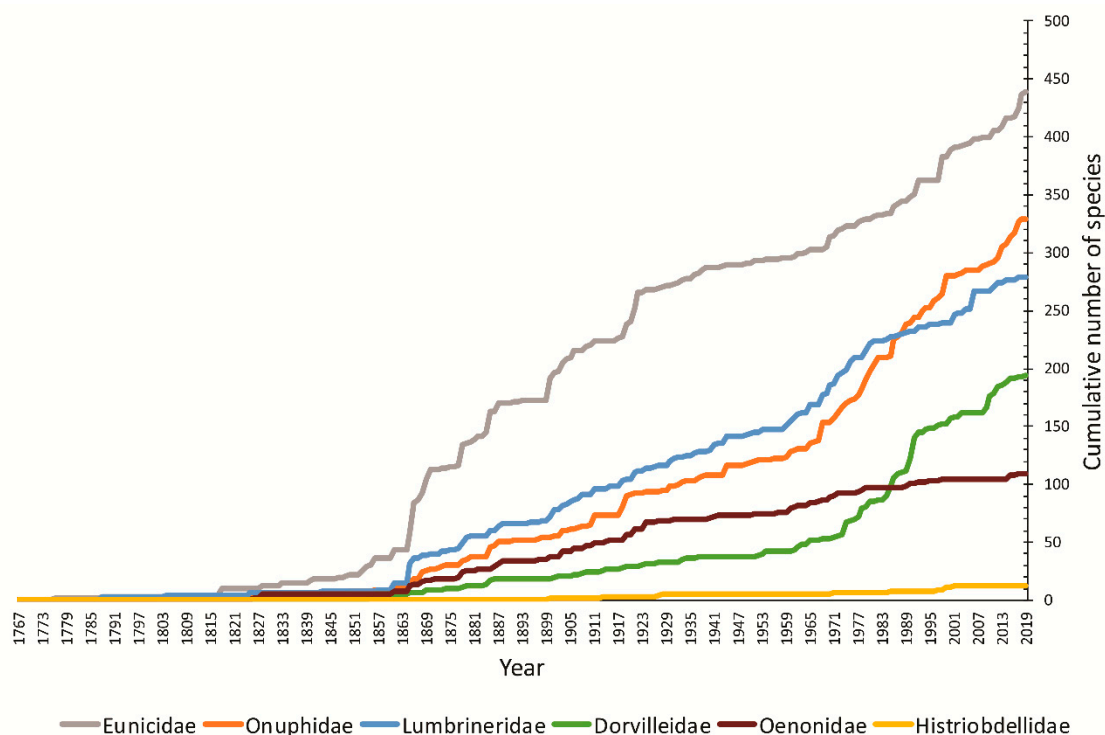


Figure 2. Cumulative number of species described in six eunicidan families, data on valid species only [15] (Hartmaniellidae not shown).

The origin and diversification of Eunicida date back to the late Cambrian, the age of the earliest fossil maxilla [27]. Maxillae compose the main fossil record of Eunicida and consist of a series of mostly paired sclerotized plates. Maxillae vary among families in relation to the number, morphology, symmetry and arrangement of the plates, and, when present, the shape of the carriers (Figure 3). The diversity of jaw morphology, which translates into the number of families, is more than twice as high in extinct than in extant taxa and is peaked in the Ordovician [27]. The general morphological patterns of maxillae are grouped in jaw-types fine-tuned along different studies considering both extinct and extant diversity [3,13,14,28,29]. Of the six jaw-types currently considered [14], two are exclusive of ten extinct families and all the other four jaw-types are shared among extinct and extant families [14]. Dorvilleidae is the recent family with the highest jaw diversity, motivating the proposition of its division into two different families (Dorvilleidae and Iphitimidae) [13,14,19] or into six informal groups [19], none supported by the only phylogenetic analyses including representatives of the dorvilleid jaw diversity [30].

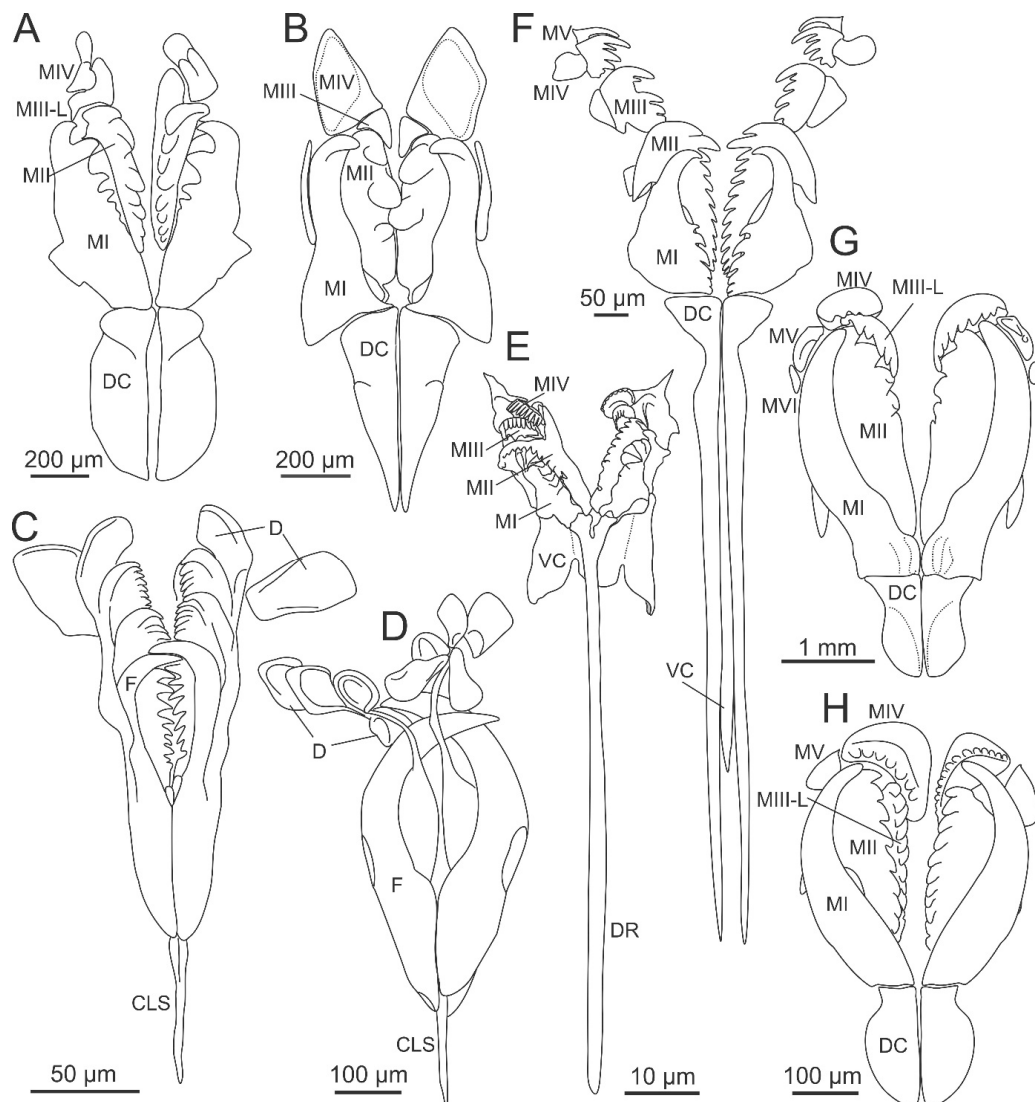


Figure 3. Diversity of maxillae in Eunicida. (A) *Hartmaniella* sp., Hartmaniellidae; (B) *Augeneria* sp., Lumbrineridae; (C) *Ophryotrocha mammillata* Ravara et al., 2015, Dorvilleidae, P-type maxillae; (D) the same, K-type maxillae (E) *Histriobdella homari* Van Beneden, 1858, Histriobdellidae; (F) *Arabella mutans* (Chamberlin, 1919), Oeononidae; (G) *Eunice roussaei* Quatrefages, 1866, Eunicidae; (H) *Paradiopatra fragosa* (Ehlers, 1887), Onuphidae. CLS—carrier-like structure, D—free denticles, DC—dorsal carrier, DR—dorsal rod, F—forceps, MIII-L—left maxillae III, MI–MV—maxillae I–V, VC—ventral carrier. (C–D) modified from Ravara et al. [31]; (H) modified from Budaeva and Fauchald [32].

The different jaw morphologies also have different biomechanics with implications for food capturing and shredding [33]. In maxillae bearing carriers of at least Lumbrineridae and Onuphidae (Figure 3B,H), those plates attached to the carriers are primary maxillae (maxillae I, II in both families and unpaired III in Onuphidae) responsible for catching and shredding (exclusive of serrated plates) food items. The unpaired serrated primary maxillae III in onuphid improves the breaking of food with different properties. The interlocking mechanism, present at the posterior end of maxillae I in both families, prevents slipping of the plates and it is an important mechanism in capturing moving food [33]. Feeding habits and food quality consumed are variable within recent and, probably, extinct Eunicida, including grazing, deposit-feeding, and predation, detritivory, herbivory, carnivory and omnivory [34]. Giant raptorial eunicidans were already present 400 million years ago [35].

Recent giant eunicidan species are among the longest annelids with up to 6 m in length (Eunicidae, *Eunice aphroditois* (Pallas, 1788) [36]). Length variation is great within Eunicida, since it also includes species among the shortest annelids with 255 μm (Dorvilleidae, *Neotenotrocha sterreri* Eibye-Jacobsen and Kristensen, 1994 [30]). The prostomium is well developed followed by a double (Dorvilleidae, Eunicidae, Hartmaniellidae, Lumbrineridae, and Oeonidae) or single (Onuphidae) ringed peristomium in all families, except for Histriobdellidae in which these structures are fused. Prostomial appendages, one to three antennae and a pair of palps, may be present on the prostomium of Dorvilleidae, Eunicidae, Histriobdellidae and Onuphidae (Figures 4, 5, 7 and 10). Lumbrineridae and Oeonidae generally have conical appendage-free prostomium with the exception of few genera bearing tiny dorsal appendages covered by the anterior fold of the peristomium or visible due to a peristomium dorsal incision (Figures 8 and 9). Buccal lips are conspicuous structures in the prostomium of Onuphidae (Figure 10E) and inconspicuous in Dorvilleidae, Eunicidae (Figure 5), Lumbrineridae, and Oeonidae [37]. The muscularized pharynx holding the maxillae contains at least homologous dorsolateral and pharyngeal folds in Dorvilleidae, Eunicidae, Lumbrineridae, Oeonidae and Onuphidae, and a dorsolateral fold anterior extension in the last four families [37,38]. Metamerism is conspicuous and the number of chaetigers is variable in all families but Histriobdellidae. Parapodia are reduced, uniramous or subbiramous with notopodia reduced to dorsal (notopodial) cirri. Capillary chaetae are present in all families, except Histriobdellidae, which lacks chaetae. Chaetae diversity increases along the evolution of Eunicida being highest in Onuphidae and Eunicidae [39]. The pygidium and two or four pygidial (anal) cirri, which may be absent, bear several nerve cell endings suggesting they have sensory function [40].

Eunicidans are mostly free-living and can be found in the majority of marine habitats in soft and hard substrates from the intertidal zone to the deep waters in all oceans. Hartmaniellidae is the only family that appears to be solely present in fine soft bottoms, sometimes with shell fragments. No other free-living family is exclusively present in one type of habitat or substrate. However, most members of some families, such as Lumbrineridae, Oeonidae and Onuphidae, prefer soft bottoms, while Eunicidae is most common in hard biogenic substrates [41,42]. Histriobdellidae is the only eunicidan family occurring in both marine and continental waters, with highest richness in the latter, and being exclusively commensals/parasites of crustaceans. Parasitic and symbiotic species are also present in the families Dorvilleidae, Eunicidae, and Oeonidae.

All families have records of widely distributed species, which deserve further investigation. Most widespread species studied in detail ended up as more than one species [43–45] or exotic species dispersed by human mediated transport [46,47]. However, some species appear to have naturally widespread distributions [48,49] despite the poor natural dispersal capability attributed to eunicidan species. Reproductive modes vary from viviparity, brooding of young in tubes or gelatinous egg masses to broadcast spawning. However, even in the latter the planktonic life span is expected to be relatively short, since all known eunicidan larvae are lecithotrophic [50]. Asexual reproduction happens at least by scissiparity (Oeonidae, [51]) and architomy (Dorvilleidae, [52]).

Eunicida includes species of economic and cultural importance. Eunicidae, Lumbrineridae, Oeononidae and Onuphidae comprise species used as baits for commercial and recreational fishing in diverse localities in Atlantic, Pacific, Adriatic, Mediterranean and Suez Canal coasts [53–58], and are also farmed to be used as bait and food supply in aquaculture (e.g., *Diopatra aciculata* Knox and Cameron, 1971, Onuphidae; [59]). Ripe swarming forms of *Palola* (Eunicidae) species are a traditional food and the source of festivals in South Pacific communities [49,60].

In this review, we analyze the current state of knowledge on extant Eunicida systematics, morphology, feeding, life history, habitat, ecology, distribution patterns, local diversity and exploitation, pointing out gaps of knowledge and future perspectives. The great diversity present in Eunicida prevents the presentation of a complete overview without considering each family separately. Thus, in the next sections, we present the current state of knowledge on the different aspects of the recent eunicidan families. Extinct families are not further considered because of the lack of information on most of the aspects considered here.

2. Dorvilleidae Chamberlin, 1919

2.1. Systematics and Phylogeny

The family Dorvilleidae comprises 32 genera and around 200 species. It includes the majority of the smaller forms of the eunicemorph polychaetes, with around 10% of the species described hitherto belonging to the interstitial fauna. Although the family name Dorvilleidae has been in common use since it was erected by Chamberlin [61], its validity remained questionable as its type genus name *Dorvillea* Parfitt, 1866 is a junior homonym of the mollusk genus name *Dorvillea* Leach in Gray, 1852. The alternative name Stauronereididae Verrill, 1900 was occasionally used (e.g., [62]), regardless the previous synonymy of its type genus *Stauronereis* Verrill, 1900 with the priority name *Dorvillea* [61]. Only recently, the genus name *Dorvillea* Parfitt, 1866 was validated as nomen protectum, based on its use in over 25 publications by more than 10 authors in the last 50 years (Article 23.9.2 of the ICZN code), while *Dorvillea* Leach, 1852 was deemed as nomen oblitum, since it has not been used as valid since 1899 [63]. This nomenclatural act also protects the family name Dorvilleidae Chamberlin, 1919.

The first dorvilleid species was described by Delle Chiaje [64] as *Nereis rudolphi* (posteriorly moved to the genus *Schistomeringos* Jumars, 1974). When Chamberlin erected the family, 21 of the currently valid dorvilleid species were already described. Two genera were included in the family: *Dorvillea* and *Ophryotrocha* Claparède and Meczniow, 1869. Although already described, the genus *Iphitime* Marenzeller, 1902 was initially ascribed to a different family (first Lysaretidae Kinberg, 1865 and later Iphitimidae Fauchald, 1970, both currently unaccepted). Not until about four decades later were other genera described for the family. The remaining 29 genera were described following important revisions [13,19,21,30,65–68], among other works. An updated key and detailed diagnoses to all dorvilleid genera is available in Wiklund et al. [69]. Over two-thirds of the dorvilleid genera include only one or a couple of species, while the largest genera, *Ophryotrocha*, *Dorvillea* and *Schistomeringos*, encompass more than half of the existing species.

Most molecular studies within the family have dealt mainly with *Ophryotrocha* [70,71], often in combination with species descriptions (e.g., [31,72–74]). In several of these restricted molecular analyses, species from different dorvilleid genera fall within *Ophryotrocha*. This is the case for *Exallopus* Jumars, 1974, *Iphitime* and *Pseudophryotrocha* Hilbig and Blake, 1991 (e.g., [31,72–74]). However, since the respective type species for these genera have not been sequenced yet, the authors have chosen to await a formal family revision rather than renaming and moving only those species that have been used in those studies. The genus *Mammiphitime* Orensanz, 1990 might also belong to *Ophryotrocha* although no molecular data is available for it yet. The erection of *Mammiphitime* was justified by the large dorsal lobes in the median and posterior segments [13], but since then, another species with similar lobes has been described, *Ophryotrocha mammillata* Ravara, Marçal, Wiklund and

Hilário, 2015, and molecular data placed it within *Ophryotrocha* [31]. Due to these, and possibly other doubtful genera, the family Dorvilleidae is in need of a comprehensive revision using a combination of morphological characteristics and molecular data.

The mono- or paraphyletic condition of the family Dorvilleidae has been a matter of discussion depending on whether some taxa such as Dinophilidae Macalister, 1876, Diurodrilidae Kristensen and Niilonen, 1982 and *Pettiboneia* Orensanz, 1973 are included or not. In their phylogenetic study using morphological characteristics, Eibye-Jacobsen and Kristensen [30] refer to Iphitimidae and Dinophilidae as belonging to Dorvilleidae. However, subsequent studies using molecular methods or ultrastructure analyses have suggested that although Iphitimidae does indeed fall within Dorvilleidae, Dinophilidae and Diurodrilidae are not closely related to Dorvilleidae (e.g., [6,75–77]). The monophyly of Dorvilleidae is achieved when excluding the genus *Pettiboneia* [6,8,39]. In fact, Paxton [14] reported *Pettibonea* as lacking base dental plates and having two rows of free denticles, corroborating the unique morphology of the genus. However, in the molecular analysis performed by Struck et al. [8] the genus was represented only by two genetic markers (18S and 16S rDNA) of a single species, *Pettiboneia urcinensis* Campoy and San Martín, 1980, that was recovered as genetically closer to Lumbrineridae. Furthermore, there are very few sequences available for species in the other dorvilleid genera preventing a large-scale family analysis. Thus, phylogenetic analyses with better taxon coverage are required to test the monophyly of the family.

2.2. Morphology

Dorvilleids share with the other eunicidan families the outstanding jaw apparatus. It is mainly the jaw morphology that allows identifying the family and is also useful for delineation of genera and species. The jaws in Dorvilleidae consist of ctenognath maxillae (upper comb-like jaws), formed by two to four rows of symmetrical or subsymmetrical dentate elements and a posterior unpaired element (carrier-like structure) (Figure 3C,D), and mandibles (lower jaws). However, species in some genera lack jaws, e.g., *Ikosipodoides* Westheide, 2000 and *Parapodrilus* Westheide, 1965. Furthermore, the shape of the prostomium and its appendages as well as the shape of parapodia and chaetae is of importance to separate genera and species within the family (see [69]). Prostomial appendages, when present, are paired. Lateral antennae can be articulated or unarticulated while palps are simple or biarticulated (Figure 4A–D). Parapodia are missing, sub-biramous or uniramous, with or without dorsal and ventral cirri (Figure 4E). Some genera lack chaetae, but most species have simple supra-acicular and simple and/or compound subacicular chaetae (Figure 4F). A detailed description of the external and internal morphology of Dorvilleidae is available in Wiklund et al. [69]. Due to their small size and frequently minor morphological differences, dorvilleids can be difficult to identify correctly, and different species are often only detected following molecular analysis (e.g., [44]).

2.3. Feeding and Life History

The feeding habits vary within the family, with some species being reported as carnivores and others as omnivorous, grazing on algae or bacterial mats or living off detritus [34,78].

In most dorvilleid genera, the sexes are separated and the species lack sexual dimorphism. However, in the genus *Ophryotrocha*, some species exhibit sexual dimorphism and many species are consecutive or simultaneous hermaphrodites (e.g., [79,80]). Epitokal modifications may occur in some species, expressed by enlarged eyes and longer chaetae [81–83]. Some dorvilleid species are broadcast spawners with swarming phases [83], other species have pseudocopulation and possibly internal fertilization [84], and a few species have been reported to have asexual reproduction [52]. In *Ophryotrocha*, pseudocopulation and brooding of the offspring is common, and viviparity occurs in a few cases [79,84]. While some dorvilleids, e.g., *Schistomeringos rudolphi* (delle Chiaje, 1828), have planktonic larvae that can spend at least a week in the water column before settling [83], others brood their

young, expressing direct development with the juveniles emerging from egg cases already resembling miniature adult worms [79].

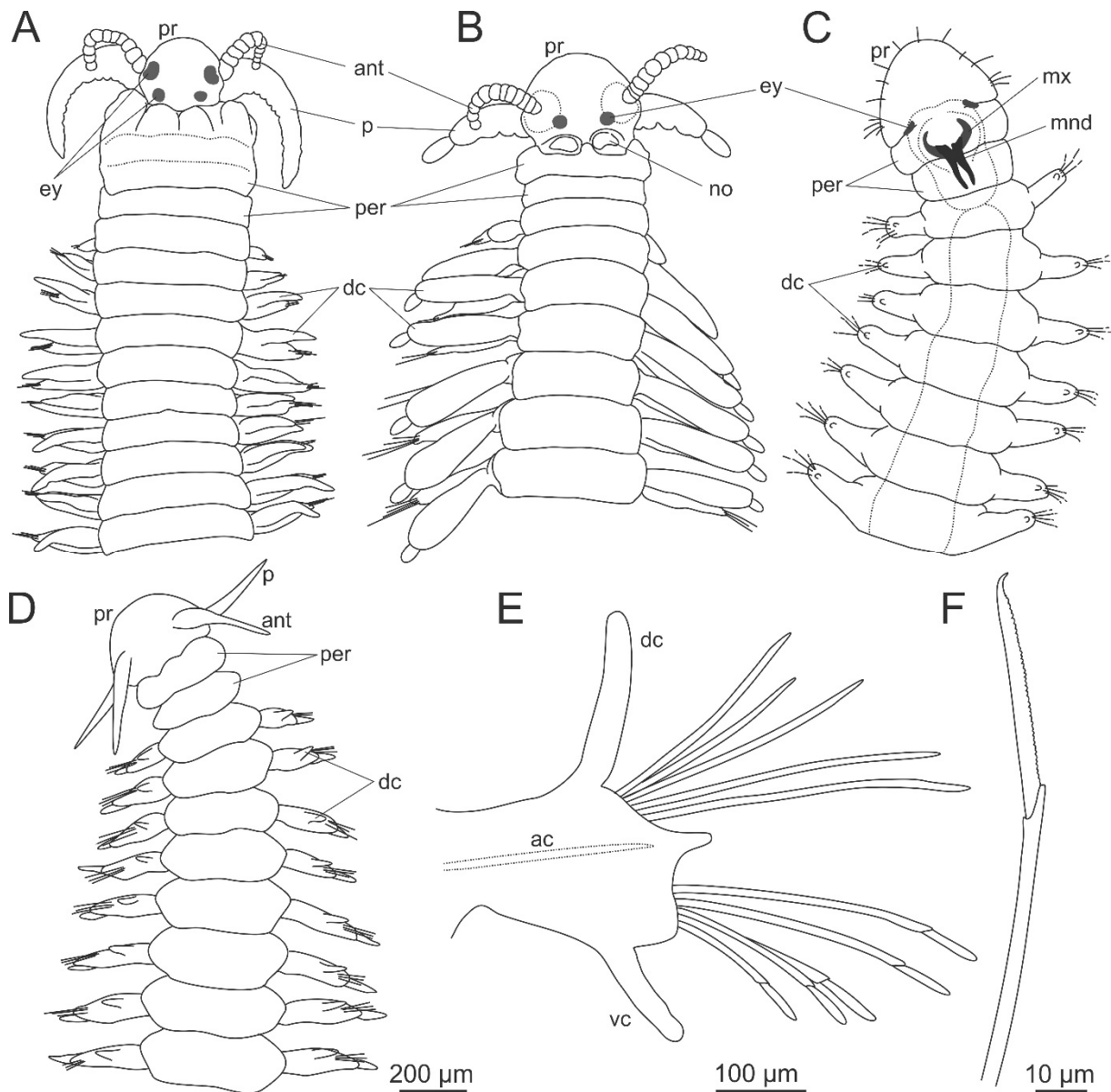


Figure 4. Morphology of Dorvilleidae. (A), (B) Dorvilleidae gen. sp. anterior end, dorsal view; (C) *Ophryotrocha* sp. Anterior end, dorsal view; (D) *Ophryotrocha langstrumpae* Wiklund, Altamira, Glover, Smith, Baco and Dahlgren, 2012, anterior end, dorsal view; (E) the same, midbody parapodium; (F) the same, compound chaeta. ac—acicula, ant—antenna, dc—dorsal cirrus, ey—eye, mnd—mandibles, mx—maxillae, no—nuchal organ, p—palp, per—peristomium, pr—prostomium, vc—ventral cirrus. (D–F) modified from Wiklund et al. [74].

2.4. Habitats and Ecology

Some of the smallest dorvilleid species are interstitial, while larger species are found on soft or hard substrates, and some are symbiotic/parasitic in e.g., crab gill chambers (species in *Iphitime* and two species in *Ophryotrocha*) or in the coelom of other polychaetes (*Veneriserva* Rossi, 1984). Free-living species can surround themselves with mucus, and some species construct tubes out of mucus [34].

Several studies indicate limited tolerance of some dorvilleid species to environmental factors such as temperature and salinity (e.g., [85,86]) although there are also records of

euryhaline species [87,88]. Nevertheless, apart from a few records of estuarine occurrence, dorvilleids seem to be predominantly fully marine organisms. Species of the genera *Ophryotrocha* and *Parougia* Wolf, 1986 are particularly common and frequently highly abundant in organically enriched habitats, such as harbors, fish farms, sewage discharges and organic-falls (wood or the carcasses of large animals sunken to the seafloor) [16,31,44,72–74,89–92], being considered by some authors as nonspecialized opportunists (e.g., [48]). These two genera, along with *Exallopus*, include the majority of the species occurring in deeper waters [19,67,93–97], often in extreme habitats such as hydrothermal vents and cold seeps [18,97–102].

2.5. Distribution Patterns and Diversity

Dorvilleid worms are widely distributed and occur from the intertidal zone to the abyss. Significant family and genera revisions covering regional geographic areas include Fauchald [103], Orensanz [13,66], Oug [81], Wolf [68,104,105], Hilbig [95,106], Paiva and Nonato [107], Imajima [108], Núñez et al. [109] and Núñez [62] (as Stauronereididae). However, the majority of these works focus mainly on the Northern Hemisphere benthic fauna, while southern geographic areas such as the South Atlantic, Southeast Pacific and Indian Ocean are very poorly documented.

The exploration of organically enriched areas led to a great increase in the number of *Ophryotrocha* and *Parougia* species (e.g., [16,18,31,44,72–74,92,96–102,110]). The occurrence of several sympatric congeners is also frequently reported for both genera (e.g., [16,18,31,44,72–74,111–113]). Furthermore, with the upswing in deep-sea exploration, more species of these and other genera have been described also from areas that seemingly were not organically enriched (e.g., [19,93,94,114–116]). It is likely that there are many more species from these and other dorvilleid genera awaiting discovery, some still unknown in the ocean while others are already collected and stored, but not properly examined and described yet.

Despite the lack of planktonic larvae, some *Ophryotrocha* species have been shown to have quite a broad distribution range. For instance, *Ophryotrocha orensanzi* Taboada, Wiklund, Glover, Dahlgren, Cristobo and Ávila, 2013, *Ophryotrocha scutellus* Wiklund, Glover and Dahlgren, 2009 and *Ophryotrocha cyclops* Salvo, Wiklund, Dufour, Hamoutene, Pohle and Worsaae, 2014 have been reported from sites with hundreds to thousands kilometers between them, with species identities confirmed by molecular data [31,48,72,90]. Some species with wide distribution ranges are suspected to have been transferred with human activities such as in ballast waters (e.g., [78]). However, many dorvilleids are small and can be difficult to identify properly to species level, and thus the possibility of them having a continuous distribution between distant localities cannot be ruled out. More rigorous taxonomic investigations, preferably in combination with molecular information, are needed before we can make any assumptions about dorvilleid dispersal capacities and species real distribution.

2.6. Exploitation

Given their small size, Dorvilleids have never been an important commercial group. However, a recent study suggested the beneficial use of *Ophryotrocha* species in pisciculture by feeding on fish feces and in turn being fed to the fish [117]. In addition, because they have a short generation time and are easily kept in laboratory conditions, *Ophryotrocha* species may be suitable candidates as test model organisms for various kinds of studies [70,79,87,118].

3. Eunicidae Berthold, 1827

3.1. Systematics and Phylogeny

The family Eunicidae comprises 12 genera and approximately 453 species. It was first recognized as a taxon by Lamarck [119] under the name of Eunica. However, until 1944 it was more inclusive and almost equivalent to the order Eunicida with variations depending

on the author. The current definition of the family was established in Hartman [28] including four of the current valid genera, *Eunice* Cuvier, 1817 (242 species), *Lysidice* Lamarck, 1818 (30 species), *Marphysa* Quatrefages, 1865 (74 species), *Palola* Gray in Stair, 1847 (14 species). The composition of the family has been stable since then. However, currently it includes eight additional genera, one extinct, *Esconites* Thompson and Johnson, 1977 (one species), and seven extant, *Aciculomarphysa* Hartmann-Schröder, 1998 in Hartmann-Schröder and Zibrowius [120] (one species), *Euniphysa* Wesenberg-Lund, 1949 (11 species), *Fauchaldius* Carrera-Parra and Salazar-Vallejo, 1998 (two species), *Leodice* Lamarck, 1818 (33 species), *Nicidion* Kinberg, 1865 (14 species), *Paucibranchia* Molina-Acevedo, 2018 (19 species), *Treadwellphysa* Molina-Acevedo and Carrera-Parra, 2017 (eight species).

Phylogenetic analyses based solely on morphological data could not recover monophyletic Eunicidae and *Eunice* [121]. Combined molecular and morphological phylogenetic analyses recovered a monophyletic Eunicidae and nonmonophyletic *Eunice*, *Lysidice*, and *Marphysa* [10,11]. Based on these results, *Leodice* and *Nicidion* were resurrected to include species previously classified as *Eunice* or *Marphysa* that made both nonmonophyletic and *Nematonereis* Schmarda, 1861 was synonymized to *Lysidice*. It was still not possible to delimit a monophyletic *Eunice* because of the inconsistent placement of several of its species, including the type species *Eunice aphroditois*. *Eunice* species, which bear branchiae starting late, inflated base of the ventral cirri as thick ventral ridges, left MxIV with teeth restricted to the dorsal portion of the plate, and bidentate compound falcigerous chaetae with inconspicuous teeth in anteriormost chaetigers, consistently formed a clade which may represent another monophyletic genus. The further division of *Leodice* in two monophyletic taxa may also be justified in future analyses including more species. The genus has two main sister clades, one comprising species with dark subacicular hooks and the other species with light subacicular hooks. Thus, further analyses including more representatives of the diversity and other molecular markers are necessary.

A taxonomic key for the identification of genera valid at the time and considering the definitions based on eunicid current phylogenetic hypothesis is provided in Zanol et al. [11]. *Marphysa* is currently more restricted because some species have been transferred to *Paucibranchia* and *Treadwellphysa*. The key to genera in Molina-Acevedo and Carrera-Parra [122] includes *Treadwellphysa*. However, it considers *Nematonereis* valid and has more restricted morphological definitions for *Eunice*, *Leodice*, *Lysidice*, *Nicidion*, and *Marphysa*, not following genera definitions based on the phylogenetic hypothesis in Zanol et al. [11].

Taxonomic revisions for species are available for *Eunice* [36], *Euniphysa* [123], *Lysidice* from the Western Caribbean [124], *Marphysa* [25,122,125,126], *Palola* [127], *Paucibranchia* [128], and *Treadwellphysa* [129]. These revisions comprise more detailed descriptions, discussions on taxonomic acts and taxonomic keys, improving the knowledge of diagnostic morphological features, undoing unjustified synonymizations and facilitating identification. The revision of *Eunice* also includes species of *Leodice* and *Nicidion*, which were classified as *Eunice* at the time. Some of these have not had their genus officially changed yet. Thus, the number of *Leodice* and *Nicidion* species is probably much higher than the current figures and that of *Eunice* is much lower. *Palola* diversity is discussed in Schulze [49] and Schulze and Timm [116]. Despite the revisions, the identification of species of the genera *Eunice*, *Leodice*, *Lysidice*, *Nicidion* and *Palola* may still be confusing, thus, further revisions including more detailed descriptions with intraspecific variation would be of great value.

3.2. Morphology

Eunicidae is defined by two synapomorphies, dorsal buccal lip fused to the dorsal side of the prostomium and dorsolateral fold anterior extensions medially connected [11] (Figure 5A–E). Additional diagnostic features are present at prostomium, peristomium and jaws. These are ventral buccal lips with median transverse groove, one (single median antenna) to five prostomial appendages (a pair of palps, a pair of lateral antennae and a single median antenna), double ringed peristomium (Figures 1A and 5A–E), and

asymmetric eulabidognath maxillae (Figure 3G). The family encompasses great length variation, bearing species from few millimeters to few meters long. All species have a variable number of chaetigers.

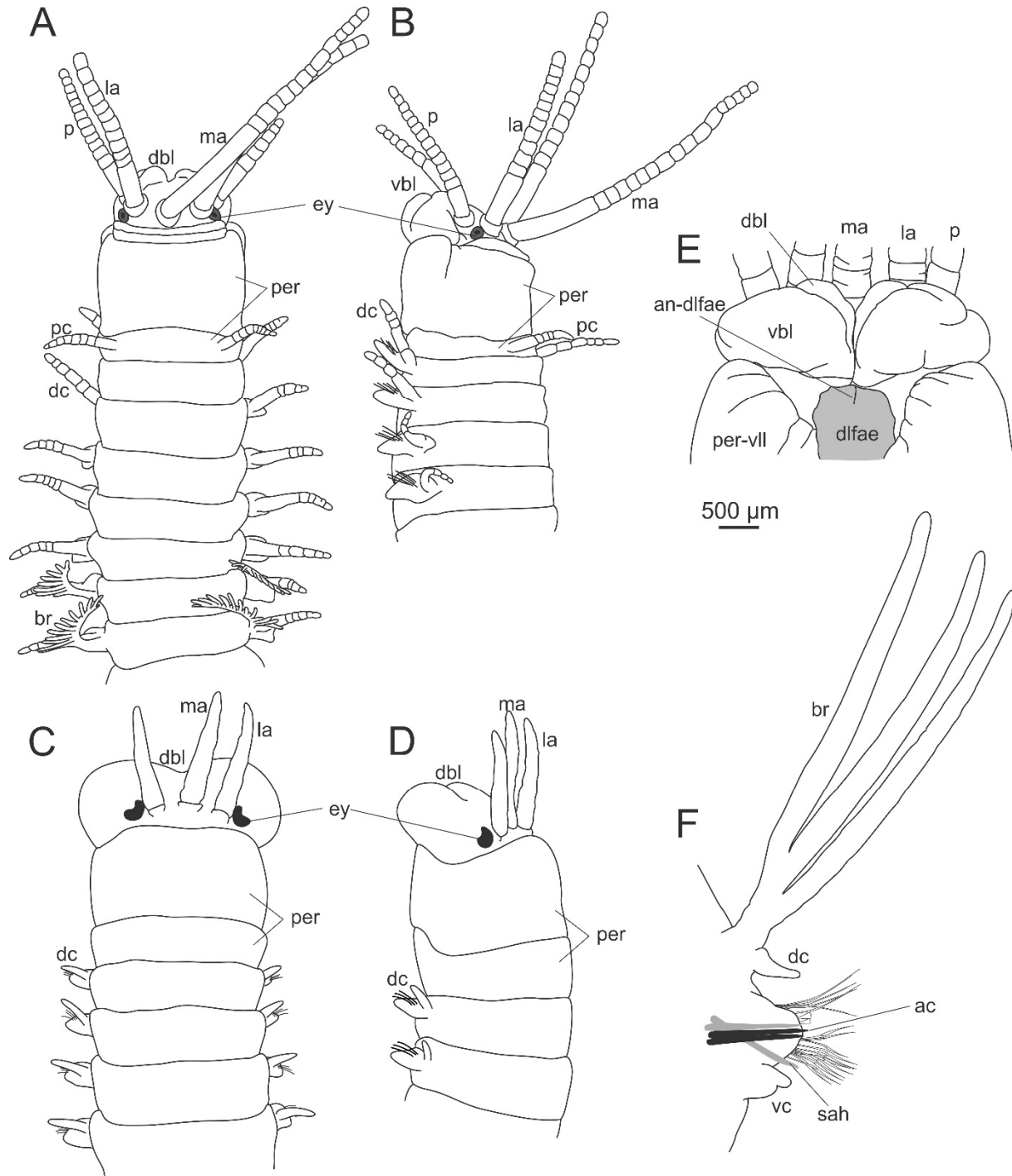


Figure 5. Morphology of Eunicidae. (A) *Leodice* sp., anterior end, dorsal view; (B) the same, lateral view; (C) *Lysidice* sp., anterior end, dorsal view; (D) the same, lateral view; (E) *Eunice violaceomaculata* Ehlers, 1887, prostomium, ventral view, dissected; (F) *Marphysa* sp., midbody parapodium. ac—acicula, an-dlfae—anterior notch of the dorsolateral fold anterior extension, br—branchia, dbl—dorsal buccal lip, dc—dorsal cirrus, dlfae—dorsolateral fold anterior extension, la—lateral antenna, ma—median antenna, p—palp, pc—peristomial cirrus, per—peristomium, per-vll—peristomial ventrolateral lips, sah—subacicular hook, vbl—ventral buccal lip, vc—ventral cirrus.

Diagnoses of extant genera take into account presence of lateral antennae and palps, articulation of prostomial appendages, presence of peristomial cirri, flat or curved mandibles, shape of maxillary plates, shape and distribution of branchiae, and presence and shape of pectinate chaetae and subacicular hooks (Figure 5F). Features present in chaetigers may vary in distribution and shape along the body. The complete set of chaetae in most genera includes limbate, pectinate, compound, subacicular hooks and aciculae. *Palola* is the only genus missing pectinate chaetae and subacicular hooks. In most genera, pectinate chaetae shafts are always thinner than limbate chaetae from the same parapodium (thin pectinate). However, in *Marphysa* and *Treadwellphysa*, they may have thick shafts (thicker than limbate chaetae in the same parapodium) and wide blades in mid and posterior chaetigers (thick and wide pectinate chaetae). The outer teeth of pectinate chaetae may be: both as long as inner teeth (anodont), just one longer (heterodont) or both longer than inner teeth (isodont *sensu* [130]).

In addition to these, features considered in the identification of species are the shape and size of prostomium, peristomium, prostomial appendages and peristomial cirri, dorsal and ventral cirri, prechaetal, chaetal, postchaetal lobes, pygidial cirri, the distribution and shape of branchiae, pectinate and compound chaetae, and the color, distribution, number and shape of aciculae and subacicular hooks. The detailed morphology of the chaetae varies along the body and is an important taxonomic feature, as in the case of pectinate chaetae in *Marphysa* species [131,132]. Compound chaetae are present in all species at least in part of the body with the exception of some species of *Marphysa*, which lack them completely. Only some species of *Euniphysa* bear pseudocompound chaetae in the anterior chaetigers.

Challenges in understanding the morphology of species are the difficulty in sampling complete specimens and the poor knowledge on intraspecific variation, known only for few species (e.g., *Leodice rubra* (Grube, 1856) in [133]; *Leodice vittata* (Chiaje, 1929) in [36,134]). Intraspecific variation, sometimes due to size variation, occurs at least in features such as the number of articles in the prostomial appendages, the presence/absence and distribution of subacicular hooks, the number of branchial filaments, the branchial distribution, and the end of inflated base of ventral cirri (e.g., [47,134–137]). In incomplete specimens, size is commonly estimated as length through chaetiger 10, and width at this chaetiger, however, at least in a few species the peristomium width is a better estimator [138]. An index of the product of the length through chaetiger 10 by the largest width at this region has also been used as a size estimator [13]. Detailed descriptions of general morphological features are available in Ehlers [3], Treadwell [139], Fauchald [36], Zanol et al. ([11] in supplementary material, [121]), Carrera-Parra [140], Zanol and Budaeva [141], of branchial distribution patterns in Miura [135] and of maxillary features in Paxton [14], Molina-Acevedo and Carrera-Parra [122] and Molina-Acevedo [128].

3.3. Feeding and Life History

Eunicids have been reported as macrophagous or microphagous omnivorous, however, some species have more restricted diets, being herbivorous or carnivorous [34]. At least one *Eunice* species is an ambush predator. It captures the preys with the maxillae, which are kept open near the substrate while waiting for the prey [142].

All the species studied have separate sexes and sexual reproduction. Sexual dimorphism of unripe individuals, hermaphroditism and asexual reproduction have not been described for the family. The reproduction biology is known for less than 10% of the species [141]. Thus, it might be more variable than our current knowledge. Free spawning by benthic or epitokous forms followed by fertilization and larval development in the water column is the most common mode of reproduction. Some epitokous forms swarm. *Palola* swarmings in the South Pacific are the most well-known because they have cultural importance to local communities [60,143,144]. Exceptions to fertilizations in the water column happen in some *Leodice*, which fertilize eggs within their burrows, and estuarine *Marphysa* species, which produce jelly egg masses attached to the substrate [145–151].

All clearly described larvae are lecithotrophic and oocyte diameters also suggest lecithotrophic development [50]. Juvenile settlement may take 10–20 days from the beginning of the development [149–152], and eunicids are expected to have poor natural dispersal capabilities. However, they may disperse via rafting in drift plastic and wood (e.g., *Eunice* and *Marphysa*; [153,154]) and in association with oysters in human-mediated transport (e.g., *Marphysa victori* Lavesque, Daffe, Bonifácio and Hutchings, 2017; [47]). Commercial oysters can also host species of *Leodice*, *Lysidice*, *Nicidion* and *Marphysa* as epibionts [155].

3.4. Habitats and Ecology

Species of eunicids are present in soft and hard substrates in estuarine and marine habitats. They also occur associated with biogenic substrates, such as coralline algae, cnidarians, oyster shells, seagrass and sponges [139,155–158], and authigenic carbonate crusts formed in cold seeps [159]. Species live in burrows or tubes; some crawl outside, usually at night. Tube building appears to be restricted to some *Eunice* and *Leodice* species. They are most commonly composed of parchment-like material—soft or stiff. Some tube building species are symbionts with cnidarian species such as *Lophelia pertusa* (Linnaeus, 1758), *Madrepora oculata* Linnaeus, 1758 and *Epizoanthus* spp [160–162]. Species associated with corals act in their bioerosion, in assembling coral reefs and in determining the reef framework through tube building, which facilitates coral growth [162–164]. The mean density of eunicids in dead coral may be as high as 315 ind/m², while a single dominant species such as *Nicidion cariboea* (Grube, 1856) may reach a density of 1219 ind/m² [165].

3.5. Distribution Patterns and Diversity

Eunicids inhabit all oceans from the intertidal zone to around 3500 m in the deep-sea, being more common and diverse in shallow tropical and subtropical hard substrates. In the Antarctic and Arctic regions, a maximum of four species has been recorded and only *Eunice* and *Leodice* are present [13,166,167]. Most genera are widespread; the exceptions are *Aciculomarphysa*, *Fauchaldius* and *Euniphysa*. *Aciculomarphysa* and *Fauchaldius* have not been recorded since their original description, thus their distribution is restricted to the depths they have been described from, respectively, 460–490 m and 150–250 m [120,130,168]. *Euniphysa* is mainly restricted to the shallow warm waters of the Northern Hemisphere, with most of the richness concentrated in the South China Sea and adjacencies [123]. The only known records for the South Atlantic Ocean are from the south and northeast of Brazil ([169], personal observation), which suggests that *Euniphysa* is widespread but not abundant.

Some local fauna studies focusing on eunicid taxa are available for the Antarctic and Subantarctic Seas [13], Argentina [170], Australia [24,131,171–175], Brazil [133,176–180], British Isles [181], the Canary Islands [182], the Caribbean Sea [25,42,122,124,130,136,139,183–186], China [187,188], the eastern Pacific [28], the El Salvador Pacific Coast [189], Fiji and Samoa [190], the French Atlantic Coast [191], the Gulf of Mexico [192,193], Hong Kong [194], the Iberian Peninsula [132,195], India [196,197], Japan [135,198–202], Korea [203], Malaysia [204], the Mediterranean Sea [205–210], the Mexican Pacific Coast [103,211,212], New Zealand [213], the Philippines [214,215], the Scandinavian and North Sea Coasts [167], South Africa [126,216,217], Taiwan [218,219], the USA's Atlantic Coast [148,220,221], the USA's Pacific Coast [222], and Venezuela [223,224]. Carrera-Parra [140] includes a taxonomic key for species registered to the warm temperate Northeast Pacific, Tropical Eastern Pacific Ocean and Tropical Northwestern Atlantic Ocean. The eunicid fauna are most poorly known for the Southeast Atlantic, Southeast Pacific and Indian Ocean.

These studies on local fauna are initial guides to the eunicid diversity. However, some of the species included should be considered with care. Several species thought to be widespread at the time of publications are currently known [e.g., *Lysidice ninetta* Audouin and Milne Edwards, 1833a [124,225], *Marphysa sanguinea* (Montagu, 1813) [45], *Palola viridis* Gray in Stair, 1847 [116]] or suspected to have restricted distribution (e.g., *Eunice afra*

Peters, 1854, *Eunice aphroditois*, *Leodice antennata* Lamarck, 1818, *Leodice pennata* (Muller, 1776), *Leodice vittata*, *Lysidice collaris* Grube, 1870, *Lysidice hebes* (Verrill, 1900), *Lysidice unicornis* (Grube, 1870), *Nicidion cariboea*, *Palola siciliensis* (Grube, 1840), *Paucibranchia bellii* (Audouin and Milne Edwards, 1833). *Eunice aphroditois* had several large (giant) species considered to be its junior synonyms, leading to the identification of most giant specimens as *E. aphroditois* [184]. The identity of most large specimens remains to be solved, as well as the diversity and evolution of giant species in the family [184,226].

The widespread status of most eunicid species is usually due to poor original descriptions, unjustified generalized synonymizations, and the use of local fauna monographs in the identification of the fauna of distinct regions as described for other polychaete groups [227]. *Palola* sp. (in [49,116,174]) and *Marphysa victori* are the only species with widespread distribution confirmed by both molecular and morphological data. *Palola* sp. is present in both Micronesia and the eastern Pacific and its means of dispersion are not fully understood [49,116,174]. Meanwhile, *M. victori* is an exotic species in France introduced in association with commercial oysters imported from Japan [47].

Taxonomic revisions of species based on type material (e.g., [36,123,127–129]) as well as designations of neotypes (e.g., *M. sanguinea* in [45]) provided the initial framework to improve the knowledge on the diversity (Figure 2) and distribution of eunicid species and to question records of species reported all over the world. Furthermore, more detailed examination of morphological features, such as jaws (e.g., [25,128]), chaetae variation along the body (e.g., [24,131]), and molecular data improved findings of misidentifications and morphologically similar species. These provide tools and encourage other authors to handle similar taxonomic issues generating a virtuous cycle as observed in *Marphysa*, eunicid genus with the highest number of species described since 2003 when the *M. sanguinea* neotype was designated in Hutchings and Karageorgopoulos [45].

Lewis and Karageorgopoulos [217] were the first to follow the lead to tackle the widespread issue in *Marphysa sanguinea* combining morphological and molecular data. They revealed high molecular diversity among species traditionally identified as *M. sanguinea*. The same pattern has also been found in *Palola* and *Lysidice*. *Palola* includes several deeply separated molecular lineages of mostly morphologically indistinct species and *Palola viridis* appears to have more restricted distribution than its records in the literature [49,116,174]. In *Lysidice*, molecular analyses [225,228] supported previously reported morphological differences between *Lysidice collaris* and *Lysidice ninetta* [229]. These are the only eunicid species subject to phylogeographic and population studies and depict different evolutionary histories. *L. collaris* has panmitic populations, while *L. ninetta* includes two genetic lineages corresponding to different color morphs separated at around 3.7–3.4 million years ago, which may be different species [225,228]. Molecular analyses using nucleotide sequences of cytochrome oxidase I (COI) and 16S rDNA have become common in papers on eunicid species [202,230]. These have aided in understanding intraspecific variation, such as the lack of a subacicular hook in large specimens of some *Marphysa* species [47], in improving species recognition and in revealing a hidden biodiversity even in well-studied places.

3.6. Exploitation

Species of *Eunice* and *Marphysa* are commonly used as bait worms. However, the species identity of many of these has just become clear in the last few years [24,132]. The clear understanding of this diversity is essential to avoid the overexploitation of species as well as the introduction of exotic species due to commercialization or the establishment of farming [24].

4. Hartmaniellidae Imajima 1977

4.1. Systematics and Phylogeny

Hartmaniellidae has only one genus and three species. The first species, *Hartmaniella erecta* Imajima, 1977, was described from Suruga Bay, Japan. A year later, Amoureux [168]

described a new genus and species from Tuléar, Madagascar, *Pseudoninoe tulearensis*, which he placed within Lumbrineridae. However, as was suspected by Pettibone [231] and Orensanz [13], this species belongs to *Hartmaniella* [232]. The third species, *Hartmaniella fujianensis* He and Wu, 1986, was described from the Taiwan Strait. Three other potential new species were described but not formally named from the Gulf of Mexico [232,233], the Andaman Sea [234], and Natuna Island, Indonesia [235].

Hartmaniellids superficially resemble Orbiniidae by having parapodia displaced dorsally (Figure 6A,C). However, they have well-developed maxillae and mandibles (Figure 3A) which unambiguously place them within Eunicida. However, several authors have debated on the classification of hartmaniellid maxillae. They have diverging views on the maxillary apparatus symmetry, homology among maxillary plates, carrier connection to maxillae I, and, thus, on hartmaniellids' closest families. Imajima [236] mistakenly described a symmetric maxillary apparatus with four plates on both sides and illustrated the carriers as being poorly connected to maxillae I. Following Imajima's description, Orensanz [13] suggested Hartmaniellidae being closely related to the fossils *Synclinophora synclinalis* Eisenack, 1975 and the *Delosites*-like scolecodonts, and with extant Eunicidae and Onuphidae. Later, based on the poor connection between the carriers and maxillae I illustrated in Imajima's description, Fauchald and Rouse [237] considered the hartmaniellids maxillary apparatus more similar to the prionognath type and the family sister group of Oeonidae and Lumbrineridae. However, illustrations of *Hartmaniella erecta* by Szaniawski and Imajima [238] and the descriptions and illustrations of *Hartmaniella tuleransis* and *Hartmaniella* sp. by Carrera-Parra [232] show that the carriers are completely attached to the base of maxillae I. Szaniawski and Imajima [238] established a remarkable similarity of *Hartmaniella* jaws with fossil of *Palurites* Kozur, 1967 by the peculiar shape of maxillae I and II. They also proposed a close relationship between Hartmaniellidae extant Lumbrineridae and extinct Kielanoprionidae (asymmetric jaws), considering that the differences in structure (symmetric vs. asymmetric) of their maxillary apparatus are diagnostic at the family level. Eibye-Jacobsen and Oug [234] described an asymmetric maxillary apparatus in specimens from the Andaman Sea, and reported the right maxillae III and IV to be fused in contrast to the left separate plates. They hypothesized that asymmetry in maxillae could have evolved independently several times within Eunicida and supported the close relationships of hartmaniellids with Oeonidae or Lumbrineridae rather than with Eunicidae and Onuphidae. Carrera-Parra [232] stated that hartmaniellids have an asymmetrical maxillary apparatus with four maxillae on the left side and only three on the right side, reinforcing the earlier idea of close relationship with the asymmetrical fossils of Kielanoprionidae and with Eunicidae/Onuphidae. The latter was also supported by the presence of dorsal and ventral cirri in the three families. Lu [239], likewise based on the revision of Japanese specimens, described an asymmetric maxillary apparatus for *H. erecta*. Paxton [14] considered hartmaniellid jaws "subsymmetrical" and closest to the extant Lumbrineridae. For both families she proposed a new type of maxillae—symmetrogna; however, the maxillary apparatus of hartmaniellids is asymmetric with four maxillae on the left side and only three on the right side [232,234,239] (Figure 3A).

A combined analysis of morphological characteristics and molecular data will help to clarify the placement of hartmaniellids within Eunicida, which, to date, has been hampered by the extremely scarce material and the lack of specimens suitable for molecular analyses.

No taxonomic revisions, key and phylogenetic analyses are available for the family.

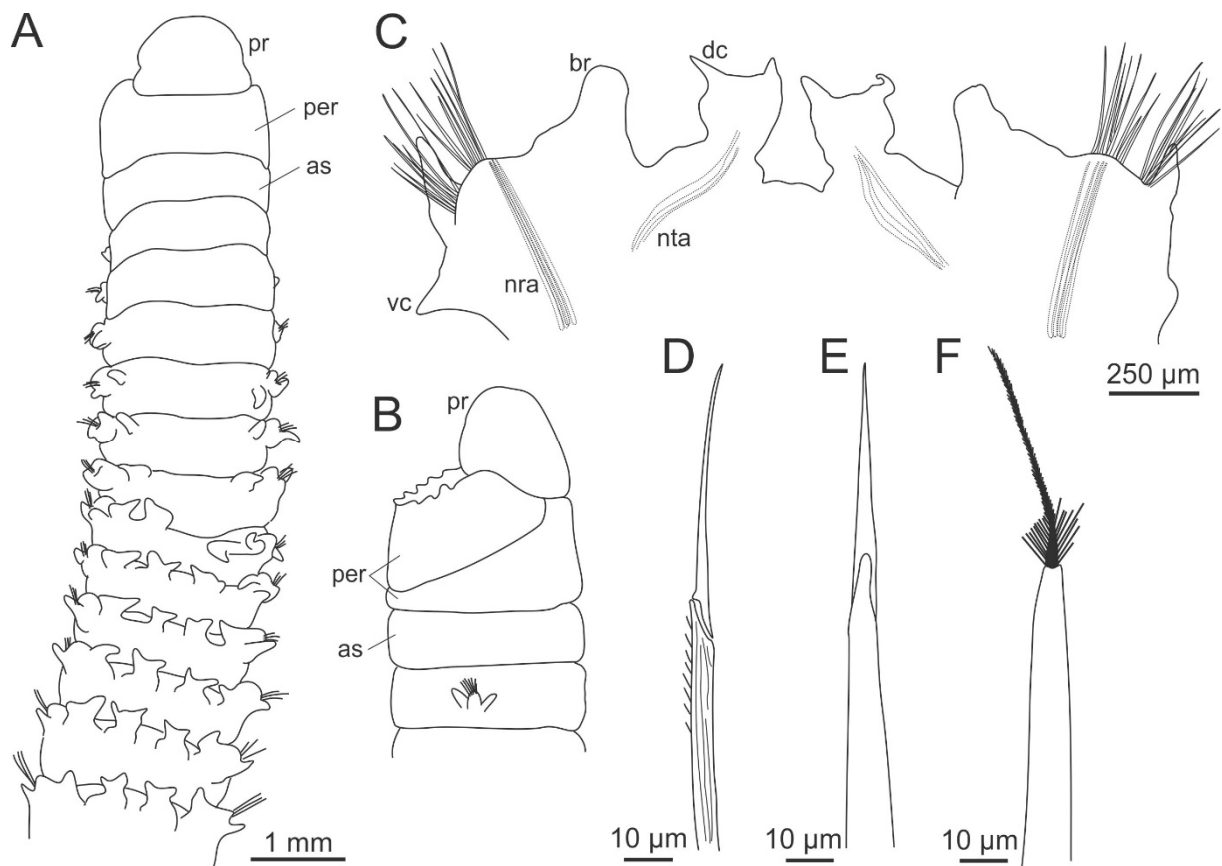


Figure 6. Morphology of Hartmaniellidae. (A) *Hartmaniella* sp., anterior end, dorsal view; (B) the same, anterior end, lateral view; (C) the same, parapodia from midbody region shifted dorsally; (D) *Hartmaniella tulearensis* (Amoureux, 1978), composite spiniger; (E) the same, acicular spine; (F) the same, acicula. as—achaetous segment, br—branchia, dc—dorsal cirrus, nra—neuropodal aciculae, nta—notopodial aciculae, per—peristomium, pr—prostomium, vc—ventral cirrus. (B), (D–F) modified from Carrera-Parra [232].

4.2. Morphology

Hartmaniellids are small worms up to 2.5 cm long; however, most of the few collected specimens are incomplete. The prostomium lacks eyes and appendages (Figure 6A). The peristomium is laterally projected over the prostomium, the first ring is dorsally reduced, and the second one is longer dorsally than ventrally (Figure 6B). The absence or presence of papillae in the peristomium may aid to species identification. The first segment is apodous. The body is divided into three regions by the morphology of parapodia. In the first region, the parapodia are lateral; the second region is characterized by having parapodia displaced over the dorsum with bifid dorsal cirri and foliose parapodial branchiae dorsal to prechaetal lobes; while in the third region, the dorsal cirri are digitiform, basally swollen and the branchiae are tapering. The relative length of the body regions might be of taxonomical value at species level; however, it should be taken with caution, as these characteristics may be size-dependent. From chaetiger 6–7, all segments are biannulated. The chaetae of hartmaniellids are limbate with a serrated margin, compound spinigers with distally spinulose shaft, internally with granulated base becoming canaliculated from the median to the distal end; acicular spines with a long mucro appear from about chaetigers 6 (Figure 6D,E). The aciculae are aristate, subdistally hirsute with a long mucro finely hairy (Figure 6F). The number of chaetae and aciculae per parapodium may be of diagnostic value at species level.

Hartmaniellids have an asymmetric maxillary apparatus with four maxillae on the left side and three on the right (Figure 3A). Maxillae I are mainly characterized by long

internal teeth and a lateral spur located on the outer posterior margin, while maxillae II are characterized by being a narrow plate with a lateral projection on the anterior outer edge. The number of teeth in maxillae I and maxillae II are important to distinguish the species.

4.3. Feeding and Life History

Jumars et al. [34] suggested hartmaniellids could be predators of meiofauna based on their size and the presence of maxillary apparatus. The only information about reproduction in hartmaniellids is the presence of deep yellow oocytes with large amounts of yolk, 150–200 µm in diameter in median parapodia, suggesting the development via lecithotrophic larvae [234].

4.4. Habitat, Distribution and Diversity

Hartmaniellids have been found in clayey and sandy silt, soft mud, sandy mud, and sandy mud with shell fragments, from depths of 40 to 210 m in six regions of the Pacific Ocean (Japan, China, Indonesia, Thailand, Madagascar, and La Réunion), while in the Atlantic Ocean, they have only been reported in the Gulf of Mexico in clayey and sandy silt at depths of 175 to 189 m. They are considered as being “living fossils”, abundant during the Mesozoic, but currently poorly represented [238].

There is no information about the ecology of the family.

5. Histriobdellidae Claus and Moquin-Tandon, 1884

5.1. Systematics and Phylogeny

The family Histriobdellidae is composed of highly specialized ectosymbionts known as “clown worms”. The prefix “histrion” (from the Etruscan word “hister”), which means actor or dancer, alludes to the performative way in which these worms move, quite similar to the actor Charlie Chaplin, in his character “Carlitos”. The species names *Stratiodrilus arreliai* Amaral and Morgado, 1997 and *Stratiodrilus circensis* Steiner and Amaral, 1999 also refer to the circus and its artists.

Histriobdellidae was first included in Hirudinea, which justifies the suffix “bdella” [240]. It has also been included among Rotifera and Archiannelida [241–244]. Mesnil and Caullery [245] have first suggested that maxillae of histriobdellids were homologous to other Eunicida, as a prionognath type. Tzetlin [246] considered the histriobdellid maxillae as of the ctenognath type. His views were recently corroborated by an extensive study of jaw morphology and ultrastructure in *Histriobdella homari* Van Beneden, 1858 showing the ultrastructure similarity of the maxillae with Dorvilleidae [247]. The inclusion of the family in Eunicida was followed by latter studies that considered histriobdellids as highly specialized commensals, lacking external resemblance to the traditional Errantia body plan [13,237,248–250].

This epizoic group is currently composed of three genera and 13 species that live within the branchial chambers (on branchiae, epipodites, or inner surfaces of carapace), in the egg masses, or, occasionally, on the general body surface (head, thorax, abdomen, or appendages) of marine and freshwater isopod and decapod crustaceans. *Histriobdella* Van Beneden, 1858 and *Steineridrilus* Zhang, 2014 are monospecific and exclusively associated with marine hosts, while *Stratiodrilus* Haswell, 1900 includes 11 species associated with freshwater hosts.

There is no phylogenetic hypothesis that deals with relationships between the genera and species within the family, only hypotheses regarding their marine or freshwater origin [251–255]. To date, most taxonomic and systematic studies on histriobdellids were based on external morphology with no molecular data available. A single study using SEM, TEM and confocal laser scanning microscopy described details of the jaw apparatus [247]. The only review was carried out by Steiner and Amaral [256] who proposed a nomenclature for some morphological structures, redescribed all species based on literature and proposed a new genus, *Dayus*, which, being preoccupied, was renamed for *Steineridrilus* [257]. Rosa et al. [255] updated the list of *Stratiodrilus* hosts based on published

data and specialized databases discussing its distribution. An identification key for all described *Stratiodrillus* was published by Amato et al. [258].

5.2. Morphology

The worm-like translucent and delicate body is small, with the maximum length of adults varying between 0.5 to 1.5 mm, indistinctly and irregularly annulated, with constrictions more visible laterally, and divided into head, trunk and posterior region (Figures 1F and 7A,B,D,E). Histriobdellids have no true segments, parapodia, chaetae or aciculae, but the ventral dark sclerotized jaws can be easily seen by transparency (Figure 7D–G). Despite the absence of metamerism, internally histriobdellids have 9 to 11 ganglia (depending on the genus) in the ventral nerve cord [248,259].

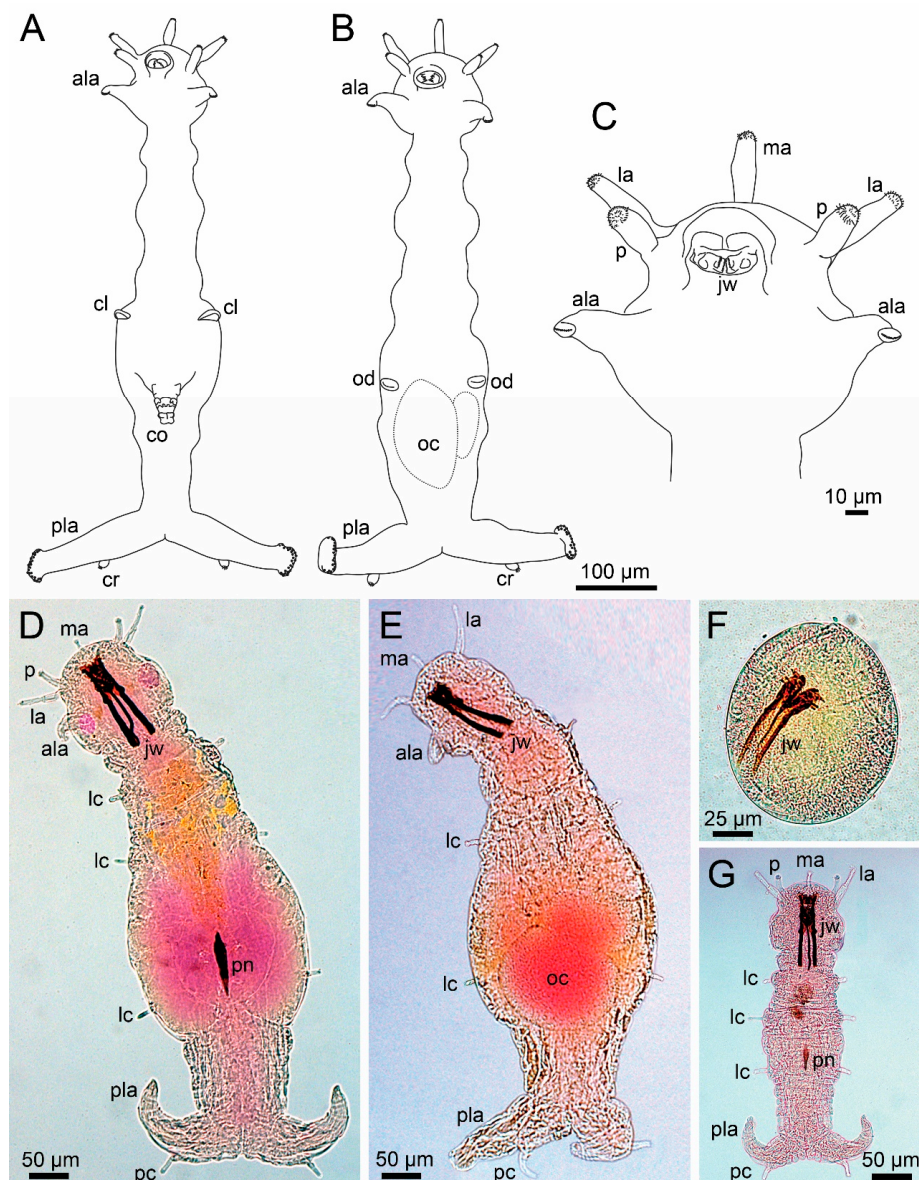


Figure 7. Morphology of Histriobdellidae. (A) *Histriobdella homari*, male, ventral view; (B) the same, female, ventral view; (C) the same, anterior end, ventral view; (D) *Stratiodrillus arreliai* Amaral and Morgado, 1997, male, ventral view; (E) the same, female, ventral view; (F) the same, early embryo; (G) the same, juvenile, ventral view. ala—anterior locomotory appendage, cl—clasper opening, co—copulatory organ, pc—posterior cirrus, jw—jaws, la—lateral antenna, lc—lateral cirrus, ma—median antenna, oc—oocyte, od—oviduct opening, p—palp, pla—posterior locomotory appendage, pn—penis. (D–G), Copyright © 2016, Editora Guanabara Koogan (Fransozo, A. & Negreiros-Fransozo, M.L., Zoologia dos Invertebrados, 1st edition, page 366), reproduced with permission of the publisher.

The head is composed of prostomium fused to peristomium, and the trunk has five segments, but only the second, third and fifth may have lateral cirri, which are probably homologous to dorsal and/or ventral cirri of other Eunicida [260] (Figure 7A–E). Nuchal organs were reported in some species [242,259]. The prostomium bears three antennae dorsally and two sensory palps frontally (Figure 7C,D). One pair of locomotory appendages with adhesive glands on the distal end is located on the lateral of the head, probably the peristomium (Figure 7A–E), retractable in most species. In the fourth trunk segment, males have one pair of lateral retractable claspers for holding females during copulation, and a penis on the ventral side of body (Figure 7A,D,G). The posterior region of the body, after the fifth segment, is composed of several fused segments without cirri or any kind of appendages and two lateral lobes, the posterior locomotory appendages, with the anus located between them (Figure 7A,B,D,E,G). These appendages have a duo-gland adhesive system [261] on their distal ends, in addition to cirri, lobes, and/or tubercles. The jaw apparatus is very complex, enclosed in the ventral pharyngeal organ. The paired mandibles are fused along the mandibular plates bearing about 10 denticles and attached to each other in the median part of the mandibular shafts, which are flattened and elongated. The maxillae consist of a single dorsal rod, a massive ventral carrier and four pairs of dentate plates–maxillae I–IV [247,249] (Figure 3E).

All known species are dioecious and sexually dimorphic when mature, one of the few examples in polychaetes. The chitinous black penis of *Stratiodrillus* is an eversible spine with a bevelled tip [260] like a hypodermic needle [262]. In *Histriobdella*, the penis is composed of two hard structures with a central duct [260], but not chitinized. Detailed descriptions of general morphological features are available in Shearer [242], Haswell [262,263], Roubaud [244], Jennings and Gelder [249], and Steiner and Amaral [256].

Histriobdella is characterized mainly by the presence of short and papillae-like antennae and palps and the absence of lateral cirri on trunk (Figure 7A–C). *Steineridrilus* and *Stratiodrillus* have lateral cirri and longer and narrower antennae and palps. In *Steineridrilus* the three antennae are biarticulated, while in *Stratiodrillus* only the lateral antennae bear two articles (Figure 7D,E). The shape of the lateral cirri and the presence or absence of cirri, lobes and tubercles in posterior locomotory appendages determine *Stratiodrillus* species, especially those from the Neotropical region. Studies that address intraspecific variations are only known for *Stratiodrillus circensis* [264] that has been widely recorded in the Neotropical region. These worms are relatively easy to collect, just by finding their hosts, which carry in their body, especially in the branchial chamber, a good amount of complete specimens.

The morphological adaptations to the commensal life habit are diverse, when compared to the Eunicida pattern. They range from the reduction in body size, absence of metamerism, parapodia, chaetae and aciculae, to the presence of a duo-gland adhesive system in the posterior region, which allows its attachment to different parts of the host's body. Sexual dimorphism and the penis also appear to be adaptations to the specific habitat of these worms.

5.3. Feeding and Life History

Histriobdellids find shelter in the host and feed on the microflora (bacteria, cyanophytic algae, diatoms, among others) that grows abundantly in the chamber and branchial filaments, bringing the benefit of always keeping these areas clean and free, so that gas exchange is carried out more efficiently. Jennings and Gelder [249] found that the relationship between *Histriobdella homari* and its crustacean host has a firm nutritional basis.

Regarding reproduction, the male hypodermically inserts its penis into the female and the sperm goes directly into the body cavity [265]. Whitish eggs in different stages of maturation are visible in the female's transparent body (Figure 7E). In all known species, there is a suppression of the larval stage, with egg-laying occurring in branchial chamber or in egg masses of the female host. The development, therefore, is direct, and immature miniatures of adult worms hatch from the eggs. Histriobdellid females attach their eggs to the host (branchial chamber, between eggs of host female, pleopods and uropods),

which allows the young worms to continue their life cycle on the host. Shearer [242] and Simon [266] stated that *Histriobdella* can migrate from the branchial chamber to the egg mass of female host and, after attaching the eggs, return to chamber. *Histriobdella homari* also has the ability to migrate from one host to another [266].

5.4. Habitats and Ecology

Histriobdellids have been treated as parasites [267,268] or commensals [260,269]. According to Bratney and Campbell [270], in most infestations *Histriobdella homari* benefits the lobster. However, if the number of individuals is very high, the benefit of microfloral grazing may decrease, as worms can reduce the oxygen flow on the branchiae, also reducing success in hatching host's eggs. On the other hand, Lerch and Uglem [271] reported success in the hatching of female hosts' eggs, even with high numbers of *H. homari* in the branchial chamber. According to Martin and Britayev [269], a symbiotic species that completes the entire life cycle in a single host has a monoxenous pattern, and they consider that *H. homari* behaves more as a cleaning symbiont rather than as a parasite. Jennings and Gelder [249] classify the species as epizotic microphagous cleaning symbiont.

Studies on species biology are still few; the mechanisms of dispersion and selectivity in host choice are still unknown, as well as the real nature or extent of the association with their hosts.

5.5. Distribution Patterns and Diversity

The differentiation between the histriobdellid genera are also reflected in their geographical distribution. The first described genus, *Histriobdella*, occurs exclusively on lobsters (*Homarus*, *Nephrops*) in the Northern Hemisphere, on both sides of the Atlantic Ocean, in Europe (Norway, Ireland, England, the Netherlands, the Irish Sea, the Clyde Sea), Canada, and the United States (mid-Atlantic Bight). *Steineridrilus* is the marine group from the Southern Hemisphere, having an intertidal isopod (*Cirolana*) as its host. It is only known from South Africa, where it occurs from the Lagebaan Lagoon to East London [272]. *Stratiodrilus* is the most speciose genus and encompasses species living on freshwater decapods from the Southern Hemisphere. It has been identified on different hosts (*Astacopsis*, *Astacoides*, *Aegla*, *Cherax*, *Parastacus*, *Samastacus*, and *Trichodactylus*) that occur in diverse freshwater environments, such as streams, brooks, flowing rivers, lagoons and caves from Australia (including Tasmania), Madagascar, Chile, Argentina, Uruguay, and Brazil.

The distribution of histriobdellids reveals interesting information that contributes to the continental drift theory, with *Histriobdella* having a Laurasian distribution, while *Stratiodrilus* and *Steineridrilus* show a Gondwanan distribution, occupying the Neotropical, Afrotropical and Australasian zoogeographic regions [254,255]. Harrison [251] suggested that *Stratiodrilus* distribution demands former land connections between Australia, Madagascar and South America, and proposed a marine ancestor for the family. The co-occurrence of *Stratiodrilus* in parastacid crayfish suggests a single colonization in continental waters, prior to the breakup of Gondwana [254,260]. Thus, *Stratiodrilus* appears to have successfully invaded continental waters either in Palaeozoic or in Mesozoic [254]. Jennings and Gelder [249] suggested that the suppression of a free-swimming larval stage is an adaptation to the freshwater environment and that *Histriobdella* and *Steineridrilus* have become secondarily adapted to a marine habitat. On the other hand, one of the strategies of some commensal species is simplification of their life cycles, either reducing or eliminating the free-living larval stage, with the adult phase being responsible for dispersion [269]. Thus, the direct development could be an adaptation to the symbiotic lifestyle and not to the freshwater environment, which would support the marine origin theory for the family.

Up to now, 44 species of nine genera of four Decapoda families have been found to host *Histriobdella* and *Stratiodrilus* species. Only one species of Isopoda hosts *Steineridrilus*, which is known only from its original description [272], including some biological information, in addition to a photographic record made by Rouse [268], from an unknown locality. Some histriobdellids do not demonstrate specificity to a single host. *Histriobdella homari*, for

example, is found in three different species of lobsters of the genera *Nephrops* and *Homarus*, on both sides of the Atlantic. *Stratiodrillus circensis* is also widely distributed, occurring in at least 10 species of Aegliidae and in some Parastacidae, in Chile, Argentina and Brazil [255]. Crabs from the genus *Aegla*, the hosts for several *Stratiodrillus* species, are widespread in the South America with 72 known species [273] of which only 20 have been studied for the histriobdellid symbionts [255]. Furthermore, other genera and species of decapods and isopods can potentially host histriobdellids. Thus, the diversity of Histriobdellidae could be highly underestimated due to the absence of systematic study covering the wide diversity of potential hosts.

It is not known how common cryptic speciation is within Histriobdellidae. Rosa et al. [255] proposed studies using molecular tools to clarify the taxonomic status of *S. circensis*, which may represent a complex of cryptic species, considering its wide distribution in four countries. Briggs et al. [274] also considered the possibility that *H. homari* from two localities of Europe are different species or subspecies. Considering that the species is reported from both sides of the Atlantic, it may represent a species complex.

Stratiodrillus gondwanian distribution suggests it may have speciated with host parastacid crayfish, which have similar distribution. However, despite early suggestions of this relationship [251,254,255] and of the connection between diversity of histriobdellids and their hosts, no study has tested these hypotheses yet. Biogeographic studies incorporating molecular analyses are necessary to study the coevolution of hosts and histriobdellid ectocommensals.

Histriobdellidae is a relatively poorly studied family with knowledge gaps in practically all areas, despite being relatively easy to collect and to observe. Until 1962, studies were limited to descriptions of new species based on external morphology [240,243,251,262,263] and investigations of the internal anatomy [241,242,244,245,259,275]. More recently, the biology and behavior of several histriobdellid species [249,258,264–266,276,277], as well as relationships with their hosts and other ectosymbionts [252,271,278] received more attention. Few studies have been carried out on the ecology of the family [249,266,267,270,271,278,279] as well as species distribution records [255,280,281]. Studies that focus on the life cycle, molecular techniques, ecology, and taxonomy will certainly help in reconstructing phylogenetic relationships among the species of the family, as well as their relationships with their hosts.

6. Lumbrineridae Schmarda, 1861

6.1. Systematics and Phylogeny

Lumbrineridae comprises 19 genera and about 279 species. The first species of Lumbrineridae was described by Müller in 1776 as *Lumbricus fragilis* (now *Scoletoma fragilis*). Previously, some authors considered the group as a subfamily of Eunicidae, but today it is regarded as an independent family [282].

Lumbrinerids have a very simple body shape, with a marked reduction of external morphological characteristics (Figure 1D). Thus, classifications based on external morphology only resulted in a simplified generic system that lumped all known species in only three or four genera [283]. Hartman [28] and Fauchald [103] treated genera *Augeneria* Monro, 1930, *Cenogenus* Chamberlin, 1919, *Eranno* Kinberg, 1865, and *Scoletoma* de Blainville, 1828 as synonyms of *Lumbrineris* de Blainville, 1828. The taxonomy of this family has changed after employing characteristics of the maxillary apparatus and mandibles, which allowed the reestablishment of all above-mentioned genera [13,283–285] and the description of 13 new genera [13,284–286]. A key to genera valid at the time is available in Carrera-Parra [286] and Carrera-Parra [282].

To date, there is only one phylogenetic study, which is based on morphological data, regarding the intergeneric relationships within Lumbrineridae. The family is divided into four main clades supported by the characteristics of the maxillary apparatus [286]. This study corroborated the inclusion of *Lysarete* Kinberg, 1865 into Lumbrineridae proposed by Orensanz [13], as well as the recognition of *Augeneria*, *Cenogenus*, *Eranno*, and

Scoletoma genera previously considered as junior synonyms of *Lumbrineris*. Furthermore, there is a phylogenetic study on interspecific relationships of *Lumbricalus* Frame, 1992 [287]. Only three genera of lumbrinerids underwent complete systematic revision: *Kuwaita* Mohammad, 1973 [288], *Lumbricalus* [289], and *Lumbrineris* [290]. The rest of the genera await revisions based on detailed study of the architecture of the maxillary apparatus and, possibly, molecular information.

6.2. Morphology

Lumbrinerids are worms of small to medium size, ranging from a few to over 60 centimeters [291,292]. Their prostomium can vary from round to conical; in most lumbrinerids, it lacks appendages (Figure 8A,B), except for *Augeneria*, *Lysarete*, and *Kuwaita*, which have three antennae (Figure 8C), as well as *Cenogenus* and *Sergioneris* Carrera-Parra, 2006, bearing a single antenna. Although *Augeneria* typically has three antennae, at least two species have multiple small antennae (*Augeneria polytentaculata* Imajima and Higuchi, 1975 and *Augeneria riojai* Aguirrezabalaga and Carrera-Parra 2007). Most lumbrinerids lack eyes, except *Lysarete*, which possess two pairs (Figure 8C). A pair of ventral pads of the dorsolateral folds anterior extension (*sensu* [37,38]; buccal lips *sensu* [284,293]), that may be well-developed, is present at the ventral posterior margin of the prostomium. The peristomium is composed of two rings and lacks appendages; dorsally, it is complete (Figure 8A,B) except in *Lysarete*, which have a dorsal incision reaching the first chaetiger (Figure 8C). Ventrally, the first peristomial ring is incomplete, and the second ring is projected forward. The parapodia are subbiramous with notopodium reduced to a small knob with notoaciculae in most lumbrinerids (Figure 8A), but well-developed dorsal cirri in *Kuwaita* and *Lysarete* (Figure 8C). Neuropodia are well developed in all lumbrinerids, constituted by prechaetal, chaetal, and postchaetal lobes, without ventral cirri (Figure 8D–F). Branchiae are absent in most genera; when present, they are associated with parapodial lobes of anterior chaetigers (Figure 8D); *Cenogenus* and *Ninnoe* Kinberg, 1865) or over dorsum in posterior chaetigers (*Kuwaita*). All genera have limbate chaetae. The presence of other chaetae varies among genera: simple and compound multidentate hooded hooks (Figure 8G,H) and compound spinigers (*Lumbricalus*); simple and compound multidentate hooded hooks (*Augeneria*, *Gallardoneris* Carrera-Parra, 2006, *Hilbigneris* Carrera-Parra, 2006, *Loboneris* Carrera-Parra, 2006, *Lumbrineris*, and *Sergioneris* Carrera-Parra, 2006); simple multidentate hooded hooks and limbate simple multidentate hooded hooks (*Abyssoninnoe* Orensanz, 1990); simple multidentate hooded hooks (*Cenogenus*, *Eranno*, *Geseneris* Carrera-Parra, 2006, *Helmutneris* Carrera-Parra, 2006, *Kuwaita*, *Ninnoe*, and *Scoletoma*); and simple bidentate hooded hooks (*Lumbrinerides* Orensanz, 1990 and *Lumbrineriopsis* Orensanz, 1990). *Arabellonereis* Hartmann-Schröder, 1979 and *Lysarete* lack hooks. The pygidium of lumbrinerids has two pairs of pygidial cirri, except in *Gallardoneris*, *Lumbrinerides*, and *Lumbrineriopsis*, which lack pygidial cirri. Until now, the pygidium shape of *Geseneris* is unknown.

The study of lumbrinerids requires careful observation of the maxillary apparatus since the recognition of genera is based mainly on the differences in this complex structure. The maxillary apparatus is symmetrical of labidognath type (*sensu* [286]) or symmetrog-nath type (*sensu* [14]); the later was suggested to distinguish the lumbrinerid symmetrical labidognath maxillae from the asymmetrical labidognath maxillae of Eunicidae and Onuphidae (Figure 3). The number of maxillary plates varies among the genera as follows: six pairs in *Lysarete*; five pairs in *Arabellonereis*, *Eranno*, *Hilbigneris*, *Kuwaita*, *Ninnoe*, *Lumbricalus*, *Lumbrineris*, and *Scoletoma*; and four pairs in *Abyssoninnoe*, *Augeneria* (Figure 3B), *Cenogenus*, *Gallardoneris*, *Geseneris*, *Helmutneris*, *Loboneris*, *Lumbrinerides*, *Lumbrineriopsis*, and *Sergioneris*. All maxillae can have either an accessory lamella, a connecting plate, or, in some cases, both structures. As a consequence, the maxillary apparatus of lumbrinerids has a great variety of shapes specific to each genus [286]. The mandibles are also an important characteristic for helping to recognize some genera such as *Gallardoneris* and *Lumbrinerides*,

which have completely fused mandibles. In contrast, all other genera have mandibles fused up to 3/4 of their length [286].

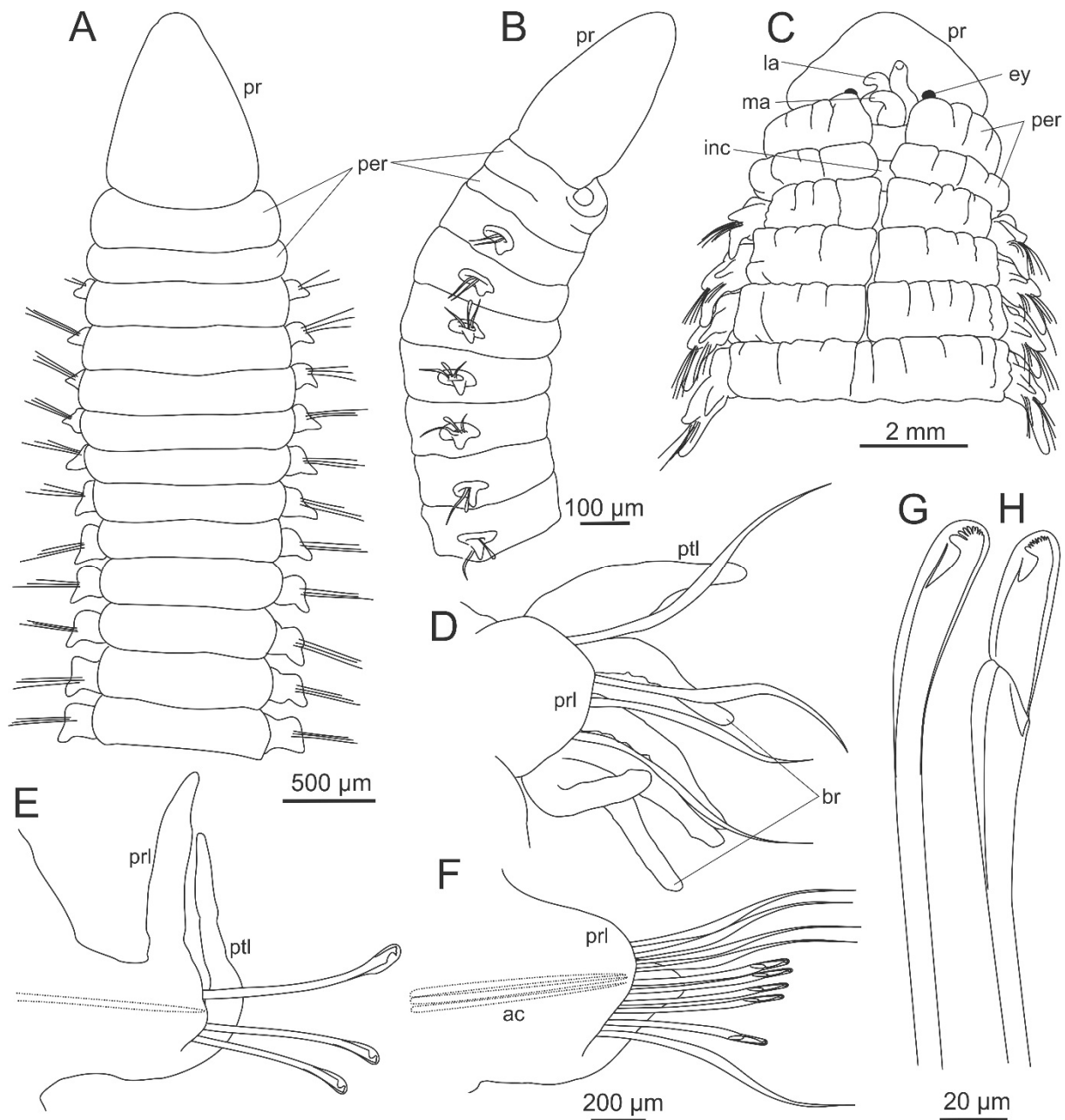


Figure 8. Morphology of Lumbrineridae. (A) *Lumbrineris mixochaeta* Oug, 1998, anterior end, dorsal view; (B) *Lumbrineriopsis* sp., anterior end, lateral view; (C) *Lysarete* sp., anterior end, dorsal view; (D) *Ninoe vargasi* Carrera-Parra, 2001, parapodium; (E) *Eranno lagunae* (Fauchald, 1970), parapodium; (F) *Lumbrineris* sp., parapodium; (G) *Scoletoma* sp., simple hook; (H) *Lumbrineris* sp., compound hook. ac-acicula, br-branchia, ey-eye, ins-dorsal incision, la-lateral antenna, ma-median antenna, per-peristomium, pr-prostomium, prl-prechaetal lobe, ptl-postchaetal lobe.

6.3. Feeding and Life History

In their feeding behavior, lumbrinerids were considered carnivores, feeding on various invertebrates, questionably herbivores [294–296] and deposit-feeders [297]. Based on the analysis of stable isotopes ($\delta^{15}\text{N}$) in species of the genera *Hilbigneris*, *Lumbrineris*, *Lumbrinerides*, and *Scoletoma*, most lumbrinerids are carnivores with a few herbivorous [34].

There is little information on the reproductive aspects of this group. However, all species with known reproduction are gonochoric without sexual dimorphism. Mature specimens of *Lumbrineris latreilli* Audouin and Milne Edwards, 1834 have been reported swimming [298]. In the few existing studies [299–301], the morphology of the sperm is described as of the ect-aquasperm type (*sensu* [302]) suggesting broadcast spawning [84]. Osman et al. [57] described three maturity stages according to yolk deposition during the oogenesis of *Scoletoma funchalensis* (Kinberg, 1865), the first previtellogenic stage and the other two within the vitellogenic phase. Oocyte diameter is known from four species. It varies from around 100 to 300 μm in diameter, *S. funchalensis* (140 μm to 280 μm , [57]), *Gallardoneris iberica* Martins, Carrera-Parra, Quintino and Rodrigues, 2012 (129 μm to 188 μm , [303]), *Lumbrineris lusitanica* Martins, Carrera-Parra, Quintino and Rodrigues, 2012 (181 μm to 191 μm [303]) and *Lumbrineris pinaster* Martins, Carrera-Parra, Quintino and Rodrigues, 2012 (98 μm to 147 μm [303]).

Messina et al. [300] studied the first stages of the development of *Scoletoma impatiens* (Claparède, 1868). They observed the appearance of protochophore larva in the 24 hours after fertilization. Three days later, it transforms into a metatrochophore with a duration of about seven days, in which time the first two segments are formed. By the eighth day, the postlarva benthic phase begins. Some species lack pelagic larvae; their gametes are deposited into the parental burrow or gelatinous masses attached to the substrate where the first development stages occur and benthic larvae emerge at different times, not allowing for a high dispersal capability [284,304–307].

6.4. Habitats and Ecology

Lumbrinerids are motile worms dwelling in soft sediment such as mud and sand; however, some species prefer hard substrates such as coral rocks. They can construct very fragile temporary tubes of sediment and mucus. Some species live in association with other invertebrates such as sponges, bryozoans, sea urchins [176,286,308,309]. The species *Helmutneris flabellicola* (Fage, 1936) and *Helmutneris corallicola* Carrera-Parra, 2006 are only found forming membranous transparent tubes in ahermatypic corals of the genera *Caryophyllia*, *Balanophyllia*, *Dendrophyllia*, and *Flabellum* [286,310]. Fossil corals with tube scars created by lumbrinerids were reported from the Miocene and Pliocene deposits in central Europe and in the Western Basin of the Mediterranean [310].

Very little is known about the ecology and population biology of the Lumbrineridae. It has been shown that some species of *Lumbrineris* and *Gallardoneris* prefer areas enriched with organic matter [303,311,312]. *Kuwaita hanneloreae* Arias and Carrera-Parra, 2014 was reported from a fine to medium sand with a mean organic matter content of 1.68%, reaching densities over 4–5 ind/ m^2 and occurring together with other lumbrinerids, *Scoletoma impatiens* and *Lumbrineris latreilli* [313].

6.5. Distribution Patterns and Diversity

Lumbrinerids have a worldwide distribution, from intertidal to abyssal zones. They are more common in temperate and tropical regions, where all genera have been reported [282,286], while in the Antarctic and Arctic regions only six genera have been found [13,290,308,314,315]. However, the taxonomic studies of lumbrinerids in the Antarctic and Arctic regions and the deep-sea habitats are scarce.

Some contributions to the regional faunas of lumbrinerid species are available for the Antarctic and Subantarctic seas [13], Argentina [284], Australia [316]; Brazil [176, 317,318], the British Isles [181]; the Canary Islands [319]; the Caribbean region [139,220, 308]; China [320–322]; Costa Rica [323]; the Eastern Pacific [28]; East Africa and the Red Sea [324]; El Salvador [325]; Fiji and Samoa [190]; the Gulf of Mexico [308,326–329]; the Iberian Peninsula [303]; India [330]; Japan [290,331–333]; the Mediterranean Sea [4,334–337]; New Zealand [338]; South California [291]; Thailand [286,339]; the USA East coast [285]; northern Europe [313,335,340,341]; western Mexico [94,103,290,342]; the Scandinavian and

North Sea coasts [315,343–346]; South Africa [216]; the southeastern Pacific [290,347–350]; Vietnam [286,351]; and West Africa [289,352–354].

Due to recent changes in the group's taxonomy, it is necessary to re-evaluate the lumbrinerid species worldwide. A number of new genera or species have been described, or other species have been re-established from their supposed synonyms even in well-studied areas [283,286,290,303,336,342]. Several lumbrinerid species have been regarded as having wide distribution (v. gr. *Scoletoma tetraura* (Schmarda, 1861), *Scoletoma impatiens*, *Lumbrineris latreilli*, *Lumbrineris inflata* Moore, 1911), most probably as a result of brief original descriptions and unjustified synonymies [283,290]. The revision of type materials with a detailed examination of the maxillary apparatus, chaetal morphology and shape of parapodia along the body is imperative to clarify these cases. Recently, some species have been re-established, and others were described as new species with restricted distributions [283,290,303,321,336].

The use of combined morphological and molecular data may help to improve the identification. Until now, only an Antarctic species identified as *Lumbrineris kerguelensis-cingulata* has been the focus of a molecular analysis [355]. The examined specimens exhibit a high range of genetic distance among 16S rDNA sequences (0–16%), suggesting the presence of more than one species. However, the poor morphological condition of the specimens and the lack of additional genetic markers in the analyses did not allow further conclusions and formal description of the obtained clades.

6.6. Exploitation

Lumbrinerids are used as bait for recreational or subsistence fishing. In the Suez Canal, *Scoletoma funchalensis* is under intensive harvesting due to its high price and local demand [57]. In the Gulf of Naples, *Scoletoma impatiens* is harvested from shallow sandy areas: this species is locally named “Esca rossa” or “Tremolina” [54]. In southwest Spain (Cádiz), sold specimens of *S. impatiens* are harvested in northwest Spain [356]; in the Canary Islands, *Lumbrineris latreilli* is a highly appreciated bait used by experienced fishers [357]. In northern Spain, *Kuwaita hanneloreae*, *S. impatiens*, and *L. latreilli* are highly appreciated as fishing bait and constitute an important natural resource from this area [313]; however, dermatitis problems have been documented when handling the latter species [358]. In Japan, *Kuwaita heteropoda* (Marenzeller, 1879) is commonly used as bait by Japanese fishers who observed that certain carnivorous insects die when they settle upon the worm. The insect death occurs by having contact with a neurotoxin called nereistoxin that is localized in the integument of the lumbrinerid [359].

7. Oeononidae Kinberg, 1865

7.1. Systematics and Phylogeny

Oeononidae comprises 12 genera and about 109 species. The first species of oeononids was described in 1804 by Montagu as *Nereis iricolor* (now *Arabella iricolor*) [360]. To date since the original family description, Oeononidae has undergone many changes in its composition, giving rise to a series of modifications and synonyms at the family level. Kinberg [361] proposed the family including four genera (*Aglaura* Savigny in Lamarck, 1818, *Andromache* Kinberg, 1865, *Danymene* Kinberg, 1865, and *Oenone* Savigny in Lamarck, 1818). Hartman [28] considered Oeononidae the synonym of Lysaretidae, another family proposed by Kinberg [361], which is currently included into Lumbrineridae. However, Colbath [362], based on the morphology and mineral composition of the maxillary apparatus, recognized Oeononidae as including the genera *Oenone*, *Halla* Costa, 1844, and *Tainoka* Knox and Green, 1972. One of the most notable changes in the delimitation of Oeononidae was the inclusion of the family Arabellidae Hartman, 1944 as its junior synonym, proposed by Orensanz [13]. Therefore, the family was expanded to 11 genera (*Arabella* Grube, 1850, *Biborin* Chamberlin, 1919, *Drilognathus* Day, 1960, *Drilonereis* Claparède, 1870, *Haematocleptes* Wirén, 1886, *Halla*, *Labrostratus* de Saint-Joseph, 1888, *Notocirrus* Schmarda, 1861, *Oenone*, *Oligognathus* Spengel, 1882, and *Tainoka*). Two years later, Dean [363] proposed one more

genus, *Pholadiphila*, bringing the total number of currently accepted genera to 12. A key to valid genera is available in Carrera-Parra [364].

Two genera, *Arabella* and *Drilonereis*, comprise 76% of the oeononid species; three genera are monospecific (*Biborin*, *Drilognathus*, and *Pholadiphila*), all parasites. Five genera have two species (*Haematocleptes*, *Halla*, *Oenone*, *Oligognathus*, and *Tainokia*), but *Oenone* includes another six species regarded as junior synonyms of the supposed cosmopolitan species *Oenone fulgida* Savigny in Lamarck, 1818 (Figure 1C). *Labrorostratus* and *Notocirrus* have six and nine species, respectively.

Phylogenetic studies based on molecular data supported the inclusion of Arabellidae into Oeononidae, finding a monophyletic group containing *Arabella*, *Drilonereis*, and *Oenone* [8]. No phylogenetic analyses focusing on the family have been carried yet.

7.2. Morphology

Oeononids are worms of variable length ranging from few centimeters to almost a meter—all of them are usually very thin. The prostomium usually lacks appendages (Figure 9A,B), except in *Tainokia*, which has one antenna, and *Halla* and *Oenone* with three antennae (Figure 9G). The peristomium is entire (Figure 9A,B,G) but can be dorsally incomplete with a median anterior incision poorly developed as in *Tainokia* or well-developed as in *Halla*. Usually, the parapodia have very small globular dorsal cirri (Figure 9C,D), but foliaceous in *Oenone* and *Halla* (Figure 9H). All oeononids lack ventral cirri. *Drilognathus* is the only genus lacking chaetae; in the other genera, all chaetae are simple, including smooth or denticulated limbate chaetae (Figure 9E,F). In some genera, there are acicular spines with or without hoods. Only *Oenone* species and one species of *Tainokia* (*Tainokia logachevae* Ravara and Cunha, 2018) have bidentate hooded hooks [364].

In addition to these important external characteristics, the study of this group of worms requires careful observation of the maxillary apparatus since its taxonomy is based mainly on the differences in this structure. The maxillary apparatus is of prionognath type, characterized by the presence of paired slender dorsal and unpaired ventral maxillary carriers, which are much longer than the maxillae themselves (Figure 3F). Due to the existence of free-living and parasitic species, the architecture of the maxillary apparatus in oeononids is highly variable. It is well developed in free-living species where several pairs of maxillae can be present, such as in *Oenone* or *Arabella*, or can be extremely reduced to only maxillary carriers and, sometimes, a pair of maxillae, as in parasitic *Drilognathus* and *Labrorostratus*.

The maxillary apparatus of oeononids is symmetrical, with the same number of maxillae on both left and right sides. In some taxa, there is a condition called asymmetric, which refers to the difference in the shape and size of maxillary elements, but not to the number of plates as in Eunicidae and Onuphidae. This type of asymmetry in the shape of the maxillary plates is usually observed in the first two maxillae. In some species, both maxillae I have similar size and falcate shape with a denticulated base, and they are similar in size to maxillae II (Figure 3F). In contrast, other species have the left maxilla I falcate with a denticulated base and the right maxilla I as a denticulated rectangular plate much shorter than maxillae II [14,364]. The mandibles of oeononids are not fused, and without calcified distal plates, lacking growth lines [13], except for *Oligognathus* (whose mandibles are fused in a single horseshoe-shaped piece), *Drilonereis* (where the mandibles may be absent in some species), or *Arabella aracaensis* Steiner and Amaral, 2009 (with growth lines on its mandibles).

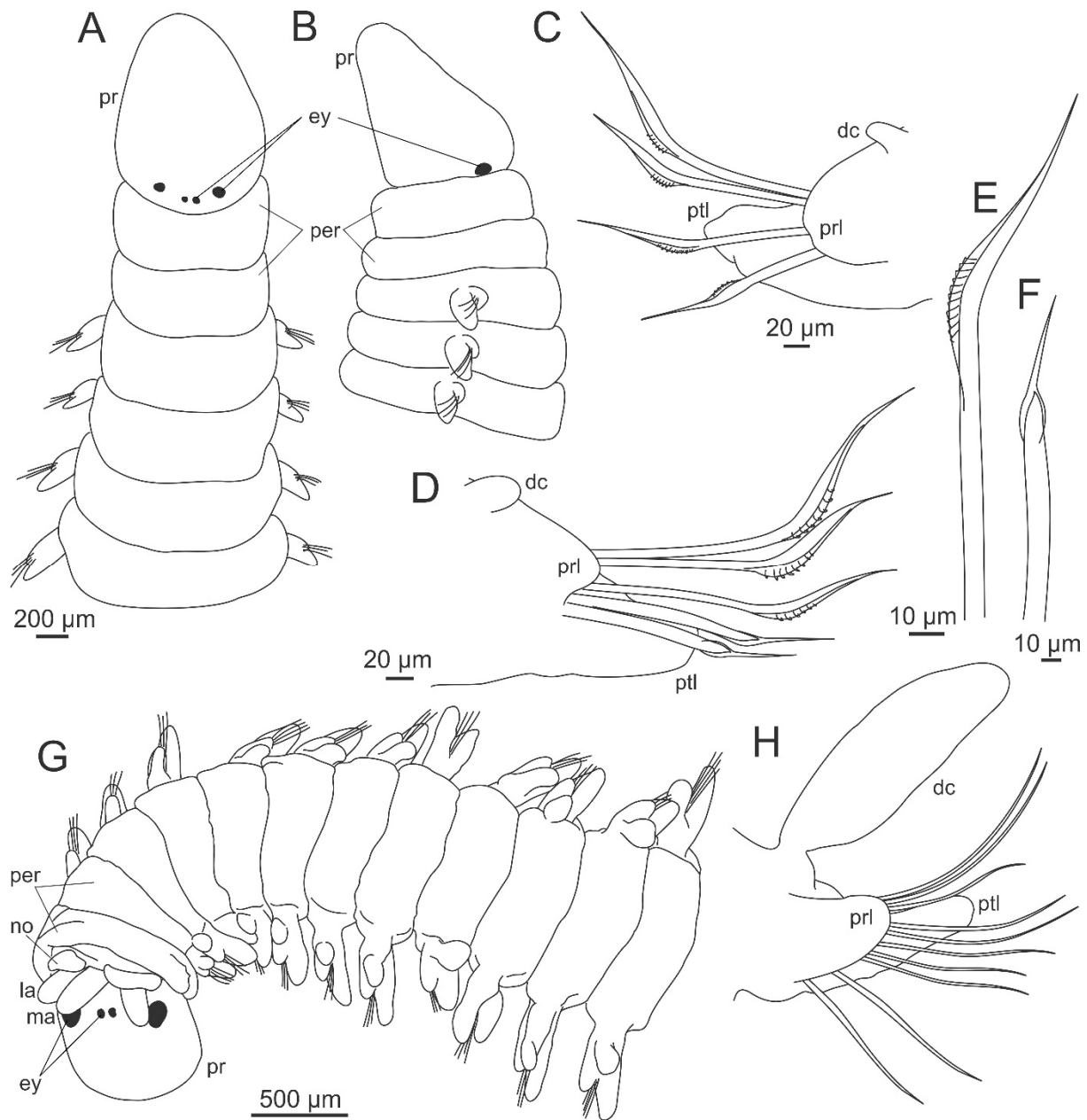


Figure 9. Morphology of Oeonidae. (A) *Arabella mutans* (Chamberlin, 1919), anterior end, dorsal view; (B) the same, lateral view; (C) the same, parapodium 5; (D) the same, parapodium 26; (E) the same, limbate chaeta; (F) the same, chaetae tapering abruptly to guards (G) *Oenone fulgida*, anterior end, dorsal view; (H) the same, parapodium from midbody region. dc—dorsal cirrus, ey—eye, la—lateral antenna, ma—median antenna, no—nuchal organ, per—peristomium, pr—prostomium, prl—prechaetal lobe, pti—postchaetal lobe. (B–F) modified from Zanol and Ruta [365].

7.3. Feeding and Life History

Oeonids were regarded as selective carnivores or surface deposit-feeders [294]. Carnivorous activity in addition to the ability to feed on their hosts has been recently corroborated based on the results obtained with stable isotopes ($\delta^{15}\text{N}$) [34]. Studies in species of the genus *Halla*, which have a marked preference for their prey, bivalves [58,366], indicate that these worms produce mucus that contains paralyzing and digestive substances that force the bivalve to open its valves, to later ingest the soft tissue [367]. Under stress conditions, *Halla* species secrete another type of purple mucus, which, when in contact with human skin, is difficult to eliminate [368]. This mucus is produced by glandular structures of the

epidermis [369], and it is considered a chemical defense mechanism [368]. Purple mucus secretion also occurs in species of *Oenone*, when they are under handling stress [370].

Very little is known about reproductive biology in oenonids. Most of the studied species are gonochoric without sexual dimorphism. Amaral [371] and Steiner and Amaral [51] reported adult individuals of the parasitic species *Labrorotratulus prolificus* Amaral, 1977 reproducing asexually by stolons. The study of the reproductive biology of *Halla parthenopeia* (delle Chiaje, 1828) showed that the appearance of mature sperm occurs in two periods, during late April and in late December; while spawning occurs in May and January [372]. The sperm of this species was described as of the ect-aquasperm type (*sensu* [302,372]). Osman et al. [58] described the oogenesis in this species with three maturity stages; the first one is a previtellogenic phase, with small racemelike oocytes, while the other two stages are vitellogenic phases, with oocytes free in the coelomic cavity.

7.4. Habitats and Ecology

Oenonidae includes free-living species, endoparasitic species, and species that, during their ontogenetic development, have an endoparasitic phase but are free-living as adults [51, 371,373,374].

Free-living species are typically soft-sediment dwellers, and although they do not construct a tube, they secrete mucus to prevent their burrow from collapsing [375]. The parasitic forms mainly infest the polychaetes of different families, for example, Terebellidae, Nereididae, Onuphidae, Eunicidae, Arenicolidae, but they have also been found in spoon worms and bivalves [51,269,363–365,376,377]. Most of the parasitic species apparently have a high degree of specificity infecting a single host [269]. They can be found from one specimen to more than 50 infecting a single host, sometimes reaching larger sizes than their host [371,373,374,376]. Pettibone [373] suggested that infections occur during the early developmental stages of the parasite, but the mechanisms of infection and the stage at which it occurs are unknown.

Information about oenonid ecology is scarce. They are not frequently recorded, and usually occur in low abundance in mud, sand, coralline rock, among algae, or as parasites.

7.5. Distribution Patterns and Diversity

Oenonids have a worldwide distribution from the intertidal zone to the abyssal depths. They are more common in tropical and temperate regions. In the Arctic and Antarctic regions, no more than eight species of *Arabella*, *Driloneries*, and *Notocirrus* have been recorded [13,378]. Some contributions to regional faunas of oenonid species are available for the Antarctic and Subantarctic seas [13], Argentina [379], Australia [365, 380]; Brazil [51,371,381], the British Isles [181]; the Caribbean region [139,220,377,382,383]; Chile [349,350]; Costa Rica, Pacific side [323,384]; the Eastern Pacific [28]; East Africa and the Red Sea [324]; Fiji and Samoa [190]; the Gulf of Cádiz [385]; the Gulf of Mexico [326,386–388]; India [330]; Japan [389–393]; the Mediterranean Sea [4,394–397]; New Zealand [398]; Norway [399]; South California [375]; Thailand [339]; western Mexico [103,376]; South Africa [216]; Vietnam [351]; and West Africa [353,354]. Some records of deep-sea oenonids in various areas of the world were reported by Chamberlin [61], Hartman [400], Hartman and Fauchald [401], and Kirkegaard [402].

Many regions of the world lack studies on oenonids, suggesting that oenonid diversity is still underestimated. Despite the low abundance of oenonids, new species have recently been found both in shallow-water and deep-sea habitats (*v gr.* [365,385]).

Some oenonid species have been regarded as widely distributed, but this distribution is usually the result of poor original description and unjustified synonymies. *Oenone fulgida*, originally described from the Red Sea, currently includes six species as junior synonyms: *Oenone diphyllidia* Schmarda, 1861 from Jamaica, *Oenone haswelli* Benham, 1915 from Australia, *Oenone pacifica* Fischli, 1900 from Ternate, *Oenone symmetrica* Fauvel, 1914 from the Gulf of Guinea, *Oenone telura* Chamberlin, 1919 from Marshall islands, and *Oenone vitiensis* Grube, 1871 from Fiji. *Arabella iricolor* (Montagu, 1804) originally described from

England has four junior synonyms: *Arabella lagunae* Chamberlin, 1919 from California, *Arabella maculosa* Verrill 1900 from the Bermudas, *Arabella multidentata* (Ehlers, 1887) from the Gulf of Mexico, and *Arabella setosa* Treadwell, 1921 from Tobago. Based on the revision of the type material, Perkins [326] found morphological differences to consider *A. multidentata* and *A. maculosa* as valid species, rejecting the synonymy with *A. iricolor*. The revision of type materials, including a detailed examination of maxillary apparatuses and chaetae, is critical to clarify the taxonomic status and distribution of oeonid species.

The use of molecular data may help to improve identification. However, until now, only seven species (*A. iricolor*, *Arabella semimaculata* (Moore, 1911), *Drilonereis longa* Webster, 1879, *Drilonereis filum* (Claparède, 1868), *Halla okudai* Imajima, 1967, *O. fulgida*, and *Tainokia logachevae*) have available molecular information in public databases. Other molecular information is available, but the specimens were identified just at family or genus level.

7.6. Exploitation

At least two species of the family are used as bait. *Halla parthenopeia* is commonly utilized for sport fishing in the Mediterranean Sea [58,372,403]. This species is locally named “cuc llobarrer” on the Catalan Maresme coast; fishers capture an average of 2.17 individuals per boat per day [403]. The second species is *Halla okudai*. It is locally named Tai-mushi in Japan, where considered an effective bait worm, reaching the highest prices among bait worms [404]. This species is also appreciated as bait in Malaysia; the specimens are harvested during low tide [405].

8. Onuphidae Kinberg, 1865

8.1. Systematics and Phylogeny

Onuphidae comprises 22 genera and approximately 340 species. Over their history, onuphids were recognized as a subfamily [4,216] or as a family [28,61] constituting 8–10 genera, with most of species belonging to *Onuphis* Audouin and Milne Edwards, 1833 and *Nothria* Malmgren, 1867. The revision of the family started from the work of Pettibone [406] who redefined *Nothria* and *Paradiopatra* Ehlers, 1887. Kucheruk [407] revised the generic diagnoses of 11 genera and described three new genera, one of which, *Aponuphis* Kucheruk, 1978, remains valid in the current system of the family. Fauchald [408] re-examined the type materials for all species of former *Onuphis*, *Nothria*, and *Paradiopatra* and described three new genera, of which *Mooreonuphis* Fauchald, 1982 and *Kinbergonuphis* Fauchald, 1982 are currently accepted. Paxton [409] provided the comprehensive revision of the whole family, redefining all accepted genera and describing five new genera. She subdivided onuphids into two monophyletic subfamilies: Onuphinae Kinberg, 1865 and Hyalinoeciinae Paxton, 1986 possessing morphological synapomorphies such as the position of subacicular hooks in the posterior parapodia and arrangement of the nurse cells in the oocytes (Figure 10D,H). Paxton’s [409] system remained largely valid to date with few minor changes: *Neonuphis* Kucheruk, 1978 was synonymized with *Leptoecia* Chamberlin, 1919 [13,17]; monotypic *Fauchaldonuphis* Paxton, 2005 was described [410]; *Epidiopatra* Augener, 1918 and *Notonuphis* Kucheruk, 1978 were synonymized with *Diopatra* Audouin and Milne Edwards, 1833 and *Paradiopatra*, respectively, and two more monotypic genera, *Paxtonia* Budaeva and Fauchald 2011 and *Protodiopatra* Budaeva and Fauchald 2011, were described [32]. A key to genera valid at the time is available in Paxton [409] and Carrera-Parra [411].

A number of onuphid genera have been revised and their taxonomy and identification are rather well resolved: *Australonuphis* Paxton, 1979 [412]; *Hirsutonuphis* Paxton, 1979 [413, 414]; *Brevibrachium* Paxton, 1986, *Longibrachium* Paxton, 1986, and *Rhamphobrachium* Ehlers, 1887 [415,416]; and *Paradiopatra* [32,417]. However, several species-rich genera, such as *Anchinotheria* Paxton, 1986, *Diopatra*, *Hyalinoecia* Malmgren, 1867, *Kinbergonuphis*, *Nothria*, and *Onuphis* await detailed revision.

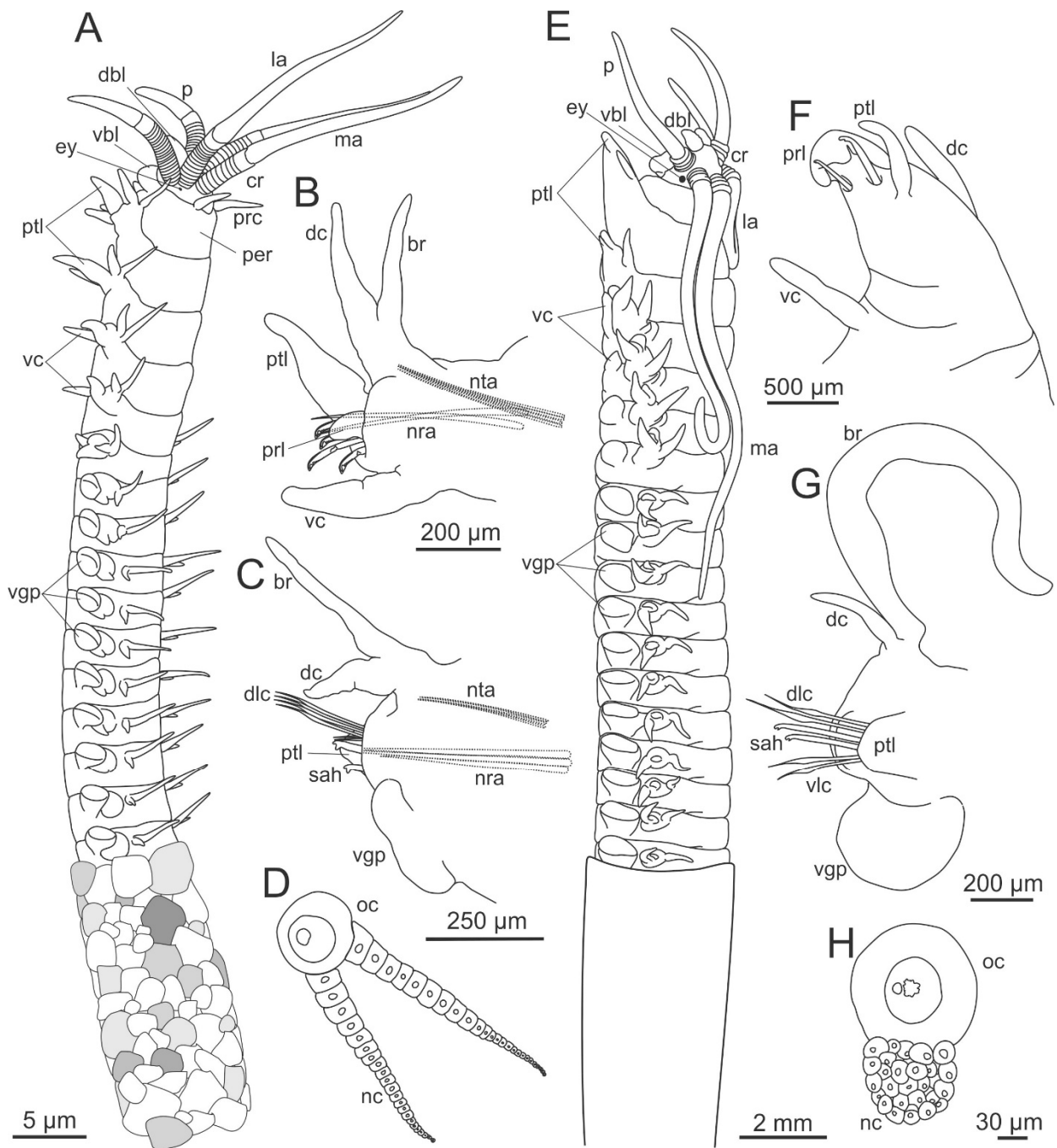


Figure 10. Morphology of Onuphidae. (A) *Onuphis* sp. (Onuphinae), anterior end, lateral view; (B) the same, anterior modified parapodium; (C) the same, posterior parapodium; (D) Onuphinae, oocyte; (E) *Hyalinoecia* sp. (Hyalinoeciinae), anterior end, lateral view; (F) the same, anterior modified parapodium, aciculae not shown; (G) the same, posterior parapodium, aciculae not shown; (H) *Leptoecia vivipara* Orensanz, 1990, oocyte. br—branchia, cr—ceratophore, dbi—dorsal buccal lip, dc—dorsal cirrus, dlc—dorsal limbate chaetae, ey—eye, la—lateral antenna, ma—median antenna, nc—nurse cells, nra—neuroaciculae, nta—notoaciculae, oc—oocyte, p, palp, per—peristomium, prc—peristomial cirrus, prl—prechaetal lobe, pti—postchaetal lobe, sah—subacicular hook, vbl—ventral buccal lip, vc—ventral cirrus, vgp—ventral glandular pad, vlc—ventral limbate chaetae.

Phylogenetic hypotheses of Onuphidae were proposed based on morphological [409] and molecular [12] data. Both studies agreed in recognizing the two subfamilies; 10 of 22 genera described based on morphology were tested with molecular tools and were recovered as monophyletic, largely supporting the accepted system of the family provided

by Paxton [409]. The hypotheses on the relationships between the genera and recognition of generic groups and complexes *sensu* Paxton [409] were not corroborated by the molecular data: nevertheless, taxon sampling was incomplete and only one nuclear (18S rDNA) and a fragment of a mitochondrial marker (16S rDNA) were used in the reconstruction [12]. Further detailed studies are required to reveal better resolution at the basal part of the onuphid tree and to assess interrelationships between the genera.

8.2. Morphology

Onuphids vary in size and number of chaetigers from 2 cm and about 100 chaetigers (e.g., *Leptoecia*, *Nothria*, and *Anchinothria*) to 70–300 cm and over 1000 chaetigers in beach worms *Australonuphis* and *Americanuphis*. The majority of species have about 200 chaetigers and are 10 cm in length [409].

Onuphids are defined by two main synapomorphies: the presence of well-delimited dorsal buccal lips (frontal lips) attached to the anterior margin of the prostomium and several pairs of modified anterior parapodia (Figure 10A,B,E,F). They have a rounded prostomium with dorsal and ventral buccal lips (frontal and upper lips), a pair of palps, a pair of lateral antennae and a single median antenna (Figure 10A,E). Both antennae and palps are placed on multiringed ceratophores consisting of 2–70 rings (Figure 10A,E). Many species possess eyes and dorsal nuchal organs in the shape of straight to semicircular ciliated grooves. The peristomium is a single ring, with (Figure 10A) or without (Figure 10E) peristomial cirri, ventrally forming a wide lower lip. The anterior 2–8 pairs of parapodia are modified, usually directed slightly anteriorly bearing special kind of chaetae: simple or pseudocompound falcigers (Figure 10B,F). Modified parapodia are used in locomotion and feeding and are highly adaptive to different lifestyles. In Hyalinoeciinae, the modified parapodia are enhanced and enlarged with auricular prechaetal lobes and short and stout falcigers (Figure 10E,F); they are used for crawling on the surface of the sea floor [418]. Species of *Rhamphobrachium*, *Longibrachium* and *Brevibrachium* have elongated modified parapodia with extremely long spiked and distally curved falcigers that can protrude anteriorly and are used in catching prey in an ambush-predator feeding strategy [419]. Australian beach worms (*Australonuphis*, *Hartmanonuphis* Paxton, 1986 and *Hirsutonuphis*) have massive anterior parapodia used for actively moving inside sandy sediments and making temporary borrows [53]. The modified parapodia may not be enlarged but always possess elongated ventral cirri (Figure 10B,F), while in following parapodia the ventral cirri are modified into glandular pads producing the organic secretion used in tube building (Figure 10C,G).

The majority of onuphid worms (except beach worms) are tubicolous dwellers and the shape and the composition of their tubes is quite diverse. Quill worms (*Hyalonoecia* and *Leptoecia*) build completely organic transparent light and firm tubes that they are able to carry along as epibenthic crawlers (Figures 1E and 10E; [418]). *Anchinothria* and *Nothria* have tubes made of a parchment-like inner layer covered by mud, sand or shell fragments; these tubes are dorsoventrally flattened, suggesting an epibenthic lifestyle for these two genera. Species of *Diopatra* construct vertical tubes with so-called “tube caps” protruding above the sediment surface and incrustated by fragments of shells, plant debris and other foreign objects. Many other species build cylindrical tubes covered by sand or mud particles, which usually are permanent and significantly exceed their inhabitants in length (Figure 10A).

The number and morphology (i.e., size and shape of various parapodia lobes) of the anterior modified parapodia, the arrangement of branchial filaments, number of rings on the ceratophores, and the presence or absence of specific chaetae are the main characteristics used in the identification of onuphid genera. The species level diagnostic characteristics are mainly the distribution of different types of chaetae and branchiae along the body, the number of denticles in the anterior falcigers, and the number of branchial filaments. Intraspecific variation in morphological characteristics is very common in onuphids, leading to difficulties in species identification and delimitation based on morphology. This is

especially prominent in species-rich genera such as *Diopatra*, *Onuphis*, *Kinbergonuphis* and *Hyalinoecia* lacking complete revisions to date. It is probably impossible to revise these genera utilizing morphology only; a complete revision would require the inclusion of molecular data.

8.3. Feeding and Life History

Omnivorous or scavenging feeding modes have been documented in onuphids with some species feeding primarily on kelp [294]. Stable isotope analysis [418] and analysis of gut content [420] suggest that quill worms are secondary consumers. Being motile predators and/or scavengers, large-bodied quill worms are able to move around in search of sources of food on the sea floor and were many times recorded on underwater photographs and video attracted by fish bait or whale falls [421]. Large-bodied beach worms (*Australonuphis* spp.) were reported to aggregate in high numbers and feed on large carrion such as washed up whale or sheep's head [53]. Ambush predator behavior was described in detail for *Longibrachium arariensis* Nishi and Kato, 2009 utilizing its extremely modified, prolonged and retractable anterior parapodia and falcigers in catching small prey [419]. *Diopatra* species were shown to feed on foraminiferans [422] or minute invertebrates inhabiting their complex tubes protruding vertically from the sediment [423,424]. Little is known about the feeding habits of the small-bodied and largely sessile onuphids dwelling in permanent tubes inside the sediment.

Onuphids display a great variety of reproductive strategies. Several cases of protandric simultaneous [425,426] or sequential [427] hermaphroditism have been observed in onuphids as well as cases of sperm transfer via spermatophores [428] and sperm storage by females [428] or hermaphrodites [427]. All species investigated so far have lecithotrophic development but many provide parental care for their young by laying eggs inside their tubes or cocoons or egg masses attached to the tubes. The broadcast spawners are also known in the family; however, they are less common, possibly due to sampling bias. Few species were shown to have short-living pelagic stages [429,430] while the majority have direct development inside parental tubes or cocoons [430–435]. At least two cases of viviparity were observed in miniature deep-sea *Leptoecia* species, with juveniles developing inside the parental body cavity up to an advanced stage [13,436].

Large-bodied species (i.e., *Diopatra ornata* Moore, 1911) were shown to serve as hosts for oeonids, another eunicidan family of bristle worms [376]. Portuguese populations of *Diopatra neapolitana* Delle Chiaje, 1841 were reported to be infected by digeneid worms [437] and myxozoans [438]. Symbiosis between onuphids and ciliates attached to their parapodia was described by Arias et al. [439] and Arias and Paxton [440].

8.4. Habitats and Ecology

All known onuphid species are free-living. They are predominantly soft-bottom dwellers, either epibenthic or infaunal, commonly found in muddy or sandy sediments. Several species of *Diopatra* can form large aggregations and were described as ecosystem engineers—species physically creating or modifying the habitat [441]. Having vertical robust and complex tubes sticking above the sediment surface, the species act as sediment stabilizers and increase the abundance and richness of the local benthic fauna [442,443]. While *Diopatra cuprea* (Bosc, 1802) was shown to reach up to 250 ind/m² at the Atlantic coast of the US [443], the Hawaiian species, *Diopatra dexiognatha* Paxton and Bailey-Brock, 1986, is able to form intertidal mounds with extreme densities of up to 21800 ind/m². These mounds enhance organic matter accumulation and provide a complex tridimensional habitat for small invertebrate species [444]. No onuphids have been reported from hydrothermal vent fields; however, in cold seeps of the US Atlantic continental margin, *Hyalinoecia artifex* Verrill, 1880 occurs in high abundancies (up to 70 ind/m²) [418].

8.5. Distribution Patterns and Diversity

Onuphids are widely distributed around the world, found in all oceans from the intertidal zone down to over 6000 m deep [445,446]. The diversity of Onuphidae in the Arctic is rather poor with only two species, *Nothria conchylega* (Sars, 1835) and *Paradiopatra pauli* (Annenkova, 1952), reported from the shelf areas [447], while the Antarctic onuphid fauna is diverse with many species found both in deep and shallow waters [13,166,448].

Regional onuphid faunas were described from Central America and adjacent waters of the East Pacific and West Atlantic [94,189,449–452], Antarctic and Subantarctic Seas [13,448]; Japan [453–456], Australia [53,413,416,417,430,457–459], South and West Africa [46,216,460–462]; South America [43,463,464] and the eastern Atlantic including Norway [343], southern Europe, the Mediterranean [440,465–468] and the Macaronesian region [469]. Large parts of the world's onuphid fauna remain poorly studied; for example, from the Indian Ocean and southeastern Asia as well as from most of the deep-sea habitats. Nonetheless, even relatively well-studied regions hold many undescribed species, which is demonstrated by the recent increase in the description of new species from Australia and the East Atlantic (Figure 2).

Deep-water onuphids were mostly described by McIntosh [445] after the HMS *Challenger* expedition, followed by the report from the USS *Albatross* Pacific expeditions by Chamberlin [61] and the USNS *Eltanin* Antarctic deep-sea expeditions by Hartman [448]. A series of works was published by Kucheruk [407,446,470,471] based on the material from the deep-sea Soviet expeditions. Deep-sea onuphids mostly belong to the genera *Anchinothria*, *Hyalinoecia*, *Leptoecia*, and *Paradiopatra*, and represent the fourth most diverse annelid family below 2000 m depth [472].

The most species-rich genera, *Onuphis*, *Nothria*, *Hyalinoecia*, and *Paradiopatra* display cosmopolitan distribution, while some others are restricted to more specific regions. Species of *Diopatra* are mostly found in intertidal and shelf tropical and subtropical areas with very few deep and temperate records. *Leptoecia* is almost exclusively a bathyal and abyssal genus distributed mainly in the Southern Hemisphere with few records in the North Atlantic and northeastern Pacific [13,17,446]. *Australonuphis*, a genus comprising seven species, is also known mostly from the Southern Hemisphere, being reported from Australia and South America and with one species known from western Mexico [412]. Until very recently, *Mooreonuphis* was restricted to the American waters; nonetheless, the detailed investigation of small-bodied onuphids from relatively well-known areas led to the description of two new species from the eastern Atlantic [461,465] and two new species from Australia [458]. Similarly, three new species of *Aponuphis*, the genus for long time known only from the North and East Atlantic, have been recently described from Australia [457].

Most onuphid species are known to have rather restricted geographical ranges; however, several examples of widely distributed species confirmed with genetic data were reported recently. *Diopatra neapolitana* originally described from the Mediterranean and widespread in Iberian Atlantic was subsequently reported from the Suez Canal, Egypt, the Brazilian Atlantic, and India [473,474]. Its sister species, *Diopatra aciculata* Knox and Cameron, 1971, common in Australian east coastal waters, has been recently reported from the South Africa estuaries and also from Egypt. Both species are broadcast spawners with larvae capable of spending some time in the water column. Thus, potential transport with ballast waters of via aquaculture could result in their recent spread due to human activities [46]. Another example of a species with a wide geographical range, but possibly not due to human mediation, is *Nothria conchylega*, a species commonly found in shelf and upper slope areas in the Arctic Ocean, the North Atlantic and the North Pacific [447]. Recent molecular investigations revealed very little genetic variation in mitochondrial markers in specimens collected across the whole range, indicating the presence of a large panmictic population in the Northern Hemisphere [475].

The vast majority of onuphid species are described based on morphological data and only a few recent studies have provided molecular support for species identification and description. This was almost exclusively done in *Diopatra* [43,476,477], the most

specious genus of onuphids with high morphological variability in diagnostic characteristics. *Diopatra neapolitana* and *D. aciculata* are two very similar species, both genetically and morphologically, which display wide but also partly sympatric distribution. Analysis of 22 morphological characteristics and five genetic markers resulted in conclusion that these two species were in the grey speciation zone. Their validity was retained for the stability of the taxonomical system [474]. A similar case has been reported in newly described *Diopatra marinae* Steiner and Amaral, in Seixas et al., 2020 and *Diopatra victoriae* Steiner and Amaral, in Seixas et al., 2020 from Brazil [43] confirming previous observations in very rapid and recent speciation within *Diopatra* (Hektoen 2020 pers. comm.). *Diopatra cryptornata* Fauchald, Berke and Woodin, 2012 was synonymized with *D. neapolitana* based on molecular data. The species was originally described due to the presence of dorsal papillae, which were later shown to be sperm storage organs in simultaneous hermaphrodite individuals of *D. neapolitana* from the northern Spanish coast [427]. Similar papillae were later described in the Brazilian population of *D. neapolitana* [473].

Cryptic species diversity, although very common in some annelids [478], has not been described as a widespread phenomenon in Onuphidae, possibly due to their complex external morphology allowing distinguishing between closely related species. None of the studies provided clear evidence of cryptic species in onuphids with detailed morphological and genetic assessment of diversity; however, few cases of species complexes are known in *Aponuphis* [26], *Diopatra* [479], *Hyalinoecia* [480] and *Nothria* [481].

Population level studies are very scarce in onuphids. A study on the deep-sea *Hyalinoecia longibranchiata* McIntosh, 1885 based on two mitochondrial markers revealed significant population structure between the worms inhabiting several deep-sea sites west of New Zealand, which was hypothesized to be a result of complex current regimes that operate in the area as well as the potential limited ability for larval dispersal [482]. In contrast, the study of Single Nucleotide Polymorphism (SNP) in Australian beach worms, *Australonuphis teres*, showed no population structure along the eastern coast of Australia, possibly due natural disturbance events, changes in currents and temperature regimes, and/or anthropogenic disturbance [483].

8.6. Exploitation

Large-bodied onuphids are widely used as bait and thus harvested by professional and recreational fishermen from the intertidal zone habitats in Australia (*Australonuphis* spp. and *Hirsutonuphis* spp., [53]), South Africa (*D. aciculata*, [46]), the Mediterranean and Portuguese coasts (*D. neapolitana*, [54,56,484]). One species, *D. aciculata*, is commercially produced in aquaculture in New South Wales, Australia and sold as food in the conditioning of prawn broodstock and as dry bait for recreational fishing [59].

9. Future Perspectives

The phylogenetic relationships between eunicidan taxa and the evolution of jaw morphology are still open questions due to the varying placement of most families in different phylogenetic hypotheses, the absence of phylogenetic analyses including both extinct and extant taxa and the highly modified families Histriobdellidae and Hartmaniellidae, as well as lack of phylogenetic hypotheses for most families. More robust phylogenetic hypotheses for Eunicida could allow estimates of time of divergence, providing better understanding of eunicidan evolution as well as calibration points to time estimates within Annelida.

Homology between the different parts of the maxillae is one of the challenges to overcome in order to understand the evolution of jaw morphology and to allow the inclusion of the extinct taxa in the analyses. Paxton [14] undertook a very thorough analysis of morphology and proposed hypotheses of homology for carriers, maxillae I and basal plate, but homologies for other parts are still unclear and in some cases controversial (e.g., Hartmaniellidae). Information on the biomechanics of extant jaw types may also provide another source of information to understand homology among plates and the feeding biology of different species.

The reproductive biology, development and ecology of most families are poorly known despite being key information for understanding the dispersal and distribution of species. Generalizations are made based on knowledge built on few species, which sometimes makes explaining observed distribution patterns a challenge (e.g., [49]). Other factors that hinder the understanding of distribution patterns are the poor information available about the diversity of some regions, such as the South Atlantic, South Pacific and Indian Ocean, and the difficulty in species identification, which may hide continuous distributions or lead to flawed wide distributions. No information is available on the initial infection of the host by eunicidan parasitic and commensal species. Such information would also be of great importance in understanding the evolution of such life modes.

Despite the existence of poorly studied areas, well-studied regions also need to be better explored regarding synonymizations and widely distributed species. Reviews of type material have uncovered diversity hidden under unjustified synonymizations (e.g., [36,122]). Moreover, detailed analyses of morphology and molecular data, especially from type specimens or specimens collected from type localities, improve the understanding of species delimitation, correct use of names and thus of diversity. However, the most important factor of all in order to understand and to reveal the diversity and distribution patterns of taxa is the presence of specialists working on the groups, which generate large leaps in the number of known species (Figure 2). Therefore, the continuous formation of specialists coupled with new views of the morphology, knowledge on the biology and ecology and the use of molecular data appears to be the path to improve the knowledge on the diversity of Eunicida.

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