Family Polynoidae

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Introduction

The Polynoidae Kinberg, 1856 is, by far, the largest family of Aphroditiformia, with 188 genera and over 900 species. This family is very genus-rich, with 174 currently valid genera, 47 % of which are monospecific (Figure 1). Another 32% of genera have between 2 and 4 species only. The most species-rich genus is *Harmothoe* Kinberg, 1856 with 156 species (16.6% of all species), followed by *Lepidonotus* Leach, 1816 (80 species), *Eunoe* Malmgren, 1865 (49 species), *Polynoe* Lamarck, 1818 (48 species), and *Lepidasthenia* Malmgren, 1867 (42 species). They inhabit a very wide range of habitats, from the intertidal to abyssal depths, from tropical waters to polar areas (Figure 2). This family has also been very successful in deep-sea hydrothermal vent ecosystems where it is the most species-rich annelid family (over 50 species), and occupies all microhabitats where metazoans are found in this very unusual habitat.
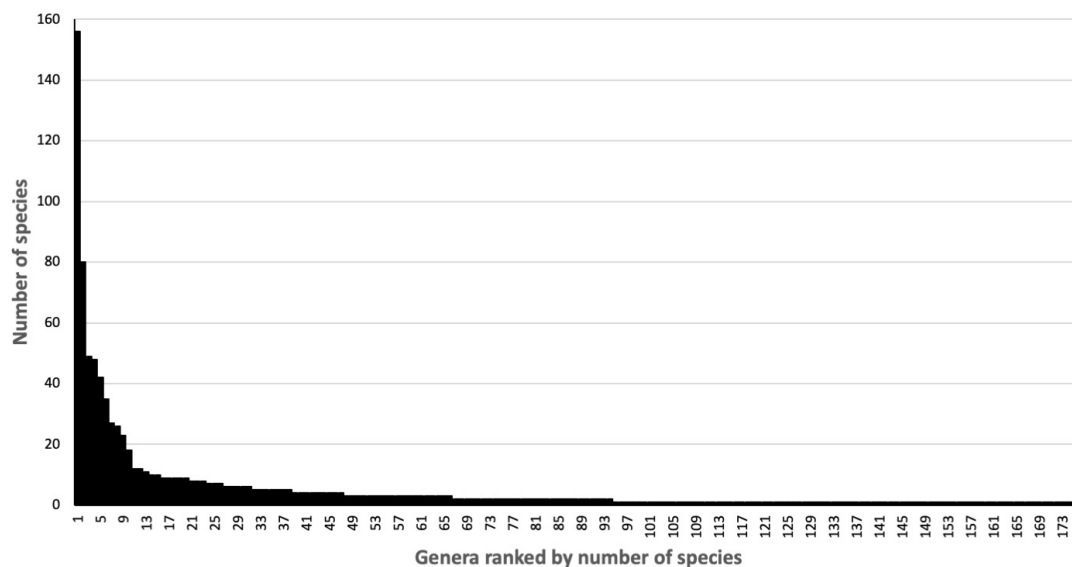
Figure 1: Distribution of the number of species per genus

Although they are good swimmers (Figure 2D), only the genera *Drieschia* Michaelsen, 1892 and *Podarmus* Chamberlin, 1919 are holopelagic, the other species only occasionally foray into the water column. *Drieschia* however is based on a larval form. Similarly, based on a barcode approach, Neal et al. (2014) have shown that *Herdmanella gracilis* Ehlers, 1908 specimens captured in the plankton actually correspond to larval forms of *Austrolaenilla*

antarctica Bergström, 1916 . They usually hide in small cavities or beneath rocks but can be found inside the tubes of other animals (see section on symbiotic relationships below). Sizes usually range between 1 and 5 cm long but the Antarctic species *Eulagisca gigantea* Monro, 1939 can reach about 30-centimeter long and 12-centimeter wide.
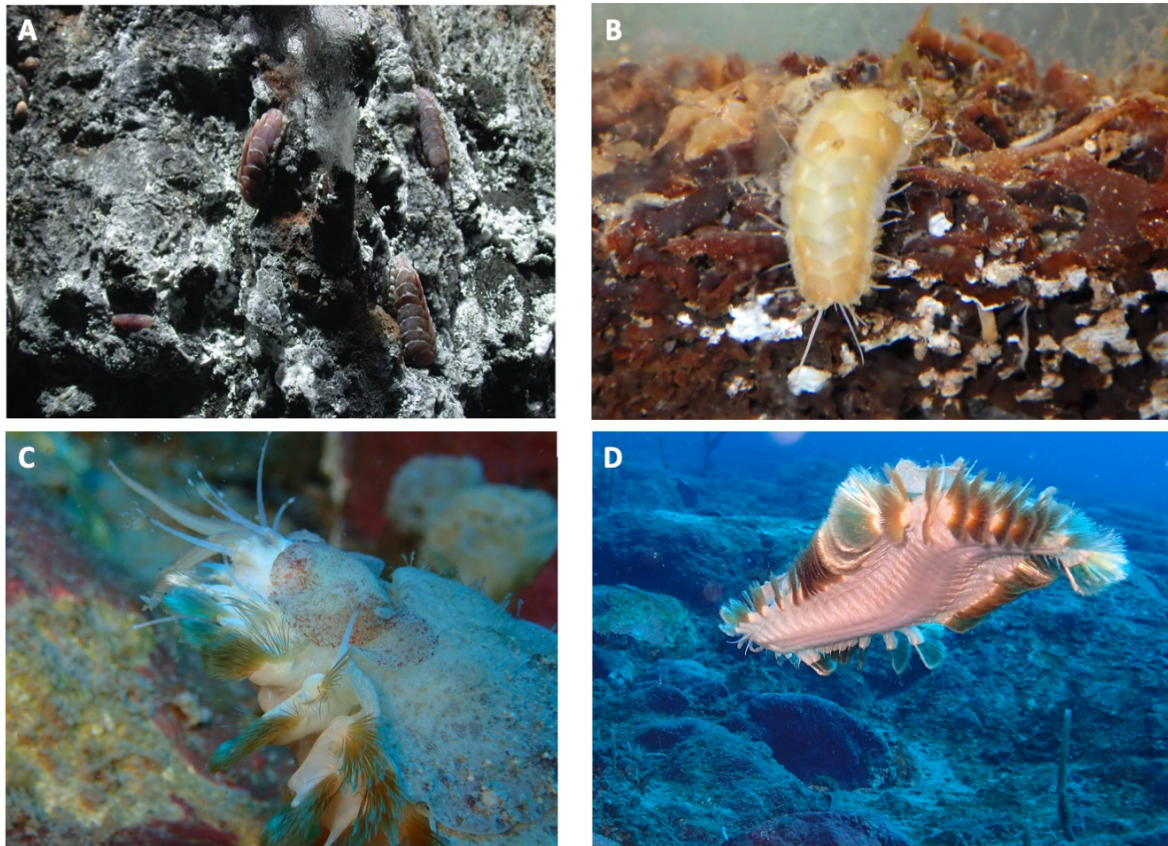

Figure 2: Polynoidae in their habitat. **A.** *Branchinotogluma segonzaci* (Miura & Desbruyères, 1995). Lau Basin, Copyright WHOI-Lau 2009. **B.** *Harmothoe fuligineum* (Baird, 1865) on the holdfast of *Himantothallus grandifolia* (A. Gepp & E.S. Gepp) Zinova, 1959. **C.** and **D**. *Eulagisca uschakovi* Pettibone, 1997. Close-up of the anteriro on the bottom (C) and swimming (D). Copyright Pierre Chevaldonné (IMBE, France). B-D: Antarctica, Adélie Land. POLARIS summer campaign series.

The relationship of Polynoidae with other families of Aphroditiformia remains unclear. There is not recognized synapomorphy in Polynoidae. Recent molecular studies, however, suggest that Iphionidae should be considered a distinct family from Polynoidae (Gonzalez et al., 2018; Norlinder et al., 2012; Zhang et al., 2018). These studies included a single Acoetidae (*Panthalis oerstedi* Kinbergg, 1856) that separated species of Iphioninae from the other

species of Polynoidae. In addition to the use of a single species to represent Acoetidae, support for this topology is relatively limited (see relevant section for further discussion). In this chapter, Iphionidae are considered as part of the Polynoidae, and referred to as the subfamily Iphioninae. Similarly, the revision of subfamilies proposed by Bonifacio and Menot (2018) will not be used here and the formerly accepted subfamily names will be used.

Morphology and taxonomically important characters

Polynoids possess numerous characters that are used in their taxonomy.

General appearance

The body can be linear or elliptical. The number of segments can be as small as 15, and reach well over 100. The numbering of segments in the past has not been consistent and modern researchers agree to count the tentacular segment as the first segment.

Prostomium and anterior area

The prostomium is usually bilobed, and can bear 0, 1, 2, or 3 antennae (Figure 3). The median antenna is always absent in the subfamily Iphioninae. The subfamilies Bathyeditinae and Polaruschakovinae are completely devoid of antennae. The presence and position of the insertion of the lateral antennae is a key character in the higher-level taxonomy, in particular at the subfamily level (Figure 3). In Lepidastheniinae, and Lepidonotinae, the lateral antennae are inserted terminally on the prostomium (Figure 3B and D). In Polynoinae, the lateral antennae are inserted ventrally or termino-ventrally (Figures 3A and 4A-C). In Iphioninae, lateral antennae can be missing as well (e.g. *Thermiphione*, Figure 3E) or inserted terminally on the prostomium (e.g. *Iphione* Figure 3F). In Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Lepidonopodinae (Figure 3C), Macellicephalinae, Macellicephaloidinae, and Macelloidinae, the lateral antennae are absent. However, some species possess frontal filaments attached to the anterior of the prostomium where lateral antennae can be attached (Figure 4D). The styles of the antennae can be smooth or papillated (Figures 3, 4C), tapering regularly, or be subulate.

On either side of the prostomium, the palps are directed forward and can sometimes display linearly disposed tufts of cilia. Next to the palps, the cirrophores of the two pairs of tentacular (= buccal) cirri can either bear short, stout chaetae (Figure 3A and B) or be smooth (Figure

3C-F). For a species, the cirri resemble those of the antennae (i.e. smooth or papillated; Figures 3 and 4).

When eyes are present, they are always sessile. Deep-sea species are usually devoid of eyes (Figure 3C and E). The eyes appear dorsally on the prostomium; the posterior pair is usually located on the posterior edge of the prostomium. The anterior pair can be located where the prostomium is widest (Figures 3A, B, D, F) or sometimes on the ventral side of the prostomium (Figure 3C).
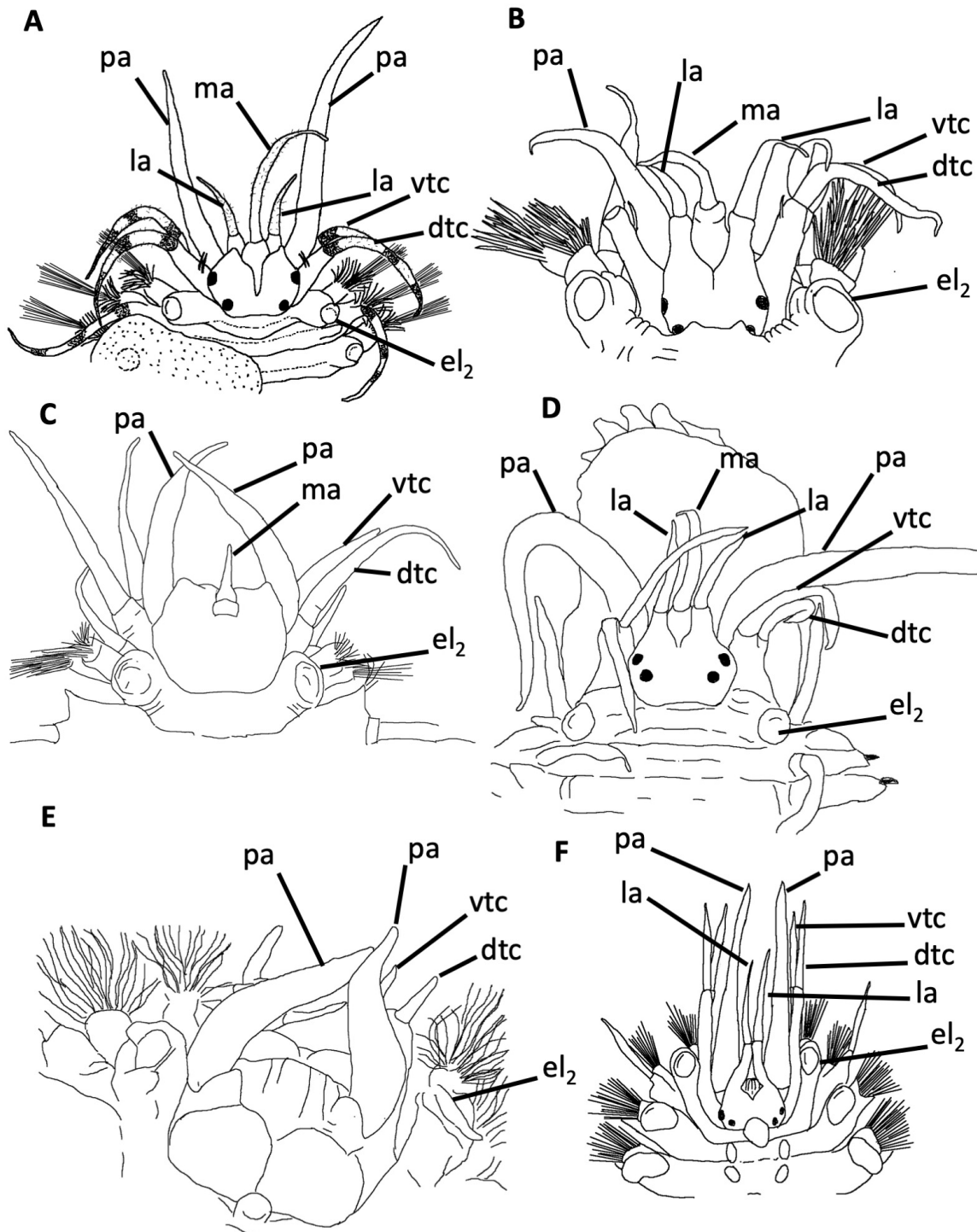
Figure 3: Anterior regions of Polynoidae with different numbers of antennae. **A.** *Harmothoe extenuata* (Grube, 1840). **B.** *Lepidonotus carinulatus* (Grube, 1869). **C.** *Lepidonotopodium atalantae* Desbruyeres & Hourdez, 2000. **D.** *Lepidasthenia loboi* Salazar-Vallejo, González & Salazar-Silva, 2015. **E.** *Thermiphione risensis* (Pettibone, 1986). **F.** *Iphione ovata* Kinberg, 1856. A redrawn after Barnich & Fiege (2003). B redrawn after Imajima (1997). F. redrawn after Pettibone (1976). dtc= dorsal tentacular cirrus, el_2= elytrophore segment 2, la= lateral antenna, ma= median antenna, pa= palp, vtc= ventral tentacular cirrus.
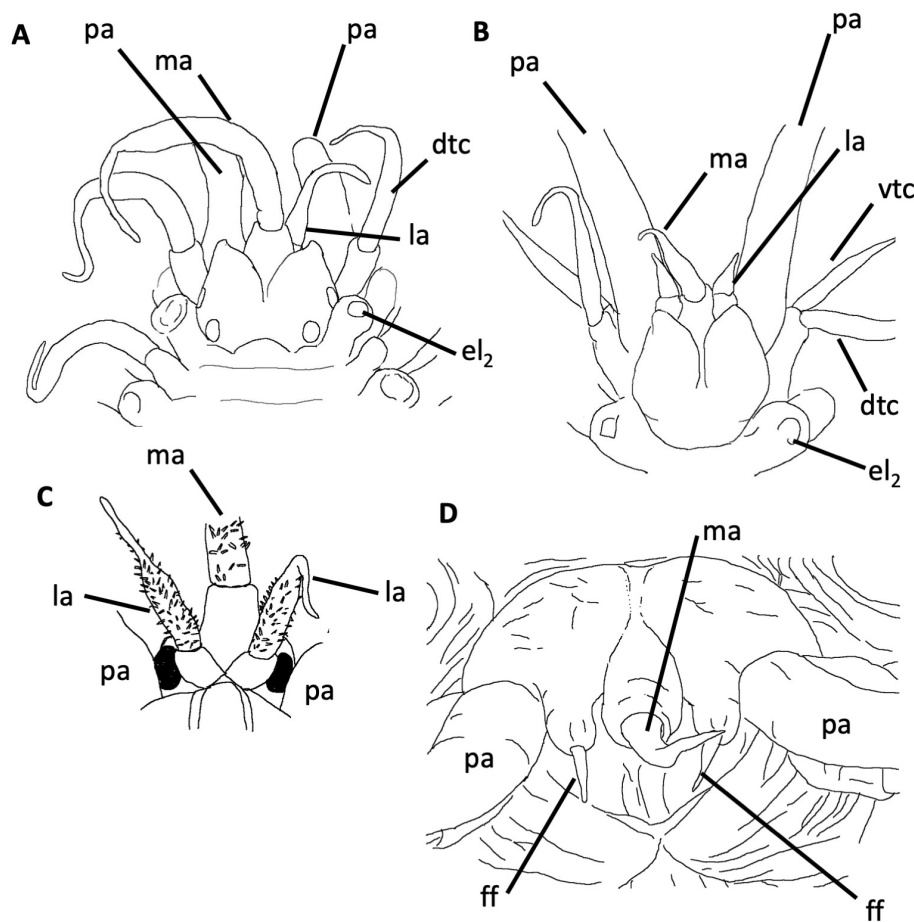
Figure 4: Insertion of lateral antennae (A-C) and of frontal filaments (D). **A.** ventral insertion (e.g. *Harmothoe* sp.). **B.** Termino-ventral insertion (e.g. *Malmgrenia* sp.). **C.** Ventral view of ventral insertion in *Harmothoe spinifera* (Ehlers, 1864). Redrawn after Imajima (1997). **D.** Frontal filaments occupy the position of lateral antennae. *Branchinotogluma sandersi* Pettibone, 1985. Frontal view. dtc= dorsal tentacular cirrus, el2= elytrophore segment 2, ff= frontal filament, la= lateral antenna, ma= median antenna, pa= palp, vtc= ventral tentacular cirrus.

Parapodia

Parapodia can bear elytra (elytrophorous) or dorsal cirri (cirregerous) (Figure 5). In *Gesiella jameensis* (Hartmann-Schröder, 1974), an additional filamentous structure (called 'accessory filamentous sensory organ' by Pettibone, 1976) is attached to the distal part of the cirrophores in addition to the dorsal cirrus. The dorsal cirri can be smooth or papillate, and can taper gradually to a fine tip or be slightly swollen close to the tip. A ventral cirrus, digitiform and usually small, is inserted near the middle of the neuropodium.
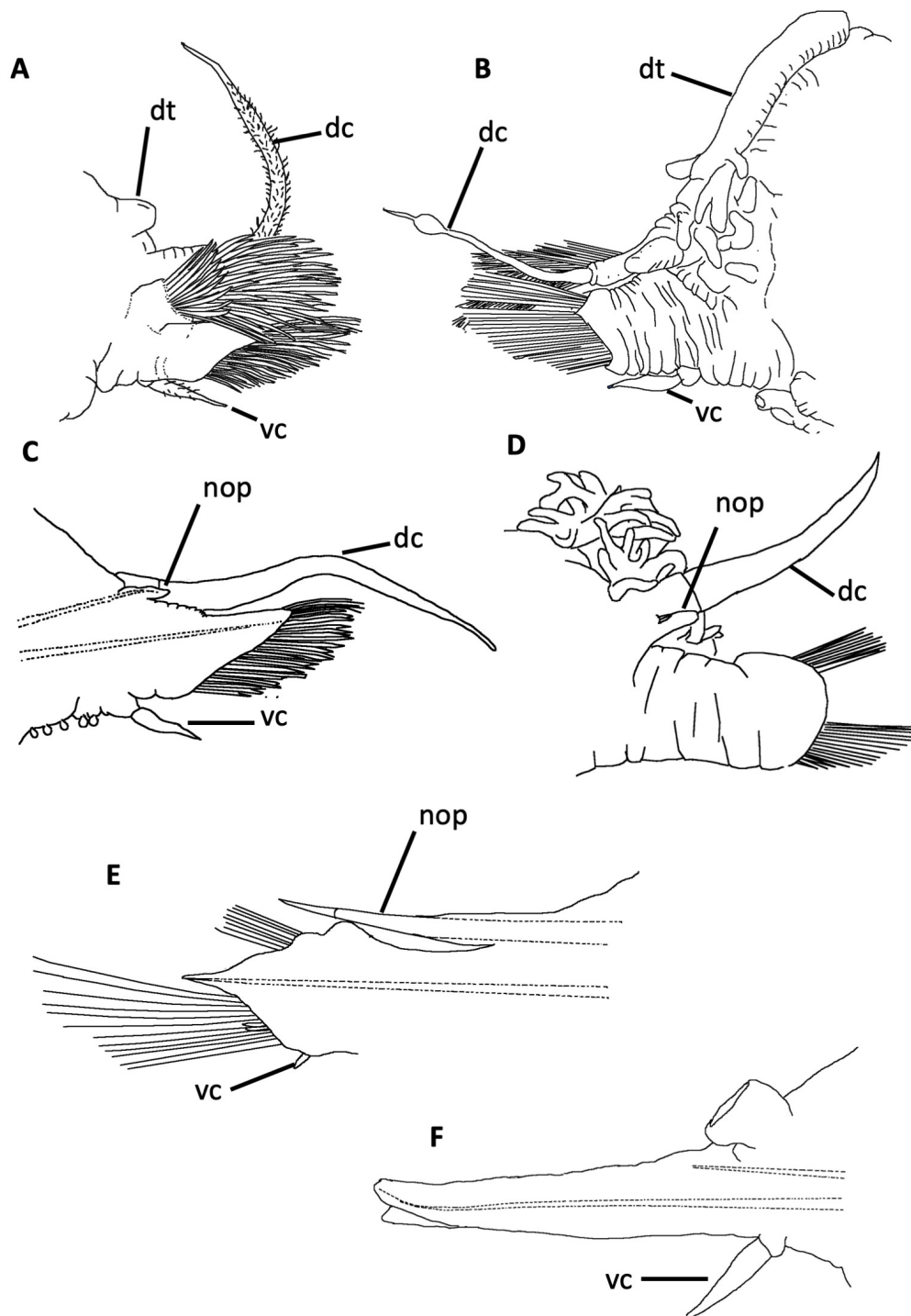
Figure 5: Parapodia of Polynoidae. Biramous parapodia of *Harmothoe imbricata* (Linnaeus, 1767) (**A**) and *Euphione chitoniformis* (Moore, 1903) (**B**). Sub-biramous parapodia from *Lepidasthenia interrupta* (Marenzeller, 1902) (**C**) and *Branchipolynoe tjiasmantoi* Lindgren, Hatch, Hourdez, Seid & Rouse, 2019 (**D**). Notopodium reduced to acicula. *Macellicephaloides uschakovi* Levenstein, 1971 (**E**). Uniramous parapodium from *Macelloides antarctica* Uschakov, 1957. Chaetae not represented (**F**). A, B, and C redrawn from Imajima (1997). E and F redrawn from Pettibone (1976). dc= dorsal cirrus, dt=dorsal tubercle, nop= notopodium, vc= ventral cirrus. Dotted lines are outlines of aciculae.

The parapodia are usually biramous but the notopodium can be reduced or absent in some genera (Figure 5). The acicula can sometimes protrude from the soft tissues (Figures 5 and 6). The neuropodium also possesses characteristics that are used for taxonomy at different levels. The neuropodial acicular lobe can be terminated by a terminal papilla (Figgure 6A), a fleshy extension above the protruding aciculum (supra-acicular process; Figure 6 B), or not have any extention. The neuropodium can be deeply incised (e.g. Lepidastheniinae; Figure 6E) or the acicular lobe and post-chaetal lobes can be short (Figure 6D). The ventral side of the neuropodium can also bear papillae (Figure 6E).

There are no compound chaetae. Notopodial and neuropodial chaetae are morphologically different. There is a great diversity of chaetal morphologies (Figure 7) that are used as a key taxonomic character defining some genera. Notochaetae can be of different types and neurochaetae are usually of different types. Supra-acicular and sub-acicular neurochaetae are often of different types.
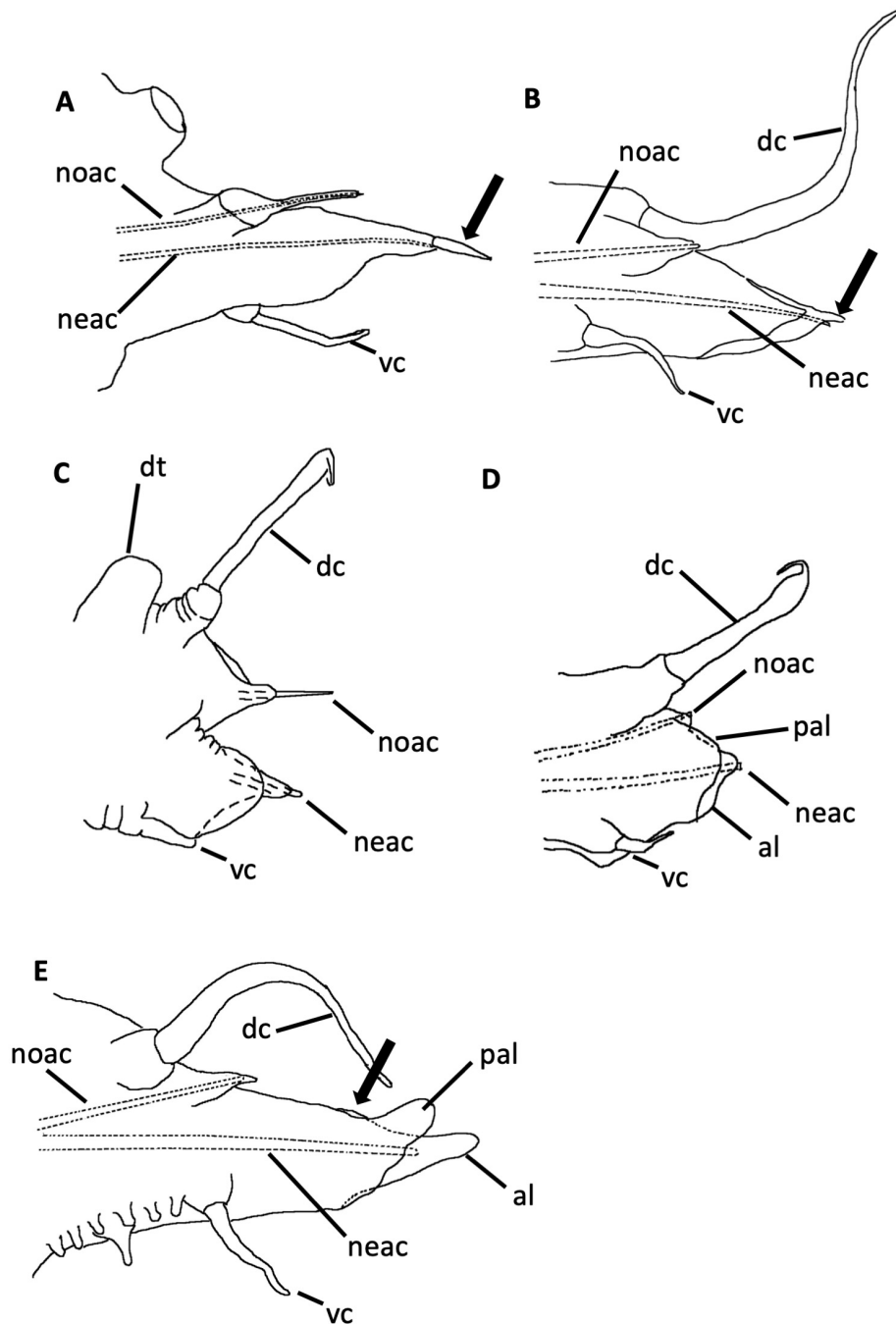
Figure 6: Parapodial features (simplified drawings, chaetae omitted). **A**. Parapodium with terminal papilla (arrow). *Neobylgides scotiensis*, Pettibone, 1993. **B**. Parapodium with supra-acicular process (arrow). *Malmgrenia lunulata* (Delle Chiaje, 1830). **C**. Parapodium without terminal processes. Only the aciculae protrude. **D**. Parapodium with a shallow incision between the pre-setal (= acicular) lobe and post-acicular lobe (e.g. Lepidonotinae). *Lepidonotus clava* (Montagu, 1808). **E**. Parapodium with a deeply incised neuropodium (e.g. Lepidastheniinae). *Lepidasthenia brunnea* Day, 1960. al= acicular lobe, dc= dorsal cirrus, dt=dorsal tubercle, neac= neuropodial acicula, noac= notopodial acicula, pal= post-acicular

lobe , vc= ventral cirrus. Dotted lines are outlines of aciculae. A Redrawn from Pettibone (1993). B, D, E Redrawn after Barnich & Fiege (2003). C Redrawn after Bock et al. (2010).

Elytra

The elytra are found on setigers 2, 4, 5, and every other segment until segment 23. The segments that do not bear elytra bear dorsal cirri instead. Their pattern beyond this segment is variable, and some species are devoid of elytra in this region (e.g. *Polynoe scolopendrina* Savigny, 1822). In Branchinotogluminae and Branchipolynoinae, the number of segments is 21 and segments 20 and 21 bear dorsal cirri only. The Macellicephalinae *Bathykurila guaymasensis* Pettibone, 1989, there are only 15 segments and the two last ones also only bear dorsal cirri. The foremost pair of elytra is often distinctly different from the following ones: they accommodate the palps, and tentacular cirri that project forward while covering the prostomium. In *Gorgoniapolynoe* Pettibone, 1991, the first pair of elytra is transparent. The elytra can completely cover the dorsum or they can be very small and leave most of the dorsum uncovered (e.g. *Branchipolynoe symmytilida* Pettibone, 1984).

The ornamentation of the scales is also a very important character to distinguish species. In particular, the presence and distribution of micro- and macro-tubercles, as well as border and surface papillae (Figure 8), are characters most often used. The species of Iphioninae have a very distinctive polygonal surface with spines or tubercles.

Posterior segments

The pygidium bears a pair of anal cirri but these are often lost when the animals are preserved. The anus can be terminal or dorsal. In male Branchinotogluminae and Branchipolynoinae, the posterior segments can be greatly modified. In association with sexually dimorphic ventral papillae, this led Pettibone to initially describe different species for males and even a different genus (*Opisthotrochopodus* Pettibone, 1985).

Biology and ecology

Symbiotic relationships

Polynoidae are, by far, the family in which most of the commensal polychaetes are found, (ca. half of the polychaetes known to be commensal). They are more often associated with echinoderms or with tube and burrow makers from several phyla, including other polychaetes

(Martin & Britayev 1998). Overall, about 20% of the Polynoidae species are commensal (Martin & Britayev 1998).

A symbiotic relationship can be accompanied by morphological modification of both partners (Martin & Britayev 1998). A reduction of parapodia and elytra is commonly observed in the genera *Branchipolynoe* Pettibone, 1984 and *Arctonoe* Chamberlin, 1910. The host can also exhibit morphological modifications, in particular, 'worm paths' have been reported in various species of cnidaria with hard skeletons (Martin & Britayev 1998)(De Assis et al., 2019)

Bioluminescence

Some Polynoidae display a bioluminescence in epidermal cells of the elytra. The luminescence is produced by a membrane photoprotein, called polynoidin, which reacts to the presence of superoxide radicals (Bassot and Nicolas 1995). These authors suggest that the tubercles on the elytra may act as lenses that focus the light emitted by special organelles, the photosomes, that are found in the cells of the basal layer of the elytra (Plyuscheva and Martin 2009). Although bioluminescence was not observed in the Lepidonotinae *Lepidonotus clava* (Montagu, 1808) and *L. squamatus* (Linnaeus, 1758), an active polynoidin was purified from their scales, and the authors suggest it could be a superoxide radical scavenger (Plyuscheva and Martin 2009).

Feeding

Polynoidae are generally predators (Jumars et al. 2015) but some vent and seep species may feed on bacterial mats (*e.g. Vampiropolynoe embleyi* Marcus and Hourdez, 2002). Many Polynoidae include algal fragments in their diet. Some commensals take advantage of their hosts diet, feeding either as kleptoparasites or by coprophagy (Jumars et al. 2015). The Polynoidae are usually active predators and they capture their preys by projecting their muscular pharynx forward. The pharynx is usually armed with two pairs of jaws that can be smooth or can bear teeth. At the base of the jaws, a structure that may be venom glands has been reported by Wolf (1986). In the species *Vampiropolynoe embleyi*, the jaws are missing and replaced by small sclerotinized plates (Figure XX, Marcus and Hourdez 2002).
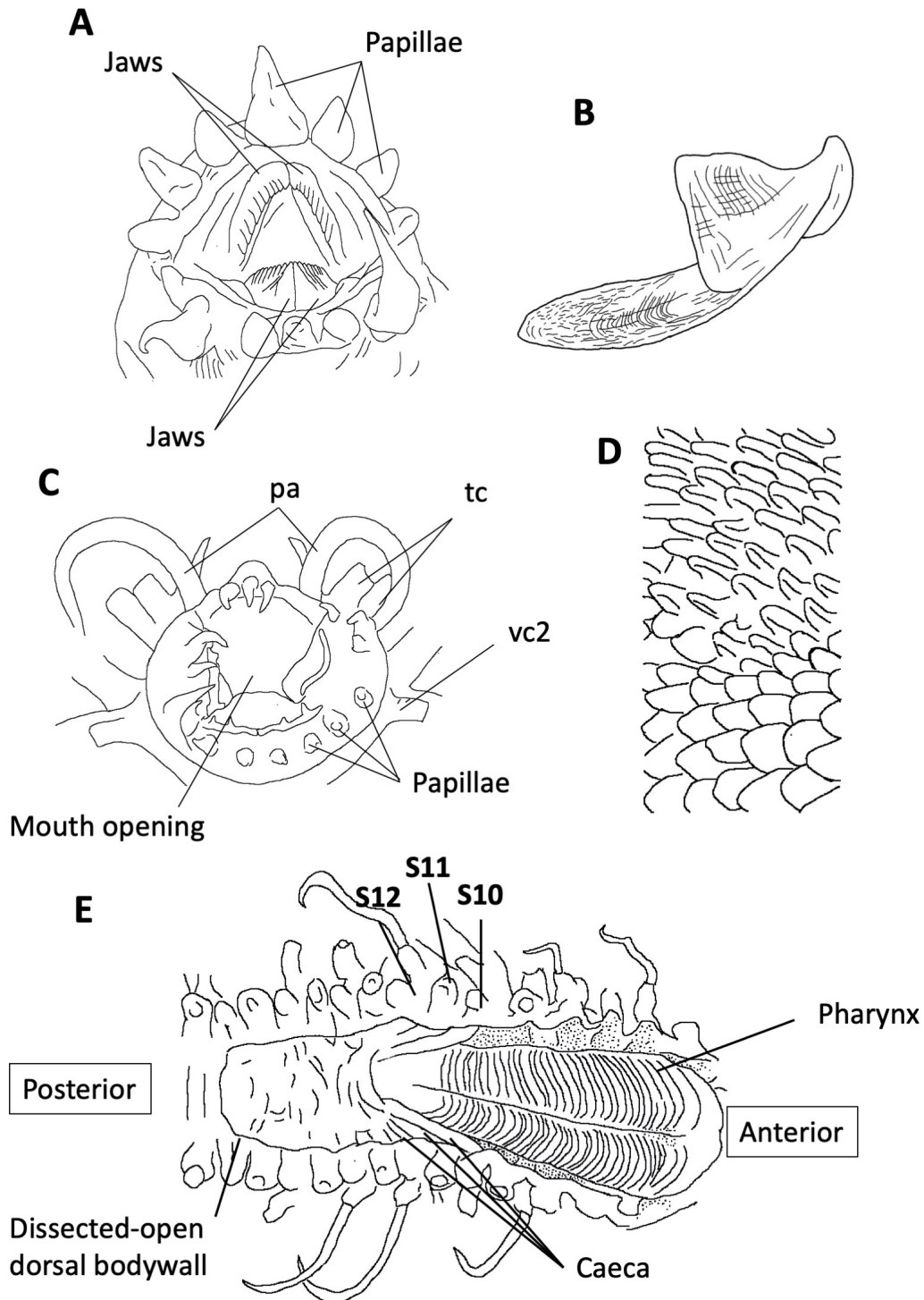
Figure 9: **A.** Pharynx opening of *Lepidonotopodium piscesae* Pettibone, 1988. **B.** Jaw from *Harmothoe* sp.. Note the growth rings on the shaft. **C.** Mouth opening of *Vampiropolynoe embleyi* Marcus & Hourdez, 2002. Note the lack of jaws and presence of keratinized plates. **D.** Keratinized teeth on the inner lining of the same species. **E.** Dissection of the anterior of *Harmothoe fuligineum* (Baird, 1865). Dorsal view showing the pharynx and bases of the first

three pairs of caeca. S10, S11, S12: Segments 10, 11, and 12. pa= palp, tc= tentacular cirrophores, vc2= ventral cirrophore of segment 2.

Respiratory exchange and respiratory pigments

Most of the Polynoidae are devoid of true gills, although some small appendages are referred to as gills in a variety of species (e.g. *Euphione* McIntosh, 1885; Figure 5B). Gills are however found in some deep sea hydrothermal vent species, in the subfamilies Branchiplicatinae, Branchinotogluminae, Branchipolynoinae, and in the species *Thermopolynoe branchiata* Miura, 1994 (subfamily Lepidonotopodinae) (Figure 10). The gills in the species *Branchipolynoe symmytilida* Pettibone, 1984 and *B.* aff. *seepensis* Pettibone, 1986 (Branchipolynoinae) correspond to thin lateral expansions of the bodywall and are not perfused by blood vessels (Figure 10). Instead, the coelomic fluid circulates inside the gills, moved by patches of cilia (Hourdez and Jouin-Toulmond, 1998).

For the species devoid gills, gas exchange likely occurs by diffusion through the bodywall. In shallow-water Polynoidae, water is renewed at the surface of the body by cilia on the surface of the body and by the motion of the elytra (Lwebuga-Mukasa 1970). Although no elytra movement was observed in the Antarctic species *Eulagisca uschakovi* Pettibone, 1997, the posterior elytra form a funnel (Figure 10A) from which water flows out, probably moved by rows of cilia found on the dorsum (pers. obs.).
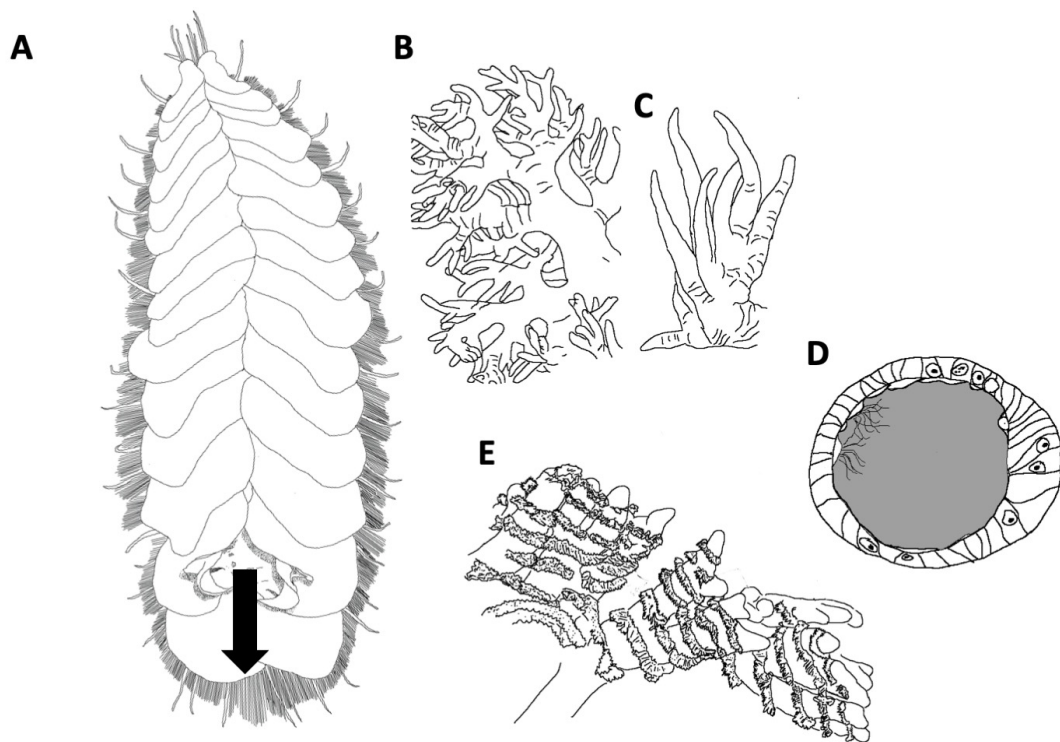
Figure 10: **A**. Dorsal view of a live specimen of *Eulagisca uschakovi* Pettibone, 1997. Arrow indicates flow of water exiting from space between dorsal body-wall and elytra. Gills from *Branchipolynoe symmytilida* Pettibone, 1984 (**B**), *B.* aff. *seepensis* Pettibone, 1986 (**C**, **D**), and (**E**) *Thermopolynoe branchiata* Miura, 1994. **D**. Cross-section through a ill filament. Grey area corresponds to coelomic fluid in the central space.

The respiratory pigments found in the Polynoidae are all heme-containing pigments. Although a small vascular system is present, most Polynoidae are devoid of true hemoglobin circulating in the body . A specific globin is however expressed the nervous system, clearly visible in the ventral nerve cord and in the cerebral ganglia (Weber, 1978; Weber and Vinogradov, 2001). In some deep-sea hydrothermal vent species, large amounts of hemoglobin (i.e. globins circulating the body) are found in the coelomic cavity. In the two species studied so far, *Branchipolynoe symmytilida* and *B. seepensis*, these hemoglobins exhibit a very high affinity for oxygen, and no cooperativity (Hourdez et al. 1999a, b). The respiratory pigments contained in the body of hydrothermal vent species represent a very significant storage of oxygen for these species that experience chronic hypoxia. In the vent species *Branchipolynoe* aff. *seepensis*, assuming fully oxygenated hemoglobins, the total bound oxygen represents a

quantity sufficient to meet the metabolic needs for about 90 minutes (Hourdez and Lallier, 2007).
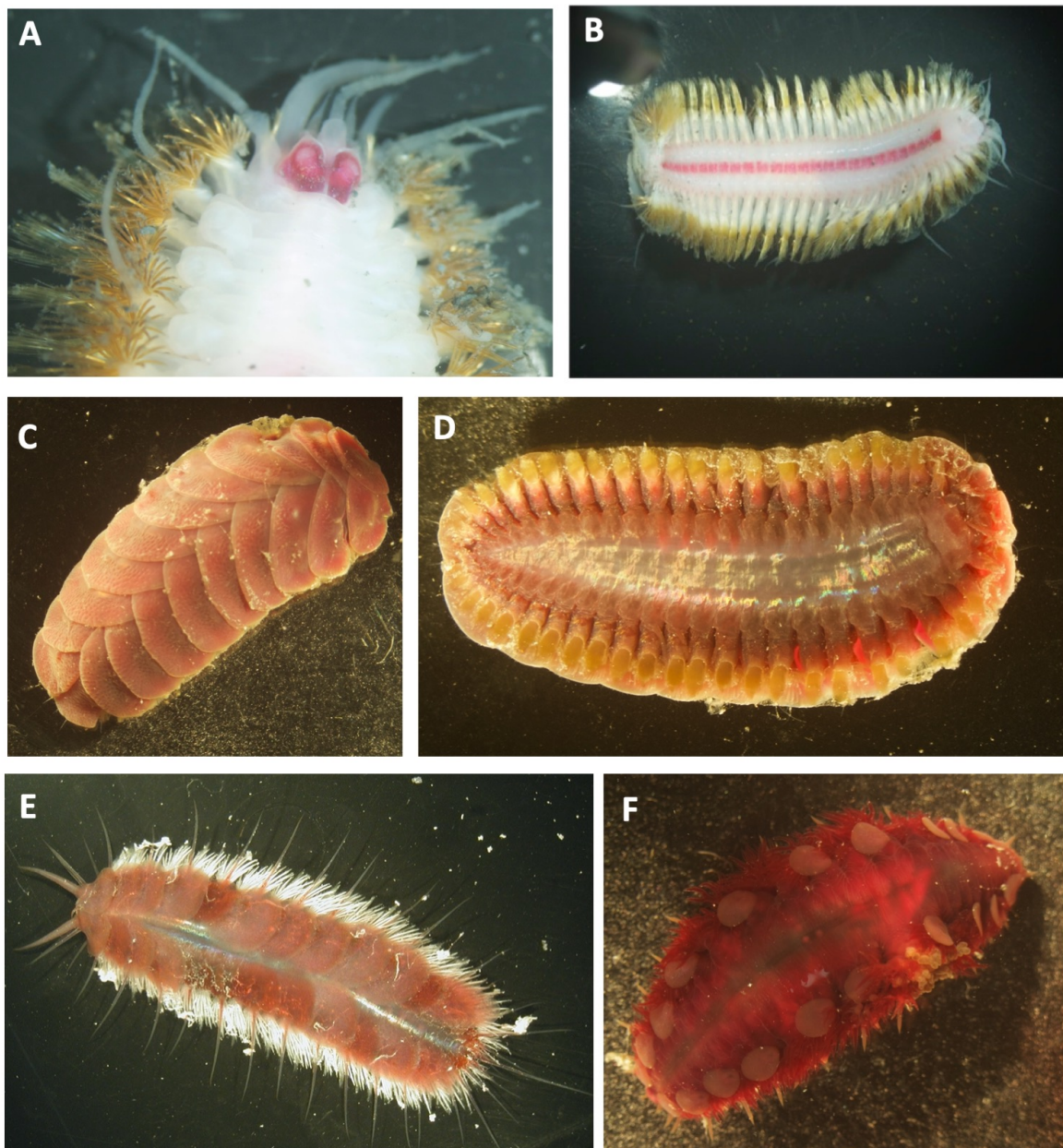
Figure 11: Globin in Polynoidae. *Harmothoe* sp. Anterior, dorsal view (**A**). Ventral side, whole body (**B**). *Lepidonotopodium williamsae* Pettibone, 1984. Dorsal view (**C**) and ventral view (**D**). **E.** *Branchiplicatus cupreus* Pettibone, 1985. **F.** *Branchipolynoe symmytilida* Pettibone, 1984.

In *Branchipolynoe*, the globins have a unique structure for annelids, with tetradomain subunits arranged into dimers and trimers (Hourdez et al. 1999a, b; Weber and Vinogradov

2001). Molecular studies indicate that this circulating globin is the result of tandem gene duplications from an intracellular single-domain globin (Projecto-Garcia et al. 2010).

Reproduction and development

As for other Aphroditiformia, sexes are separate in the Polynoidae (Wilson, 1991). The gametes develop in the epithelium that lines the coelomic cavity and nearly mature gametes are released in the coelomic cavity where their maturation progresses (Daly 1974). Mature oocytes found in the coelomic cavity usually cannot be directly fertilized, and a maturation factor seems to be necessary (Howie 1961; Bentley and Pacey 1992). In *Lepidonotus sublevis* Verrill, 1873, however, the oocytes are fertilizable after a brief incubation in seawater (Simon 1965). In the deep-sea hydrothermal vent species *Branchipolynoe* aff. *seepensis* Pettibone 1986, Jollivet et al. (2000) also report the presence of ovaries with oocytes at different stages of maturation, and ovisacs to store the large mature oocytes.

The reproduction and development of at least 18 species of Polynoidae have been studied (Wilson 1991; Phillips and Pernet 1996; Giangrande 1997; Van Dover et al. 1999). Most of these species free-spawn their gametes into the surrounding water, where fertilization occurs and development takes place. For a few species however, sperm is transferred by pseudocopulation (e.g. *Harmothoe imbricata* (Linnaeus, 1767), *Branchipolynoe* spp.; Daly 1972; Van Dover et al. 1999; Jollivet et al. 2000). The shallow-water species *H. imbricata* broods its embryos under the maternal elytra until they are released as larvae. The produced larvae usually feed in the plankton but the large size of the oocytes suggests that the larvae are lecitotrophic and disperse over long distances (Jollivet et al. 2000; Daguin and Jollivet 2005; Plouviez et al. 2008).

The most detailed recent study of larval development of an Aphroditiformia is probably that of Pernet (2000) who worked on the three closely related symbiotic Polynoidae *Arctonoe vittata* (Grube, 1855), *A. pulchra* (Johnson, 1897), and *A. fragilis* (Baird, 1863). The development is essentially the same for all Aphroditiformia that have been studied to date. These species produce planktonotrophic larvae with a prototroch but no metatroch or food groove cilia. Feeding starts after the development of episphere cilia. After 6-12 weeks, metamorphosis occurs, with the development of anterior appendages (palps, antennae, and tentacular cirri), and the beginning of elytra and dorsal cirri. The morphology of the larvae at different stages for 8 other species was also reported (Bhaud & Cazaux, 1987).

Growth

Very few studies of the growth and longevity of the Polynoidae have been published so far. A possible tool for such studies in the Polynoidae is the use of growth rings on the jaw base (Figure 9B) as a proxy of the age of animals (Britayev and Belov, 1993). The authors established a correlation between these growth rings and duration since the beginning of a colonization experiment in the White Sea. This can in turn be used to estimate the age of the animals in population dynamics studies (e.g. Plyuscheva et al. 2004).

Phylogeny and taxonomy

The taxonomy of the Polynoidae is in need of

Recent molecular studies, however, suggest that Iphionidae should be considered a distinct family from Polynoidae (Gonzalez et al., 2018; Norlinder et al., 2012; Zhang et al., 2018).

There are currently 19 subfamilies

Table 1: Polynoid subfamilies, authority, depth range and known habitat. Sub-littoral (0-200 m), bathyal (200-2 000 m), abyssal (2 000-6 000 m), hadal (deeper than 6 000 m).

Sub-family	Authority	Habitat	Number of genera	Number of species
Admetellinae	Uschakov, 1977	Bathyal	2	4
Arctonoinae	Hanley, 1989	Sub-littoral	15	19
Bathyedithinae	Pettibone, 1976	Abyssal	2	3
Bathymacellinae	Pettibone, 1976	Abyssal	2	4
Branchinotogluminae	Pettibone, 1985	Bathyal, Abyssal (hydrothermal vents and organic matter)	2	18
Branchiplicatinae	Pettibone, 1985	Bathyal, Abyssal (hydrothermal vents)	1	1
Branchipolynoinae	Pettibone, 1984	Bathyal, Abyssal (hydrothermal vents, cold seeps)	1	9
Eulagiscinae	Pettibone, 1997	Sub-littoral, Bathyal, Abyssal	3	8
Gesiellinae	Muir, 1982	Sub-littoral (anchialine caves)	1	1
Iphioninae	Baird, 1865	Sub-littoral, Bathyal, Abyssal	3	13

		(hydrothermal vents and organic matter)		
Lepidastheniinae	Pettibone, 1989	Sub-littoral	12	65
Lepidonotinae	Willey, 1902	Sub-littoral	26	175
Lepidonotopodinae	Pettibone, 1983	Bathyal, Abyssal (hydrothermal vents)	2	9
Macellicephalinae	Hartmann-Schröder, 1971	Sub-littoral, Bathyal, Abyssal (hydrothermal vents anchialine caves)	18	65
Macellicephaloidinae	Pettibone, 1976	Abyssal, Hadal	1	9
Macelloidinae	Pettibone, 1976	Bathyal, Abyssal	1	1
Polaruschakovinae	Pettibone, 1976	Abyssal	5	9
Polynoinae	Kinberg, 1856	Sub-littoral, Bathyal, Abyssal	58	487
Uncopolynoinae	Wehe, 2006	Sub-littoral	1	1
Vampiropolynoinae	Marcus & Hourdez, 2002	Bathyal, Abyssal (hydrothermal vents)	1	1

List of subfamilies, the genera they comprise, and number of valid species is each genus.

The following taxonomic list is based on the current status in the World Record of Marine Species (WoRMS). Because of the issues on the basis for synonymization of some deep-sea families in Bonifácio & Menot (2018) mentioned earlier in this chapter, the following list does not completely follow the current status in WoRMS and maintains the subfamilies recognized before (Bonifácio & Menot, 2019).

Subfamily Admetellinae Uschakov, 1977

Currently valid genera: 2

Genus *Admetella* McIntosh, 1885

    Number of currently valid species: 3

Genus *Bathyadmetella* Pettibone, 1967

    Number of currently valid species: 1

Subfamily Arctonoinae Hanley, 1989

Currently valid genera: 15

Genus *Adyte* Saint-Joseph, 1899

Number of currently valid species: 1

Genus *Arctonoe* Chamberlin, 1920

Number of currently valid species: 3

Genus *Asterophilia* Hanley, 1989

Number of currently valid species: 2

Genus *Australaugeneria* Pettibone, 1969

Number of currently valid species: 4

Genus Bathynoe Ditlevsen, 1917

Number of currently valid species: 6

Genus *Capitulatinoe* Hanley & Burke, 1989

Number of currently valid species: 1

Genus *Disconatis* Hanley & Burke, 1988

Number of currently valid species: 2

Genus *Gastrolepidia* Schmarda, 1861

Number of currently valid species: 1

Genus *Medioantenna* Imajima, 1997

Number of currently valid species: 2

Genus *Minusculisquama* Pettibone, 1983

Number of currently valid species: 1

Genus *Neohololepidella* Pettibone, 1969

Number of currently valid species: 2

Genus *Parabathynoe* Pettibone, 1990

Number of currently valid species: 1

Genus *Parahololepidella* Pettibone, 1969

Number of currently valid species: 1

Genus *Pottsiscalisetosus* Pettibone, 1969

Number of currently valid species: 1

Genus *Showascalisetosus* Imajima, 1997

Number of currently valid species: 1

Subfamily Bathyedithinae Pettibone, 1976

Currently valid genera: 2

Genus *Bathyedithia* Pettibone, 1976

Number of currently valid species: 3

Genus *Bathymariana* Levenstein, 1978

    Number of currently valid species: 1

Subfamily Branchinotogluminae Pettibone, 1985

Currently valid genera: 2

Genus *Branchinotogluma* Pettibone, 1985

    Number of currently valid species: 12

Genus *Peinaleopolynoe* Desbruyères & Laubier, 1988

    Number of currently valid species: 6

Subfamily Branchiplicatinae Pettibone, 1985

Currently valid genera: 1

Genus *Branchiplicatus* Pettibone, 1985

    Number of currently valid species: 1

Subfamily Branchipolynoinae Pettibone, 1984

Currently valid genera: 1

Genus *Branchipolynoe* Pettibone, 1984

    Number of currently valid species: 9

Subfamily Eulagiscinae Pettibone, 1997

Currently valid genera: 3

Genus *Bathymoorea* Pettibone, 1967

    Number of currently valid species: 2

Genus *Eulagisca* McIntosh, 1885

    Number of currently valid species: 5

Genus *Pareulagisca* Pettibone, 1997

    Number of currently valid species: 1

Subfamily Gesiellinae Muir, 1982

Currently valid genera: 1

Genus *Gesiella* Pettibone, 1976

    Number of currently valid species: 1

Subfamily Iphioninae Kinberg, 1856

Currently valid genera: 3

Genus *Iphione* Kinberg, 1856

    Number of currently valid species: 7

Genus *Iphionella* McIntosh, 1885

    Number of currently valid species: 1

Genus *Iphionides* Hartmann-Schröder, 1977

    Number of currently valid species: 1

Genus *Thermiphione* Hartmann-Schröder, 1992

    Number of currently valid species: 4

Subfamily Lepidastheniinae Pettibone, 1989

Currently valid genera: 12

Genus *Alentiana* Hartman, 1942

    Number of currently valid species: 1

Genus *Anotochaetonoe* Britayev & Martin, 2006

    Number of currently valid species: 1

Genus *Benhamipolynoe* Pettibone, 1970

    Number of currently valid species: 2

Genus *Hyperhalosydna* Augener, 1922

    Number of currently valid species: 3

Genus *Lepidasthenia* Malmgren, 1867

    Number of currently valid species: 42

Genus *Lepidastheniella* Monro, 1924

    Number of currently valid species: 4

Genus *Lepidofimbria* Hartman, 1967

    Number of currently valid species: 1

Genus *Parahalosydna* Horst, 1915

    Number of currently valid species: 3

Genus *Perolepis* Ehlers, 1908

    Number of currently valid species: 4

Genus *Pseudopolynoe* Day, 1962

    Number of currently valid species: 1

Genus *Showapolynoe* Imajima, 1997

Number of currently valid species: 2

Genus *Telolepidasthenia* Augener & Pettibone, 1970

Number of currently valid species: 1

Subfamily Lepidonotinae Willey, 1902

Currently valid genera: 26

Genus *Alentia* Malmgren, 1865

Number of currently valid species: 1

Genus *Allmaniella* McIntosh, 1885

Number of currently valid species: 2

Genus *Augenerilepidonotus* Pettibone, 1995

Number of currently valid species: 1

Genus *Cervilia* Frickhinger, 1916

Number of currently valid species: 1

Genus *Chaetacanthus* Seidler, 1922

Number of currently valid species: 3

Genus *Dilepidonotus* Hartman, 1967

Number of currently valid species: 1

Genus *Drieschiopsis* Støp-Bowitz, 1991

Number of currently valid species: 1

Genus *Euphione* McIntosh, 1885

Number of currently valid species: 6

Genus *Euphionella* Monro, 1936

Number of currently valid species: 4

Genus *Halosydna* Kinberg, 1856

Number of currently valid species: 35

Genus *Halosydnella* Hartman, 1938

Number of currently valid species: 6

Genus *Halosydnopsis* Uschakov & Wu, 1959

Number of currently valid species: 1

Genus *Hermenia* Grube, 1856

Number of currently valid species: 3

Genus *Hermilepidonotus* Uschakov, 1974

Number of currently valid species: 2

Genus *Heteralentia* Hanley & Burke, 1991

    Number of currently valid species: 1

Genus *Hololepida* Moore, 1905

    Number of currently valid species: 5

Genus *Lepidametria* Webster, 1879

    Number of currently valid species: 4

Genus *Lepidonopsis* Pettibone, 1977

    Number of currently valid species: 3

Genus *Lepidonotus* Leach, 1816

    Number of currently valid species: 80

Genus *Nonparahalosydna* Uschakov, 1982

    Number of currently valid species: 1

Genus *Olgalepidonotus* Pettibone, 1995

    Number of currently valid species: 1

Genus *Parahalosydnopsis* Pettibone, 1977

    Number of currently valid species: 3

Genus *Pseudohalosydna* Fauvel, 1913

    Number of currently valid species: 1

Genus *Sheila* Monro, 1930

    Number of currently valid species: 1

Genus *Telodrieschia* Kirkegaard, 1995

    Number of currently valid species: 1

Genus *Thormora* Baird, 1865

    Number of currently valid species: 9

Subfamily Lepidonotopodinae Pettibone, 1983

Currently valid genera: 2

Genus *Lepidonotopodium* Pettibone, 1983

    Number of currently valid species: 8

Genus *Thermopolynoe* Miura, 1994

    Number of currently valid species: 1

Subfamily Macellicephalinae Hartmann-Schröder, 1971

Currently valid genera: 18

Genus *Abyssarya* Bonifácio & Menot, 2018

    Number of currently valid species: 1

Genus *Bathybahamas* Pettibone, 1985

    Number of currently valid species: 1

Genus *Bathycatalina* Pettibone, 1976

    Number of currently valid species: 1

Genus *Bathyeliasona* Pettibone, 1976

    Number of currently valid species: 4

Genus *Bathyfauvelia* Pettibone, 1976

    Number of currently valid species: 4

Genus *Bathykermadeca* Pettibone, 1976

    Number of currently valid species: 3

Genus *Bathykurila* Pettibone, 1976

    Number of currently valid species: 2

Genus *Bathylevensteina* Pettibone, 1976

    Number of currently valid species: 1

Genus *Bathymacella* Pettibone, 1976

    Number of currently valid species: 1

Genus *Bathypolaria* Levenstein, 1981

    Number of currently valid species: 3

Genus *Bathytasmania* Levenstein, 1982

    Number of currently valid species: 1

Genus *Bathyvitiazia* Pettibone, 1976

    Number of currently valid species: 2

Genus *Bruunilla* Hartman, 1971

    Number of currently valid species: 2

Genus *Levensteiniella* Pettibone, 1985

    Number of currently valid species: 7

Genus *Macellicephala* McIntosh, 1885

    Number of currently valid species: 26

Genus *Natopolynoe* Pettibone, 1985

    Number of currently valid species: 1

Genus *Pelagomacellicephala* Pettibone, 1985

    Number of currently valid species: 1

Genus *Yodanoe* Bonifácio & Menot, 2018

    Number of currently valid species: 1

Subfamily Macellicephaloidinae Pettibone, 1976

Currently valid genera: 1

Genus *Macellicephaloides* Uschakov, 1955

    Number of currently valid species: 9

Subfamily Macelloidinae Pettibone, 1976

Genus *Macelloides* Uschakov, 1957

    Number of currently valid species: 1

Subfamily Polaruschakovinae Pettibone, 1976

Currently valid genera: 6

Genus *Bathycanadia* Levenstein, 1981

    Number of currently valid species: 1

Genus *Bathymiranda* Levenstein, 1981

    Number of currently valid species: 1

Genus *Diplaconotum* Loshamn, 1981

    Number of currently valid species: 1

Genus *Nu* Bonifácio & Menot, 2018

    Number of currently valid species: 1

Genus *Polaruschakov* Pettibone, 1976

    Number of currently valid species: 5

Subfamily Polynoinae Kinberg, 1856

Currently valid genera: 58

Genus *Acanthicolepis* McIntosh, 1900

    Number of currently valid species: 2

Genus *Acholoe* Claparède, 1870

    Number of currently valid species: 1

Genus *Antarctinoe* Barnich, Fiege, Micaletto & Gambi, 2006

    Number of currently valid species: 2

Genus *Antinoe* Kinberg, 1856

Number of currently valid species: 6

Genus *Antipathipolyeunoa* Pettibone, 1991

Number of currently valid species: 1

Genus *Arcteobia* Annenkova, 1937

Number of currently valid species: 2

Genus *Arctonoella* Buzhinskaja, 1967

Number of currently valid species: 1

Genus *Australonoe* Hanley, 1993

Number of currently valid species: 1

Genus *Austrolaenilla* Bergström, 1916

Number of currently valid species: 10

Genus *Barrukia* Bergström, 1916

Number of currently valid species: 2

Genus *Bathynotalia* Levenstein, 1982

Number of currently valid species: 1

Genus *Bayerpolynoe* Pettibone, 1991

Number of currently valid species: 1

Genus *Brychionoe* Hanley & Burke, 1991

Number of currently valid species: 1

Genus *Bylgides* Chamberlin, 1919

Number of currently valid species: 9

Genus *Enipo* Malmgren, 1865

Number of currently valid species: 10

Genus *Eucranta* Malmgren, 1865

Number of currently valid species: 5

Genus *Eunoe* Malmgren, 1865

Number of currently valid species: 49, including 2 taxon inquirendum which are indeterminable due to holotype in poor condition

Genus *Gattyana* McIntosh, 1897

Number of currently valid species: 11

Genus *Gaudichaudius* Pettibone, 1986

Number of currently valid species: 2

Genus *Gorekia* Bergström, 1916

Number of currently valid species: 1

Genus *Gorgoniapolynoe* Pettibone, 1991

Number of currently valid species: 9, including one *nomen dubium* (indeterminable juvenile)

Genus *Grubeopolynoe* Pettibone, 1969

Number of currently valid species: 2

Genus *Harmothoe* Kinberg, 1856

Number of currently valid species: 156, including 2 *taxon inquirendum* (indeterminable due to insufficient description) and 4 *nomen dubium.*

Genus *Hartmania* Pettibone, 1955

Number of currently valid species: 1

Genus *Hemilepidia* Schmarda, 1861

Number of currently valid species: 3

Genus *Hermadion* Kinberg, 1856

Number of currently valid species: 3, including 1 *taxon inquirendum* and 1 *nomen dubium*

Genus *Hermadionella* Uschakov, 1982

Number of currently valid species: 3

Genus *Hesperonoe* Chamberlin, 1919

Number of currently valid species: 7

Genus *Heteropolynoe* Bidenkap, 1907

Number of currently valid species: 1

Genus *Hololepidella* Willey, 1905

Number of currently valid species: 12

Genus *Intoshella* Darboux, 1899

Number of currently valid species: 3

Genus *Kermadecella* Darboux, 1899

Number of currently valid species: 1

Genus *Lagisca* Malmgren, 1865

Number of currently valid species: 23, including 5 *taxon inquirendum* (indeterminable due to loss or poor condition of type, and insufficient description)

Genus *Leucia* Malmgren, 1867

Number of currently valid species: 2

Genus *Lobopelma* Hanley, 1987

Number of currently valid species: 1

Genus *Malmgrenia* McIntosh, 1874

Number of currently valid species: 18, including 2 *nomen dubium* due to poor condition of type

Genus *Malmgreniella* Hartman, 1967

Number of currently valid species: 27

Genus *Melaenis* Malmgren, 1865

Number of currently valid species: 2

Genus *Neobylgides* Pettibone, 1993

Number of currently valid species: 1

Genus *Neolagisca* Barnich & Fiege, 2000

Number of currently valid species: 1

Genus *Neopolynoe* Loshamn, 1981

Number of currently valid species: 4

Genus *Paradyte* Pettibone, 1969

Number of currently valid species: 3

Genus *Paragattyana* Pettibone, 1993

Number of currently valid species: 2

Genus *Paralentia* Uschakov, 1982

Number of currently valid species: 1

Genus *Paralepidonotus* Horst, 1915

Number of currently valid species: 5

Genus *Pararctonoella* Pettibone, 1996

Number of currently valid species: 3

Genus *Pettibonesia* Nemésio, 2006

Number of currently valid species: 1

Genus *Polyeunoa* McIntosh, 1885

Number of currently valid species: 2

Genus *Polynoe* Lamarck, 1818

Number of currently valid species: 48, including 21 taxon inquirendum (insufficiently described and loss of types) and 1 nomen dubium and 3 nomen nudum (no associated description and type)

Genus *Robertianella* McIntosh, 1885

Number of currently valid species: 2

Genus *Rullieriella* Pettibone, 1993

Number of currently valid species: 1

Genus *Russellhanleya* Barnich, Sun & Fiege, 2004

    Number of currently valid species: 1

Genus *Scalisetosus* McIntosh, 1885

    Number of currently valid species: 5

Genus *Subadyte* Pettibone, 1969

    Number of currently valid species: 8

Genus *Tenonia* Nichols, 1969

    Number of currently valid species: 2

Genus *Tottonpolynoe* Pettibone, 1991

    Number of currently valid species: 1

Genus *Verrucapelma* Hanley & Burke, 1991

    Number of currently valid species: 3

Genus *Ysideria* Ruff, 1995

    Number of currently valid species: 1

Subfamily Uncopolynoinae Wehe, 2006

Currently valid genera: 1

Genus *Uncopolynoe* Hartmann-Schröder, 1960

    Number of currently valid species: 1

Subfamily Vampiropolynoinae Marcus &Hourdez, 2002

Currently valid genera: 1

Genus *Vampiropolynoe* Marcus & Hourdez, 2002

    Number of currently valid species: 1

Subfamily Polynoidae *incertae sedis*

The following genera have not been placed in current subfamilies because their affinities were not clear.

Currently valid genera in this group: 19, including 3 taxon inquirendum based on larval forms, 1 nomen dubium

Genus *Bathyhololepidella* Buzhinskaya, 1992

    Number of currently valid species: 1

Genus *Benhamisetosus* Averincev, 1978

    Number of currently valid species: 1

Genus *Drieschella* Augener & Pettibone, 1970

    Number of currently valid species: 1

Genus *Hodor* Bonifácio & Menot, 2018

    Number of currently valid species: 2

Genus *Lepidogyra* Hartman, 1967

    Number of currently valid species: 1

Genus *Ophthalmonoe* Petersen & Britayev, 1997

    Number of currently valid species: 2

Genus *Parapolyeunoa* Barnich, Gambi & Fiege, 2012

    Number of currently valid species: 1

Genus *Phyllantinoe* McIntosh, 1876

    Number of currently valid species: 1

Genus *Phyllohartmania* Pettibone, 1961

    Number of currently valid species: 1

Genus *Phyllosheila* Pettibone, 1961

    Number of currently valid species: 1

Genus *Podarmus* Chamberlin, 1919

    Number of currently valid species: 1

Genus *Polynoella* McIntosh, 1885

    Number of currently valid species: 3

Genus *Polynoina* Nolte, 1936

    Number of currently valid species: 1

Genus *Chaetosphaera* Häcker, 1898 (*taxon inquirendum*, based on a larval form)

    Number of currently valid species: 1

Genus *Drieschia* Michaelsen, 1892 (*taxon inquirendum*, based on a larval form)

    Number of currently valid species: 5

Genus *Eumolphe* Risso, 1826 (*taxon inquirendum*, insufficiently described)

    Number of currently valid species: 1

Genus *Frennia* Viguier, 1912 (*taxon inquirendum*, insufficiently described)

    Number of currently valid species: 2

Genus *Quetieria* Viguier, 1911 (*taxon inquirendum*, based on a larval form)

    Number of currently valid species: 1

Genus *Sinantenna* Hartmann-Schröder, 1974 (*taxon inquirendum*)

    Number of currently valid species: 1

Genus *Herdmanella* Darboux, 1899 (*nomen dubium*)

Number of currently valid species: 2

The following genera have no valid species and should therefore not be considered valid

Genus *Eupolynoe* McIntosh, 1874

Number of currently valid species: 0

Genus *Hylosydna* Moore, 1903

Number of currently valid species: 0

References

Barnich, R., Fiege, D., 2003. The Aphroditoidea (Annelida:Polychaeta) of the Mediterranean Sea, in: Abhandlungen (Senckenbergische Naturforschende Gesellschaft). Stuttgart Schweizerbart, pp. 1–167.

Bock, G., Fiege, D., Barnich, R., 2010. Revision Of Hermadion Kinberg, 1856, With A Redescription Of Hermadion Magalhaensi Kinberg, 1856, Adyte Hyalina (G. O. Sars, 1873) N. Comb. And Neopolynoe Acanellae (Verrill, 1881) N. Comb. (Polychaeta: Polynoidae). https://doi.org/10.5281/ZENODO.196874

Bonifácio, P., Menot, L., 2019. New genera and species from the Equatorial Pacific provide phylogenetic insights into deep-sea Polynoidae (Annelida). Zool. J. Linn. Soc. 185, 555–635. https://doi.org/10.1093/zoolinnean/zly063

De Assis, J., Souza, J., Lima, M., Lima, G., Cordeiro, R., Pérez, C., 2019. Association between deep-water scale-worms (Annelida: Polynoidae) and black corals (Cnidaria: Antipatharia) in the Southwestern Atlantic. Zoologia 36, 1–13. https://doi.org/10.3897/zoologia.36.e28714

Gonzalez, B.C., Worsaae, K., Fontaneto, D., Martínez, A., 2018. Anophthalmia and elongation of body appendages in cave scale worms (Annelida: Aphroditiformia). Zool. Scr. 47, 106–121. https://doi.org/10.1111/zsc.12258

Imajima, N.S.M.M., 1997. Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo. Families Polynoidae and Acoetidae 13, 1–131.

Neal, L., Wiklund, H., Muir, A.I., Linse, K., Glover, A.G., 2014. The identity of juvenile Polynoidae (Annelida) in the Southern Ocean revealed by DNA taxonomy, with notes on the status of Herdmanella gracilis Ehlers sensu Augener. Mem. Mus. Vic. 71, 203–216. https://doi.org/10.24199/j.mmv.2014.71.16

Norlinder, E., Nygren, A., Wiklund, H., Pleijel, F., 2012. Phylogeny of scale-worms (Aphroditiformia, Annelida), assessed from 18SrRNA, 28SrRNA, 16SrRNA, mitochondrial cytochrome c oxidase subunit I (COI), and morphology. Mol. Phylogenet. Evol. 65, 490–500. https://doi.org/10.1016/j.ympev.2012.07.002

Pettibone, M.H., 1993. Revision of some species referred to Antinoe, Antinoella, Antinoana, Bylgides, and Harmothoe (Polychaeta: Polynoidae: Harmothoinae). Smithson. Contrib. Zool. 1–41. https://doi.org/10.5479/si.00810282.545

Pettibone, M.H., 1976. Revision of the genus Macellicephala McIntosh and the subfamily Macellicephalinae Hartmann-SchrAder (Polychaeta: Polynoidae). Smithson. Contrib. Zool. 1–71. https://doi.org/10.5479/si.00810282.229

Zhang, Y., Sun, J., Rouse, G.W., Wiklund, H., Pleijel, F., Watanabe, H.K., Chen, C., Qian, P.-Y., Qiu, J.-W., 2018. Phylogeny, evolution and mitochondrial gene order rearrangement in scale worms (Aphroditiformia, Annelida). Mol. Phylogenet. Evol. 125, 220–231. https://doi.org/10.1016/j.ympev.2018.04.002