# Annelida: Pleistoannelida, Errantia II, Phyllodocida. Section 7.13.1 Aphroditiformia

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# Aphroditiformia

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## Introduction

Collectively referred to as scale worms, Aphroditiformia includes six traditionally recognized families: Acoetidae Kinberg, 1856; Aphroditidae Malmgren, 1867; Eulepethidae Chamberlin, 1919; Pholoidae Kinberg, 1958; Polynoidae Kinberg, 1856; and Sigalionidae Malmgren, 1867. The status of some lineages is however currently changing. In a recent molecular study, Norlinder et al. (2012) erected the family Iphionidae Kinberg, 1856 to replace Iphioninae, once a subfamily positioned in Polynoidae. Gonzalez et al. (2018) showed that the family Pholoidae should also be considered a subfamily in Sigalionidae. In this handbook, however, the Iphionidae will be treated in the chapter on Polynoidae.

Aphroditiformia belong~~s~~ to the order Phyllodocida (Rouse & Pleijel 2001) and are characterized by the presence of elytra on some segments that may cover parts of the dorsum, and usually alternate with dorsal cirri on non-elytrigerous segments. The developmental origin of these elytra is still widely debated; they could correspond to either greatly modified dorsal cirrus that forms a scale, or, could correspond to the development of dorsal tubercles (Rouse & Pleijel 2001). There are however some exceptions to this iconic character. Species formerly described as belonging to the family 'Pisionidae' have been shown to have secondarily lost their elytra, and are now considered part of Sigalionidae (Gonzalez et al. 2017; Norlinder et al. 2012). Similarly, *Metaxypsamma uebelackerae* Wolf, 1986 (Sigalionidae) are also scaleless. Finally, the species *Palmyra aurifera* Savigny in Lamarck, 1818 is included in Aphroditidae (Wiklund et al. 2005; Norlinder et al. 2012), while other species of the genus are included in the family Chrysopetalidae.

Together, scale worm families comprise 237 recognized genera, and nearly 1385 species (Table 1). The most speciose family is Polynoidae, with 930 species, followed by Sigalionidae with 218 species, and Aphroditidae with 125 species. Aphroditiforms have a worldwide distribution, from the intertidal to abyssal depths, and with numerous habitat specializations. Adult sizes in Aphroditiformia range from about a millimeter for some Sigalionidae, to about two meters long for some of the long-bodied Acoetidae. Within Polynoidae, size ranges from a few millimeters for a large number of species to about 30 centimeters long and 12 centimeters wide in the Antarctic species *Eulagisca gigantea* Monro, 1939.

Table 1: Number of genera and species for the five families of Aphroditiformia. Numbers drawn from World Register of Marine Species (WoRMS Editorial Board 2017)

| **Family** | **Number of genera** | **Number of species** |
|---|---|---|
| Acoetidae | 10 | 58 |
| Aphroditidae | 13 | 108 |
| Eulepethidae | 6 | 24 |
| Polynoidae | 176 | 943 |
| Sigalionidae | 32 | 252 |
| Total | 237 | 1385 |

In the past, Aphroditiformia were the focus of a large treatise written by Darboux (1900), which offers a wealth of information on this group. Since that treatise, numerous studies have focused on taxonomy, morphology, biology, development, and evolution of this annelid group. In this chapter, we aim to give an overview of these characters for Aphroditiformia in general. Families will then be the focus of dedicated chapters.

## Morphology

### *Prostomium and peristomial appendages*

The structure of the prostomium is a key character in the distinction between the different families of Aphroditiformia (Figure 1). This region is usually covered by elytra and the associated appendages protrude anteriorly. The basic structure is the same for all families: the prostomium is surrounded by the first segment, which may be achaetous, and usually bears two pairs of tentacular cirri (a ventral pair and a dorsal pair). Although morphologically associated with the first segment, the pair of large palps is of protostomial origin. The number of antennae varies between zero and three, including a median and two lateral. The prostomium can be either deeply bilobed as in most Polynoidae or Acoetidae, or can more commonly form a single lobe. Some groups however differ from the typical anterior design. In the Pholoinae, the prostomium is typically rounded and fused to the first segment. In the genera formerly associated with the family 'Pisionidae' (now included in Sigalionidae, see Gonzalez et al. 2017), the prostomium is reduced and the first segment modified. Eyes are present and sessile in most families, on small mounds as in some Aphroditidae, or, directed anteriorly on a pair of large structures called ommatophores as in some Acoetidae. The mouth opens ventrally and a facial tubercle may be present.

Studies on brain structures in the aphroditid *Aphrodita aculeata* Linnaeus, 1758, the polynoids *Lepidonotus clava* (Montagu, 1808) and *Harmothoe areolata* (Grube, 1860), and the sigalionids *Neoleanira tetragona* (Örsted, 1845) and *Sthenelais* cf. *limicola*, showed that in accordance their active errant lifestyle, aphroditiforms have complex brain structures, morphologically reminiscent to that of insects, with paired mushroom body neuropils, unpaired midline neuropils, and olfactory glomeruli (Heuer & Loesel 2009; Heuer et al. 2010).

*Elytral pattern*

The presence of elytra (= scales) is a defining character of Aphroditiformia. These elytra vary in size along the body, and may cover the dorsum completely or leave most of it exposed, as is the case in some symbiotic species (*e.g.* genera *Arctonoe*, *Branchipolynoe*, *Lepidasthenia*). The anterior elytral pattern is common to all families until segment 19. Short-bodied species such as some members of the polynoid subfamilies Macellicephalinae and Branchinotogluminae deviate from this pattern. In particular, the posteriormost elytra may be missing in some males of the polynoid genus *Branchinotogluma* (Figure 2). The following segment, segment 2, bears the first pair of elytra. Segment 3 bears a pair of dorsal cirri and the two following segments (4 and 5) each bear a pair of elytra. The following segments alternate between having cirri (even-numbered segments) and elytra (odd-numbered segments). In Eulepethidae, dorsal cirri are present only on segments 3 and 6, with branchiae starting on segment 8 onwards, while in Pholoinae, there are no dorsal cirri. Sigalionidae exhibit the most variability in the positioning of the dorsal cirri, either on all segments (*e.g.*, *Pisione* sp.), only on segment 3 (*e.g.*, *Pelogenia* sp.), or lacking dorsal cirri completely (most genera).

Beyond segment 19, the pattern varies throughout Aphroditiformia. In Aphroditidae, the segments alternate between elytra and cirri until the end of the body. In the polynoid sub-family Branchinotogluminae, the two last segments (20 and 21) both bear a pair of cirri, while the remaining members of the family with more than 19 segments have alternating cirri and elytra until segment 23, then the segments alternate between two with cirri, one with elytra, and so on until the last segment. Some polynoid genera lack elytra entirely on their posterior region (*e.g.* *Polynoe scolopendrina* Savigny, 1822), bearing only dorsal cirri. Sigalionidae have alternating elytra until segment 26, beyond which all segments bear elytra. In the genus *Pholoe* (Pholoinae), all segments beyond 23 bear elytra. In Acoetidae, segments having elytra or cirri alternate until segment 25, followed by two segments with cirri, one with elytra, two with cirri, one with elytra, and three segments with cirri.

All genera forming the sigalionid subfamily Pisioninae, as well as in *Metaxypsamma uebelackerae* (Sigalionidae), and in *P. aurifera* (Aphroditidae), elytra have been secondarily lost. In the latter, segments with palaeal fans and dorsal cirri alternate, following the typical pattern for Aphroditidae. Dorsal cirri are reduced but present on all segments in species found within the Pisioninae.

In addition to their position on the body, the overall shape of the elytra and their surface and border ornamentation are important taxonomic characters in species identification, but not at higher taxonomic levels.

### *Parapodia and chaetae*

Parapodia are most often biramous but the notopodium can be reduced or absent in some genera (Figure 3). The segments can either be elytrigerous (bearing a pair of elytra) or cirrigerous (bearing a pair of dorsal cirri). Instances of parapodia bearing both a dorsal cirrus and an elytron have been reported (see Darboux 1900) but probably correspond to developmental anomalies. The elytrigerous parapodia bear a pair of thick elytrophores on their dorsal side, directed dorsally, and on which the elytra are attached, while those cirrigerous parapodia bear cirriphores that are directed laterally. Ventral cirri are present on all parapodia, usually digitiform. The supporting notoaciculum is usually clearly visible, stout, pointed, and sometimes protruding in most families. In Eulepethidae, the neuroaciculum is T-shaped and never protrudes. Notochaetae are all simple, with a great diversity of shapes, thickness, and number. In the family Sigalionidae, most or all neurochaetae are compound, either in the form of spinigers (long, apically pointed terminal article) or falcigers (short, apically blunt terminal article).

### *Digestive system*

The digestive system is linear, with the mouth opening followed by a muscular proboscis (pharynx) connected to an intestine that contains paired, segmental lateral caeca (Figure 4C). The latter extend into the parapodia, showing ramification and exhibiting physiological differentiation (Darboux 1900; Fauvel 1959; Dales & Pell 1971). Studies have shown that the pharynx, intestinal wall, and the caeca contain digestive enzymes that exhibit absorptive characteristics (Welsch & Storch 1970).

### *Pharynx and jaws*

In most aphroditiforms, when extended, the pharynx opening is usually surrounded by papillae, and is armed with two pairs of beak-like jaws (Figure 4A). In Aphroditidae, some genera (e.g., *Aphrodita* and *Laetmonice*) lack jaws (Day 1962; pers. obs.), while in others, including those of Eulepethidae, are reported to be plate-like (Pettibone 1986). Beak-like jaws are also absent in the polynoid *Vampiropolynoe embleyi* Marcus & Hourdez, 2002, in which only plates remain (Marcus & Hourdez 2002).

In some members of the families Acoetidae, Polynoidae, and Sigalionidae, structures interpreted as venom glands have been observed at the base of the jaws (Wolf 1986). Contrary to the best-known example of piercing jaws in annelids (Glyceridae), the jaws studied by Wolf (1986) do possess a canal but no openings were present at the tip. In the families devoid of piercing jaws (Eulepethidae and Aphroditidae), Wolf (1986) did not observe any structure that is reminiscent of venom glands. Since then, no further studies have been carried out on the venom of aphroditiforms. In their review on venomics, von Reumont et al. (2014a) mentioned ongoing research on two species, a Polynoidae (*Harmothoe imbricata* (Linnaeus, 1767)) and a Sigalionidae (*Sthenelais boa* (Johnston, 1833)), in which preliminary data shows that scale worms seem to possess a diverse set of putative toxin homologs, similar to what was observed in the well-studied *Glycera* (Glyceridae) (von Reumont et al. 2014b).

## Biology and Ecology

### *Feeding*

The great majority of Aphroditiformia are predators, feeding on other annelids, small crustaceans, and mollusks (Fauchald & Jumar 1979; Jumars et al. 2015). Most are motile predators, but those that are commensal, or live inside tubes (*i.e.,* Acoetidae and some Eulepethidae and Sigalionidae) are mostly sit-and-wait predators.

### *Respiratory exchange and respiratory pigment*

Although Aphroditiformia have a small, closed vascular system, it contains no circulating respiratory pigment. Scale worms typically lack branchiae; however, some groups do possess these structures (*i.e.,* Eulepethidae, Polynoidae, Sigalionidae). In Eulepethidae, branchiae start on segment 8 and continue onwards, while in some hydrothermal vent Polynoidae (subfamilies Branchipolynoinae, Branchiplicatinae, Branchinotogluminae, and the branchiate *Thermopolynoe* (Lepidonotopodinae)) branchiae are present in addition to dorsal cirri and elytra, and are considered as an adaptation to the chronic hypoxia they experience (Hourdez & Lallier 2007). In scale worms, oxygen diffuses through the body wall, and it has been shown that in shallow-water Polynoidae, water is renewed along the surface of the body by cilia and not the oscillating motion of the elytra (Lwebuga-Mukasa 1970). The elytra form a roof under which water flow is directional.

Aphroditiformia were previously well known for lacking circulating respiratory pigments (Weber 1978); however, a globin is present and is located within the nerve cells (neuroglobin). Its function is unclear but it gives the nerve cord and prostomium a typical red color. Subsequently, the discovery of deep-sea hydrothermal vent polynoid species has changed this view. Most vent species are indeed red-colored and contain large amounts of hemoglobin (*i.e.* circulating globin) in their coelomic fluid (Hourdez et al. 1999a, b; unpublished data).

### *Reproduction and development*

Sexes are separate in Aphroditiformia (Wilson 1991). Gametes develop in the epithelium that lines the coelomic cavity and nearly mature gametes are released into the coelomic cavity where their maturation progresses (Daly 1974). Oocytes contained in the coelomic cavity usually cannot be directly fertilized, and studies suggest that an endocrine factor may be necessary for oocytes to finish maturation and be fertilizable, in a way similar to that of *Arenicola marina* (Linnaeus, 1758) (Howie 1961; Bentley & Pacey 1992). In the polynoid *Lepidonotus sublevis* Verrill, 1873, however, the oocytes are fertilizable after a brief incubation in seawater (Simon 1965). Copulation takes place in members of the sigalionid subfamily Pisioninae (details in corresponding chapter). The presence of spermathecae in the polynoid genus *Branchipolynoe* suggests copulation also occurs in this lineage (Jollivet et al. 2000).

One of the most detailed studies of larval development in Aphroditiformia is that of Pernet (2000) who worked on the three closely related symbiotic polynoids *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 (Bhaud & Cazaux 1987). These species produce planktotrophic larvae with a prototroch but no metatroch or food groove cilia. Feeding starts after the development of episphere cilia (Figure 5). 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 (Figure 6).

The presence of elytra on late-stage larvae is a key character to identifying Aphroditiformia in the plankton. These are, however, absent in the scaleless Pisioninae (Åkesson 1961). In *Pisione remota* (Southern, 1914), although the young larvae resemble those of Polynoidae (*e.g.* no metatroch) during metamorphosis, strong morphological differences appear. In particular, the first parapodia move forward and the prostomium retracts between these parapodia. The dorsal cirri are also found on all segments but remain short.

For annelids, five larval stages are described in the literature (Cazaux 1968; Bhaud et al. 1999): trochophore I, trochophore II, metatrochophore I, metatrochophore II, and nectochaete (bearing chaetae). While the trochophore stages are very similar for all annelid families, at the metatrochophore stage in scale worms, some adult characters are present and can be used to identify families. Among larval Aphroditiformia, Sigalionidae is the only family with compound chaetae while Acoetidae and Aphroditidae share the presence of thin, silken notochaetae, and in Eulepethidae, wide, distally truncated neuropodia bear the characteristic T-shaped acicula supporting the edge. Larval Polynoidae are identified, however, by the absence of these characters.

## Phylogeny and Evolution

### *Fossil record*

As for all soft-bodied animals, fossilization is rare and very few fossils are available. There are currently eleven species of fossils dating from 86 to 300 million years in age with clear affinities to Aphroditiformia (Table 2). Affinities to lower taxonomic levels remain uncertain, as distinctive characters are usually not well preserved or are too small. Most paleoaphroditiforms described to date have about 24 segments, except *Dryptoscolex matthiesae* Thompson, 1979 which has up to 52 segments (Fitzhugh et al. 1997). Luque et al. (2015) distinguished three basic body shapes in the currently described fossil species (Table 2): an oval shape reminiscent of Aphroditidae, a more elongated and flexible shape that is reminiscent of Polynoidae or Sigalionidae, and a slender and possibly stiff shape that could correspond to Pholoinae or other short-bodied Sigalionidae. Additional work and probably a revision are needed to better interpret the relationships among these three shapes. In particular, species with two of these basic shapes are attributed to the same name.

Table 2: General morphology and age of fossil species of Aphroditiformia known to date.

| Species | Morphology | Age (My) | Reference |
|---|---|---|---|
| *Dryptoscolex matthiesae* | Elongated and flexible | 300 | Fitzhugh et al. 1997 |
| *Fatuoscolex gemmatus* | Oval | 300 | Fitzhugh et al. 1997 |

| | | | |
|---|---|---|---|
| *Hystriciola delicatula* | Oval | 300 | Fitzhugh et al. 1997 |
| *Palaeoaphrodite adeliae* | Oval | 165 | Alessandrello et al. 2004 |
| *Palaeoaphrodite anaboranoensis* | Elongated and flexible | 250 | Alessandrello 1990 |
| *Palaeoaphrodite briggsiana* | Oval | 165 | Alessandrello et al. 2004 |
| *Palaeoaphrodite gallica* | Elongated and flexible | 165 | Alessandrello et al 2004 |
| *Palaeoaphrodite libanotica* | Oval | 94-100 | Bracchi & Alessandrello 2005 |
| *Palaeoaphrodite raetica* | Oval | 201-208 | Alessandrello & Teruzzi 1986 |
| *Protopholoe colombiana* | Slender and stiff | 86-90 | Luque et al. 2015 |
| *Protopholoe rhodanitis* | Slender and stiff | 165 | Alessandrello et al. 2004 |

### *Molecular phylogenies and major taxonomic changes*

In recent phylogenetic studies of Annelida, Aphroditiformia maintained its position within Errantia as part of Phyllodocida, a lineage that also includes Syllidae (Struck et al. 2015; Weigert and Bleidorn 2016). Aphroditiformia needs a systematic revision, and molecular studies combined with morphological data have been used to suggest some important modifications. In particular, studies such as Norlinder et al. (2012), Wiklund et al. (2005), and Struck et al. (2005) all strongly support the interpretation of the species formerly belonging to 'Pisionidae' as scaleless Sigalionidae, and that of *P. aurifera* as a scaleless member of Aphroditidae. Polynoidae forms the largest family, possibly a result of the fact that this family can be called the 'default' family. Essentially, the species placed in this family lack morphological synapomorphies. Although this situation is not satisfactory, Polynoidae does form a monophyletic group in combined molecular and morphological studies (Norlinder et al. 2012; Gonzalez et al. 2018). Since 2012, the subfamily Iphioninae has been recovered independent of Polynoidae, often forming a clade with Acoetidae, and, as a consequence, Norlinder et al. (2012) elevated the polynoid subfamily Iphioninae to the family level (= Iphionidae).

It is important to note however that the relationship and position of Acoetidae with respect to Iphionidae (Iphioninae) and Polynoidae warrants further detailed molecular and morphological studies. Acoetidae and Iphionidae were recovered in a clade sister to Polynoidae by Gonzalez et al. (2018) using combined molecular and morphological analyses, and again by Zhang et al. (2018) using only molecules, both with higher support than first reported by Norlinder et al. (2012).

Based on the phylogenetic studies published by Zhang et al. (2018) and Gonzalez et al. (2018), Eulepethidae and Aphroditidae are deeply positioned in relationship to other aphroditiform families (Figure 5). While the relationships between the latter two families is unresolved in Norlinder et al. (2012), both Zhang et al. (2018) and Gonzalez et al. (2018) show good support for Eulepethidae being sister to all remaining scale worm families. Sigalionidae is consistently recovered as a sister group to Polynoidae, and morphological analyses indicate their compound chaetae are secondarily derived. 'Pholoidae' forms a clade within Sigalionidae that is sister group to Acoetidae – Polynoidae. Based on these results, Gonzalez et al. (2018) suggested that Pholoidae be treated as members of family Sigalionidae.

The following chapters deal with the separate families of Aphroditiformia in greater depth.

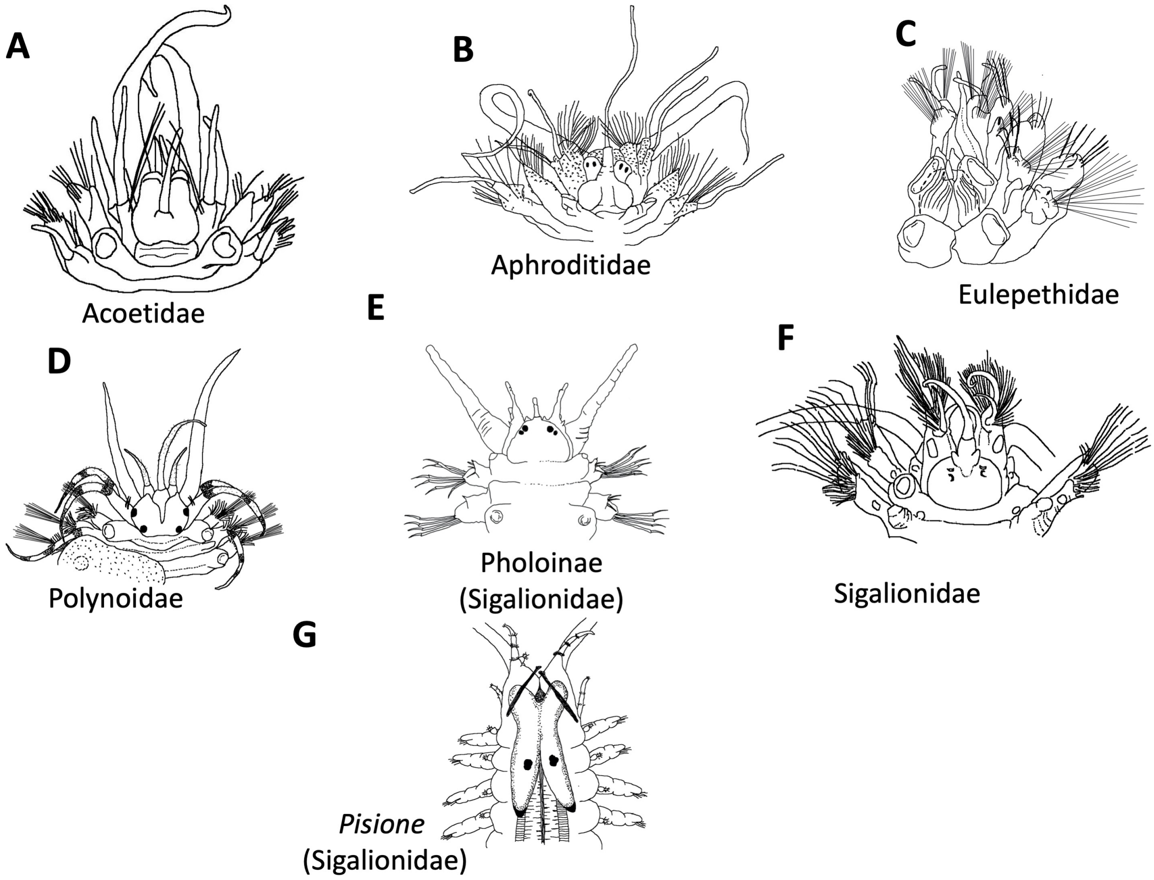

Figure 1: Dorsal view of the anterior parts of different Aphroditiformia showing the prostomium. A. *Panthalis oerstedi* Kinberg, 1856 (Acoetidae); B. *Laetmonice hystrix* (Savigny & Lamarck, 1818) (Aphroditidae); C. *Grubeulepis augeneri* Pettibone, 1969 (Eulepethidae); D. *Harmothoe extenuata* (Grube, 1840) (Polynoidae); E. *Laubierpholoe swedwarki* (Laubier, 1975) (Sigalionidae, Pholoinae); F. *Sthenelais brachiata* Imajima, 2003 (Sigalionidae); G. *Pisione remota* (Southern, 1914) (Sigalionidae). Redrawn after Barnich and Fiege, 2003 (A, C, D), Laubier 1975 (E); Imajima, 2003 (F), Akesson, 1961 (G).

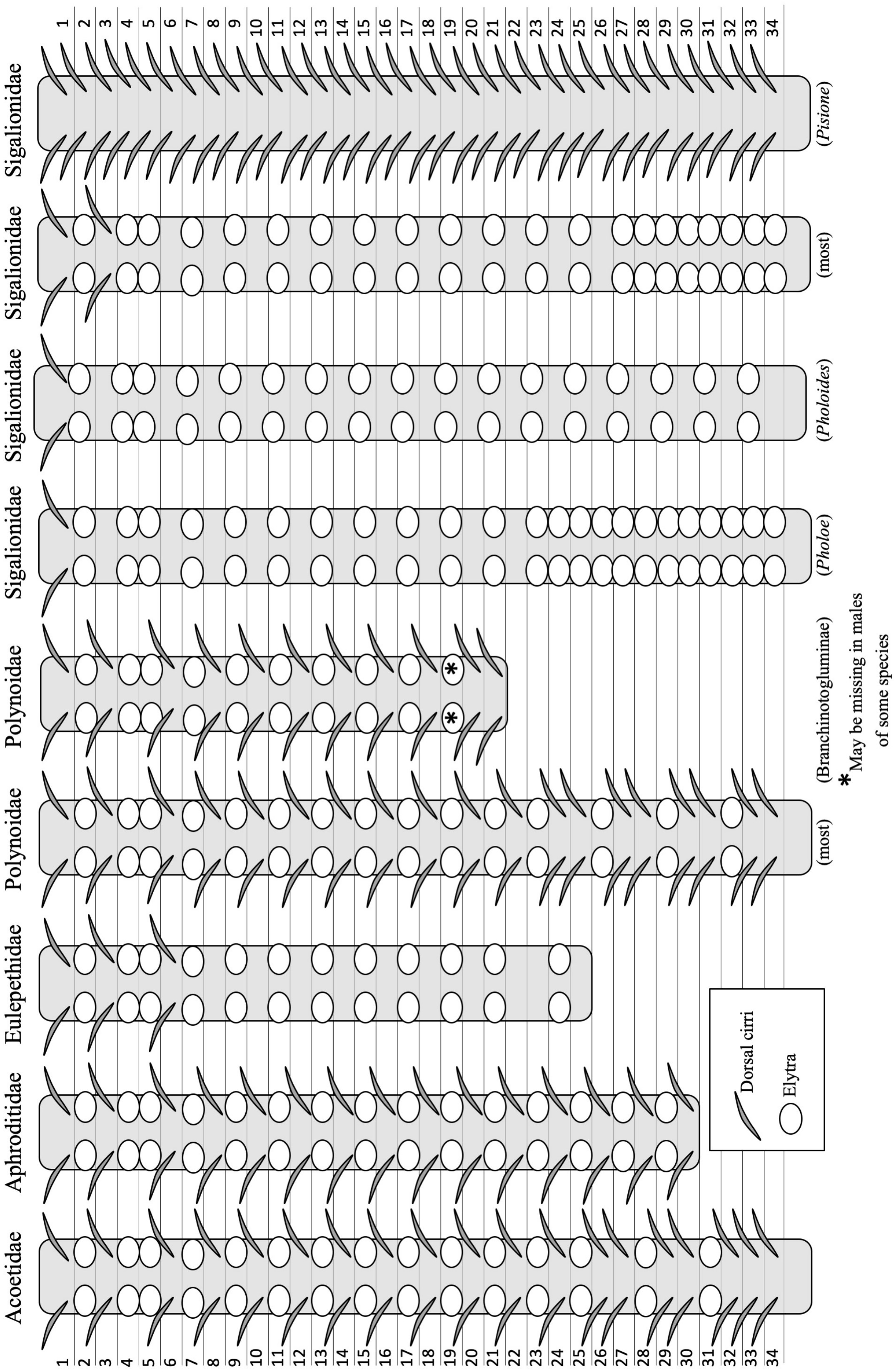

Figure 2: Elytral patterns and position of dorsal cirri in Aphroditiformia for the first 34 segments.

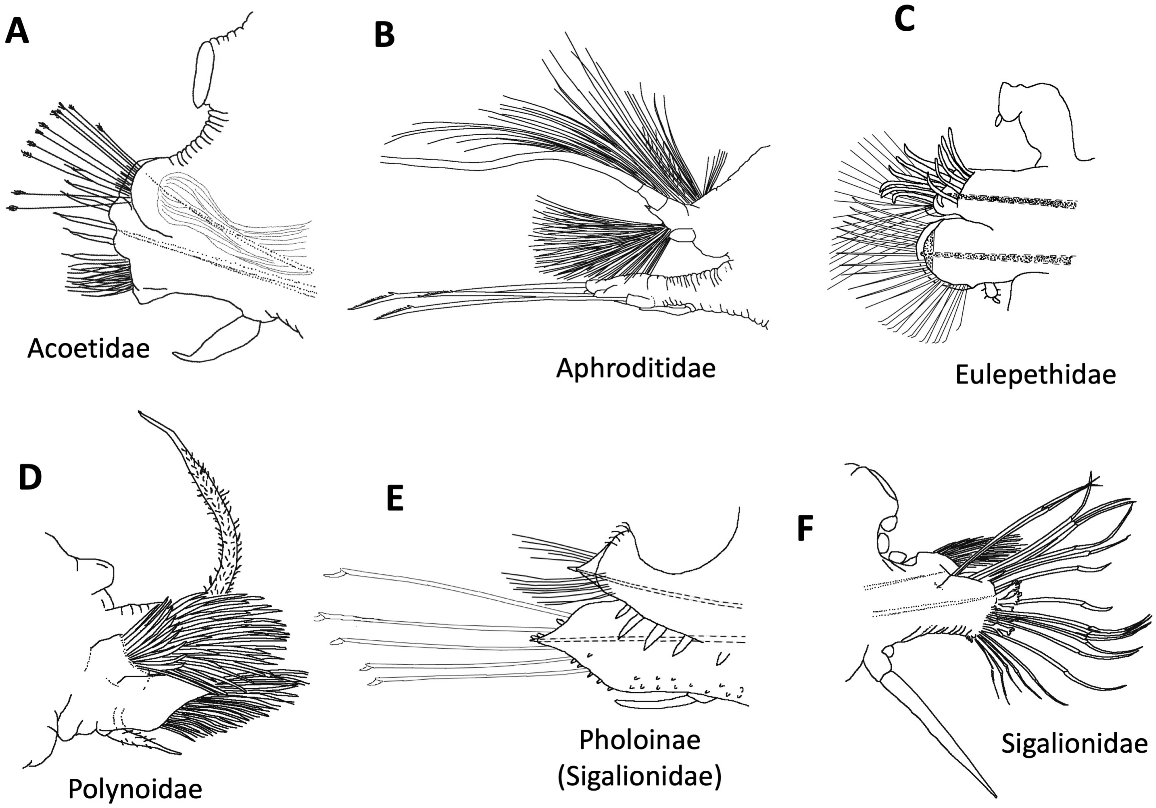

Figure 3: Parapodial morphology in Aphroditiformia. A. *Acoetes jogasimae* (Izuka, 1912) (Acoetidae); B. *Laetmonice producta* Grube, 1877 (Aphroditidae); C. *Grubeulepis augeneri* Pettibone, 1969 (Eulepethidae); D. *Harmothoe imbricata* (Linnaeus, 1767) (Polynoidae); E. *Pholoe longa* (O.F. Müller, 1776) (Sigalionidae Pholoinae); F. *Sthenelais brachiata* Imajima, 2003 (Sigalionidae). Redrawn after Barnich and Fiege 2003 (C), Imajima 1997a (A, D), Imajima 1997b (B, F), Pettibone 1992 (E).

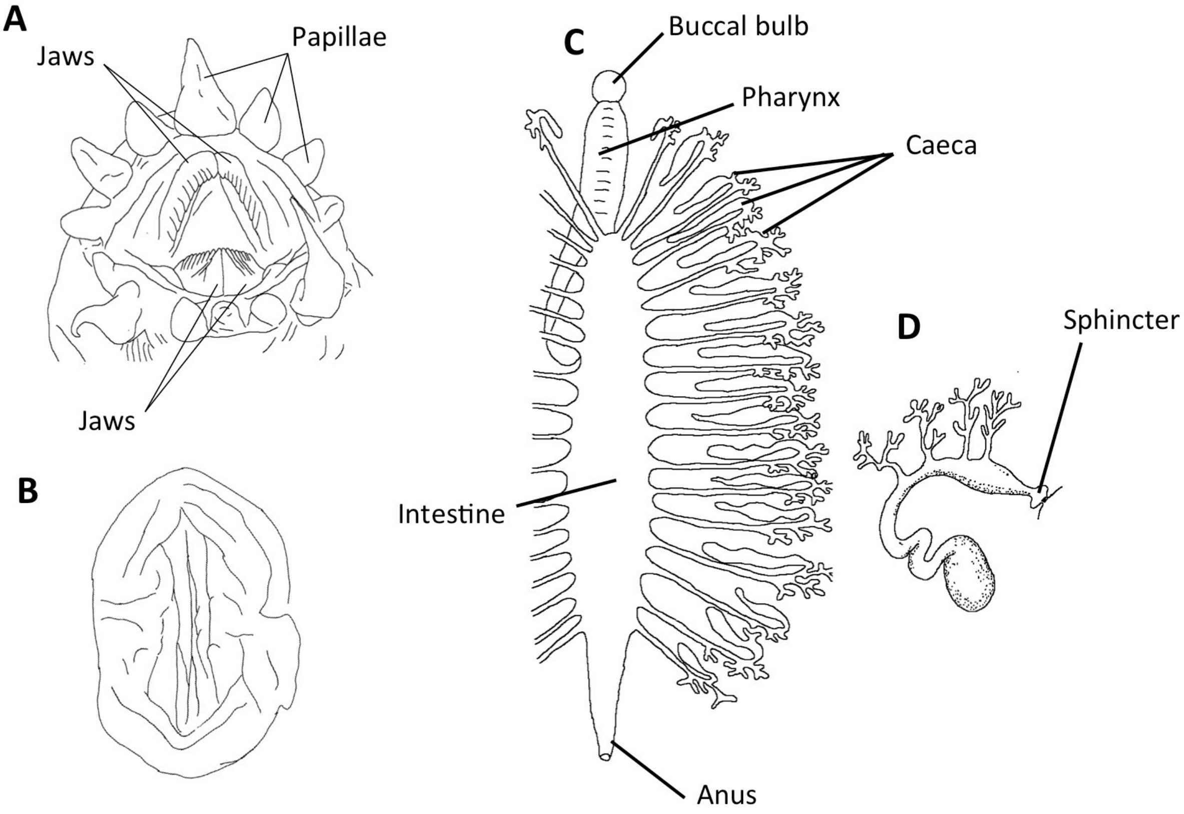

Figure 4: Pharynx and digestive system. A. Pharynx opening of the polynoid *Lepidonotopodium piscesae* Pettibone, 1988. B. Pharynx opening of the aphroditid *Laetmonice producta* Grube, 1877. C. Digestive system of the aphroditid *Aphrodita aculeata* Linnaeus, 1758 (redrawn after Brusca and Brusca 1990). D. Detail of a caecum from *A. aculeata* (redrawn after Darboux 1900).

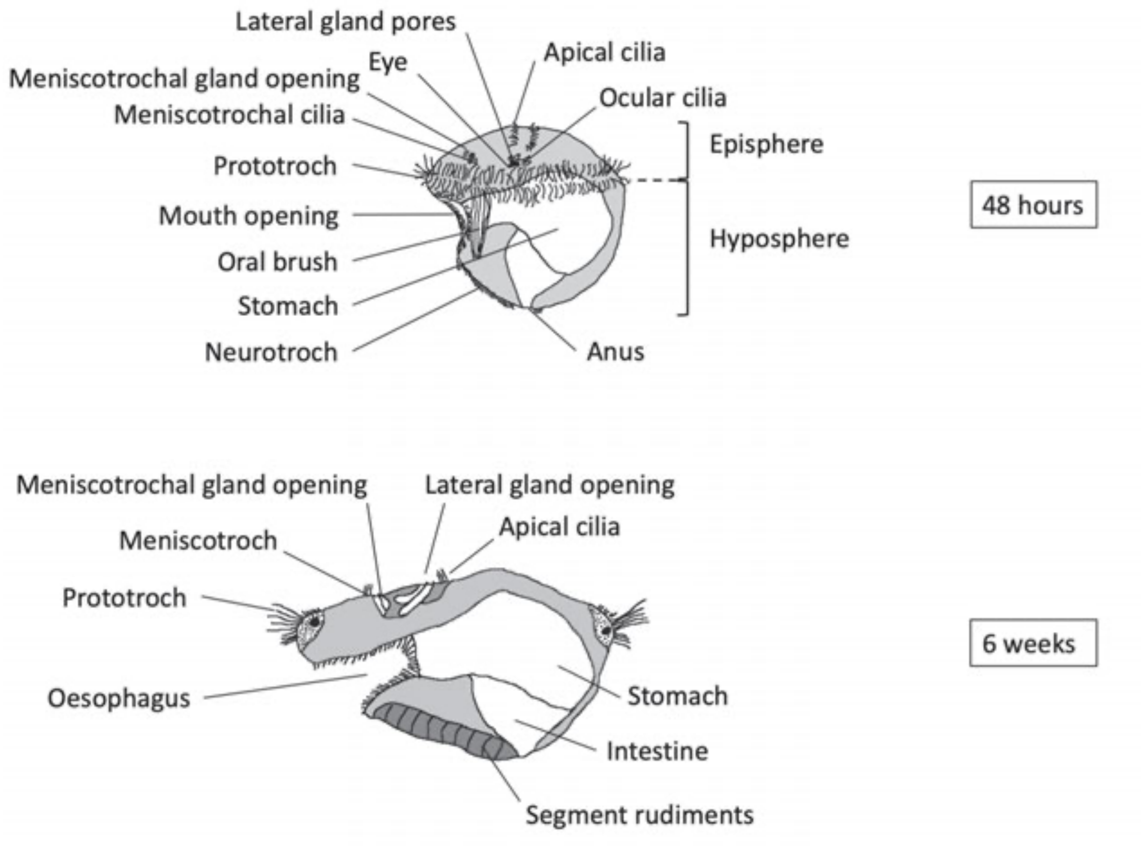

Figure 5: Early development of *Arctonoe* spp. after 48 hours and 6 weeks (schematized after Pernet 2000).

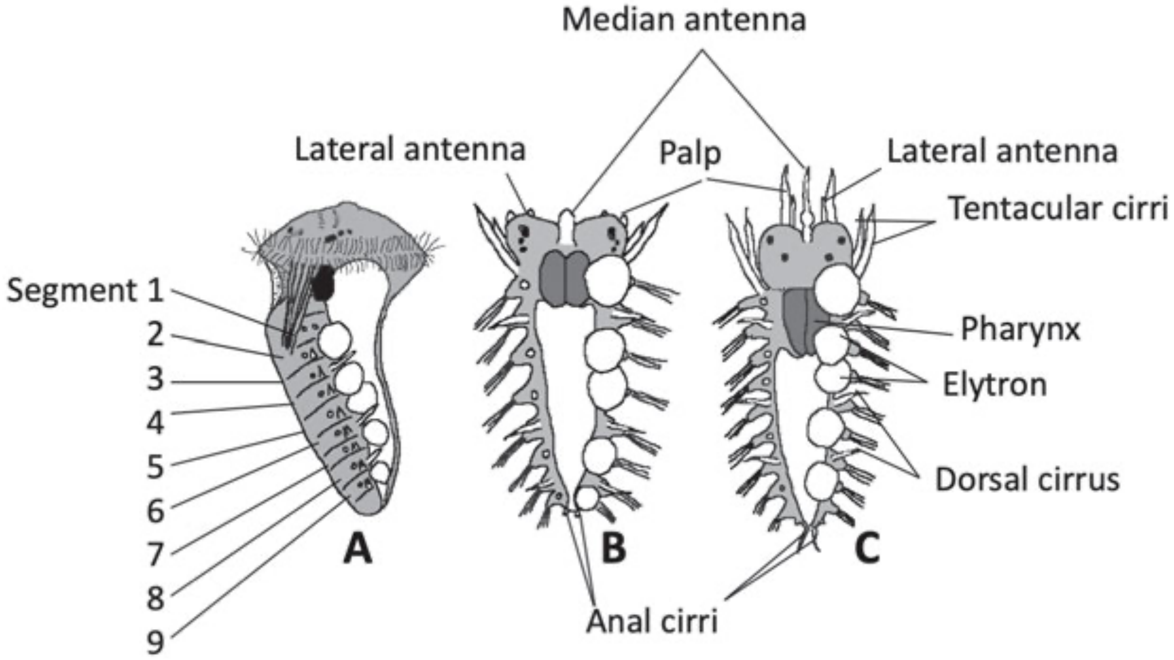

Figure 6: Metamorphosis of *Arctonoe* spp. (schematized after Pernet 2000). A, Early metamorphosis with a now elongated hyposphere and appearance of dorsal cirri and elytra. Lateral view. B, appearance of adult head appendages. Prototroch and oral brush have disappeared. Dorsal view. C, Juvenile. Dorsal view.

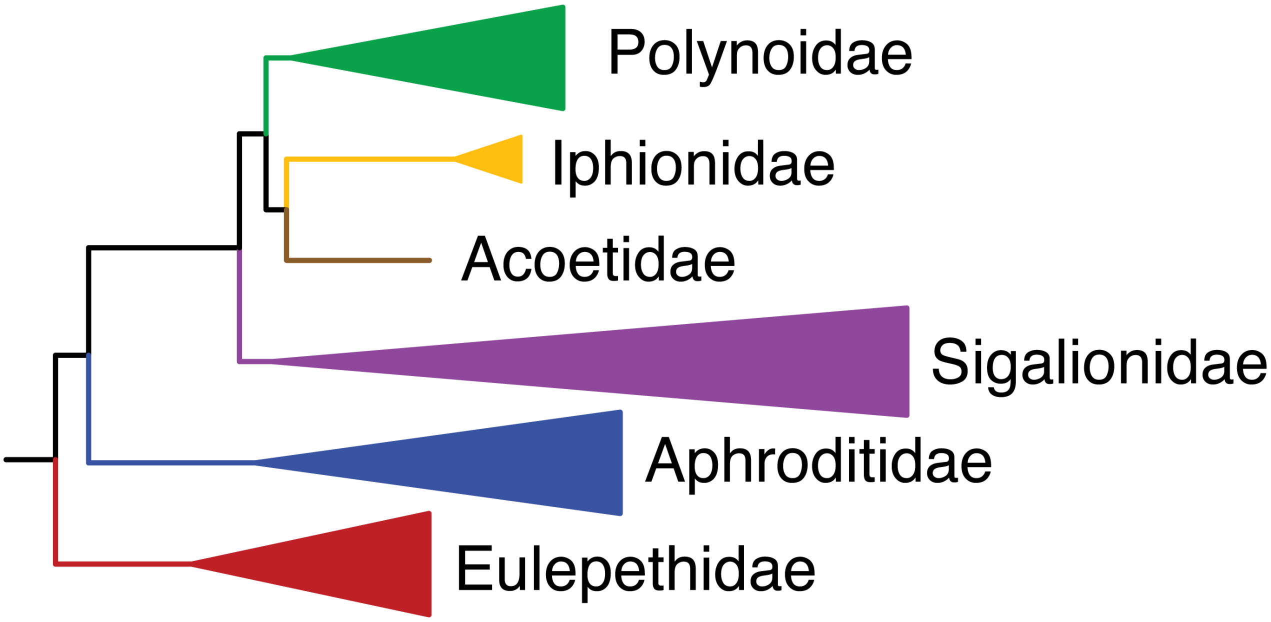

Figure 7: Schematic representation of the current phylogenetic and systematic view of Aphroditiformia based on combined molecular and morphological analyses (from Gonzalez et al. 2018). Status of Iphionidae remains in question, but continues to be recovered independent of Polynoidae (see Zhang et al. 2018). This lineage is here considered as subfamily Iphioninae in the handbook chapter on Polynoidae. Sigalionidae includes 'Pholoidae' (see Gonzalez et al. 2018; Zhang et al. 2018) and the former 'Pisionidae' (see Norlinder et al. 2012).

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