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## Acoetidae Kinberg, 1856

Stéphane Hourdez, Karen J. Osborn and Brett C. Gonzalez

### Introduction

Acoetidae is the fourth largest family within Aphroditiformia and includes eight genera and 58 species (Figs. 1-10). Species discovery was most prominent between 1817-1899 (n=16) and between 1900-1988 (n=25). In Pettibone's (1989) revision of Acoetidae, an additional 13 species were added, however, since then, only four species have been described. The most recent acoetid description was by Jimi et al. (2019) for a new species of *Polyodontes* from Japan. Most of our knowledge on Acoetidae stems from *Panthalis oerstedii* Kinberg, 1856 – being used by early scientists to understand structures of the brain, nervous system and various morphological novelties.

Acoetidae comprises annelids with an unusually elongated body ( $\leq 2$  m) and a prolific number of segments ( $> 300$ ). The true diversity of Acoetidae is unknown, but they have been found so far in diverse bottom types between the intertidal zone and 1500 m. The morphology of Acoetidae largely agrees with Polynoidae and Aphroditidae, possessing only simple chaetae and having dorsal cirri on nonelytragerous segments. Acoetids only inhabit self-constructed tubes, which they make from tightly woven feltage notochaetae and sediment (Fig. 4A-B). Unlike other scale worms, acoetids may possess highly modified prostomiums bearing large elaborate eyes (ommatophores), probably an adaptation to their sit-and-wait predatory lifestyle (Figs. 1-3, 4B-C). These highly evolved structures may occupy the entire width of the prostomium or be pedunculate. Early literature suggested that Acoetidae possessed several morphological apomorphies (*i.e.*, ommatophores, feltage chaetae, denticulate jaws), but continued discovery across scale worms has proven that these structures are not unique, since they are now known to be shared among the aphroditiform families.

### Morphology

Acoetids are among the largest of the scale worms, having a dorsoventrally flattened body that is relatively broad in its entirety, reaching upwards of 300 segments or more. In cross section they appear rectangular, with blunt subconical parapodia and elytra positioned towards their lateral borders (Pettibone 1989).

Nearly all described Acoetidae are from partial specimens, however, in general, acoetids have a considerable size range, being up to 1 m or more in length and over 40 mm wide. Since acoetids are rarely collected whole, maximums and minimums in size and segment number is often unknown. *Polyodontes maxillosus* (Ranzani, 1817) is considered one of the largest acoetids, reportedly reaching a length of 2 m (Saint-Loup 1889), while *Eupolyodontes batabanoensis* Ibarzábal, 1988 is known to have upwards of 400 or more segments.

Body coloration is minimal in acoetids, often stated as being “without” (Fig. 4D). However, dark transverse bands along the dorsum are common throughout Acoetidae and hues of brown and yellow are reported from several species of *Polyodontes*. Pigmentation is most noticeable on the elytra, often exhibiting bright colours and patterns (e.g., *Polyodontes kuroshio* Jimi, Tomioka, Orita & Kajihara, 2019; Fig. 4D). Both the dorsum and venter are smooth and lacking papillae. Papillae may be present on the prostomium and prostomial appendages, including tentaculophores, ceratophore of the median antenna and nuchal regions. The dorsal body surface is often transversely grooved and may obscure segmental boundaries. The ventral nerve cord is protected by a median longitudinal ridge.

Similar to other scale worms, elytra in Acoetidae are attached to bulbous elytraphores on segments 2, 4, 5, 7 and then alternate until segment 23. Beyond that point, the pattern can be variable among families (See Aphroditiformia chapter). In acoetids, elytra and dorsal cirri usually alternate until the end of the body (Fig. 4D). Jimi et al. (2019), however, reported changes to this pattern in *Polyodontes kuroshio* where the alternating pattern stopped on segment 23, followed by consecutive elytra being present on segments 23-26, then returning to an alternating pattern posteriorly to the end, but on every other even segment. On segments without elytra, indistinct dorsal tubercles are present.

Generally, the head and prostomial region in Acoetidae is highly developed and contains well-developed sense organs (Figs. 1-3). The tentacular segment (segment 1) is directed anteriorly, fused to the prostomium (Fig. 2I). The palps are ventral in all acoetids and are often long and tapered, being smooth, papillate or a combination of both. In *Eupolyodontes*, palps are much smaller than in other genera and rarely longer than the ommatophores.

According to Pettibone (1989), there are four distinct types of prostomia, each correlated to the degree of ommatophore development. The simplest prostomial type (type 1) is found in species of *Euarche* (Figs. 1B, 3A) and *Eupanthalis* (Figs. 1C, 3E), being oval or bilobed and having two pairs of sessile eyes. At a quick glance, members of this form resemble Polynoidae. The sessile eyes may be lacking (e.g., *Euarche mexicana* Pettibone, 1989), or, with the anterior pair slightly larger (e.g., *Eupanthalis aena* (Moore, 1903)). The second prostomial type (type 2) is found in *Zachsiella* (Fig. 2H) and *Eupolyodontes* (Figs. 1D, 3B), being wide and bilobed with large anteriorly projecting ommatophores that occupy most of the prostomium. Sessile eyes are lacking in *Eupolyodontes* but are present in *Zachsiella*. The third prostomial type (type 3) is present in *Acoetes* (Figs. 1A, 3D), *Panthalis* (Fig. 1F) and *Polyodontes* (Figs. 1G, 3C). Within these genera, the prostomium is bilobed, bearing a pair of bulbous ommatophores that extend anteriorly. The ommatophores may have a narrow neck like in *Acoetes* and *Polyodontes* (e.g., *Acoetes melanonota* (Grube, 1876)), or, as in *Panthalis*, lack a narrow neck completely (e.g., *Panthalis alaminosae* Pettibone, 1989). Ommatophores lack colour in *Panthalis*, but are coloured in *Acoetes* and *Polyodontes*. Sessile eyes are present in *Acoetes* and *Polyodontes*, but absent in *Panthalis*. The most peculiar type of prostomium (type 4) is represented by *Neopanthalis* (Fig. 1E), having anteriorly extended ommatophores that are fused along their midline. Sessile eyes are absent.

Most acoetids have three prostomial antennae; a pair of lateral antennae and a median antenna. The position of the lateral antennae corresponds to the prostomial type: type 1, lateral antennae are visible and anteriorly positioned (Fig. 1C); type 2, they are anteriorly positioned between the ommatophores (Fig. 1D); type 3, they are attached ventrally on the ommatophores, barely visible dorsally (Fig. 2J); and in type 4, the lateral antennae are attached on the distal tip of the fused ommatophores (Fig. 1E). Lateral antennae may be

hidden completely from dorsal view in some species (*e.g.*, *Acoetes congoensis* Pettibone, 1989). The median antenna in Acoetidae consists of a basal ceratophore and a distal ceratostyle, often referred to as the median occipital antenna. All genera except *Eupanthalis* have a well-developed median antenna (Fig. 1C). In some species of *Eupolyodontes*, the median antenna is small or even absent (*e.g.*, *Eupolyodontes thomassini* Pettibone, 1989). Prostomial branchiae (fleshy appendages) may be present in some species of *Eupolyodontes* (*e.g.*, *Eupolyodontes amboinensis* Malaquin & Dehorne, 1907), however, the true function of these structures is unknown (Figs. 4B-C).

Nuchal organs in Acoetidae are referred to as nuchal lobes, presumed to be present in some form in all acoetids. These lobes are positioned between the posterior region of the prostomium and the dorsal surface of segment 2. In most genera, only a single nuchal lobe is present, but in *Eupolyodontes* it can be bilobed (Figs. 1D, 3B). Nuchal lobes may be papillate and often are the attachment point for the occipital antenna.

Segment 1 envelops the prostomium laterally. The tentaculophores of the dorsal- and ventral tentacular cirri are positioned lateral or ventral to the prostomium (Figs. 2I, 6A) and are supported by one or two aciculae (*e.g.*, *Panthalis*). If present, notochaetae may be found in single or multiple groups along the tentaculophores (*e.g.*, *Neopanthalis*, *Panthalis*, *Acoetes* and *Polyodontes*). Acicular lobes may be present (*e.g.*, *Eupolyodontes amboinensis*) as well as papillae. The ventral tentacular cirrus is usually longer than the dorsal tentacular cirrus, but is variable, as is the case in *Eupolyodontes cornishii* Buchanan, 1894 where the dorsal tentacular cirrus is longer. In *Acoetes southcarolinensis* Pettibone, 1989, the tentacular cirri are bulbous with filamentous tips. Pigment along the tentacular cirri may be present as either spots or bands.

Acoetids have a ventrally positioned mouth, posterior to any prostomial appendage. Like other scale worms, the lips are the only vestige of the peristomium (Rouse and Pleijel 2001). The anterior, lateral and posterior lips of the mouth are formed by the first three segments. Radial folds are often present. All acoetids have an eversible large muscular pharynx that greatly extends beyond the palps or tentacular cirri (Fig. 5). The distal border of the pharynx is crowned by a circle of terminal papillae: 13 pairs in *Euarche* and *Eupanthalis*; 15 pairs in

*Panthalis* and *Acoetes* with middorsal and midventral papillae longer and situated on lobulated bases; 19 pairs in *Polyodontes* with middorsal and midventral papillae longer and situated on lobulated bases; and up to 39 pairs of closely-set papillae in *Eupolyodontes* with both middorsal and midventral papillae long and tapered.

As in most scale worms, acoetids have four strongly hooked jaws (Fig. 5C-D), presented as one dorsal and one ventral pair, positioned just inside the lumen of the everted pharynx. Each jaw has 7-17 lateral teeth, but may be as little as two depending on the size of the animal. *Acoetes mohammadi* Pettibone, 1989 is reported to lack lateral teeth, but it was noted in the description that it may be due to wear. In his study of jaws, Wolf (1986) noted that acoetid (referred to as polyodontid) jaws differ from Polynoidae and Sigalionidae in that the ventrolateral plate is fused to the concave margin of the fang, being dentate along the outer edge.

Segment 2, or buccal segment (Fig. 6B), is modified similarly as in other scale worms and is the first elytragerous segment. The ventral buccal cirri are enlarged, anteriorly directed and lateral to the mouth. Resembling the tentacular cirri, both the cirrophore and style are thicker and longer than they ventral cirri of the following segments. The parapodia are biramous or subbiramous and are oriented laterally. Watson (1895) noted that segment 2 parapodia were quite important in the manipulation of feltage chaetae for tube construction (see Anatomy section for terminology), referring to them as 'weaving feet'. The notopodium is supported by a thin aciculum and notochaetae may be present (Fig. 8A). The neuropodium has a stout aciculum and neurochaetae are often lanceolate and slender. Various prechaetal and postchaetal lobes may be present. Pettibone (1989) referred to these structures as anteroventral bracts, but "bract" is a botany term referencing leaf structures. In an attempt to remove confusion, the term 'neuropodial lobe' (*sensu* Aungtonya 2005) should be implemented for any structure covering the base of the chaetae, similar to what has been implemented in Sigalionidae genera.

Acoetid elytra generally have a simple oval or round shape that is occasionally elongated transversely (Fig. 4D). The elytra are small in comparison to the size of the worms, attached to bulbous, sometimes papillated, elytraphores positioned on the lateral borders of the

body (Fig. 6C,E). Their position often leaves the midline of the dorsum uncovered. The elytra do overlap anteriorly to protect the prostomial appendages and are often found overlapping in the narrowed, posteriormost segments. Most acoetids have thin transparent elytra that are smooth and flexible, but thick opaque elytra occur in *Eupolyodontes thomassinia* Pettibone, 1989, and *Eupanthalis edriophthalma* (Potts, 1910) is reported to have slightly inflated elytra. Similar to the deep incisions found throughout the Pelogeniinae (Sigalionidae), acoetids bear lateral pouches on their posterior elytra. These pouches (=pockets) may begin as early as the third elytral pair (e.g., *Eupolyodontes hartmanae* Pettibone, 1989), or, may be absent completely (e.g., *Acoetes congoensis*). Surface ornamentation is rarely documented, but microtubercles were identified in *Euarche tubifex* Ehlers, 1887 (Salazar-Vallejo et al. 2014) and surface areolae are common throughout species of *Acoetes* and *Polyodontes*. Colour is highly variable on acoetid elytra, and may be restricted to the lateral and posterior margins, or throughout the surface of the elytra. Colour patterns are also present in some species and may be a single repeating pigment spot or coloured crescent shape along the interior elytron border as in *Zachsiella nigromaculata* (Grube, 1878), yellow margins as in *Polyodontes lupinus* (Stimpson, 1856) or completely bright orange with light spots as in *Polyodontes vanderloosi* Barnich & Steene, 2003.

In addition to the dorsal (tentacular) cirri of segment 1, dorsal cirri are located on all nonelytragerous segments (Fig. 6C-D,F), generally consisting of a short cirrophore and styles that do not project beyond the tips of the neurochaetae. An exception to this exists on segments 3, 6 and 8, where styles may extend beyond the neurochaetae as the parapodia become modified. From segment 9 posteriorly (Fig. 6E), cirrophores are wide and appear inflated, having short subulate or wide conical styles. Aside from the buccal cirri (segment 2), the ventral cirri are all short and subulate, most often attached near the base of the parapodia (Fig. 6).

Parapodial branchiae are common throughout Acoetidae, forming on the anterior, dorsal and posterior sides of the parapodia and the base of the elytraphores/cirrophores (Fig. 7A-B). In *Polyodontes vanderloosi*, these branchiae can also be found ventrally. Acoetid branchiae have a thick cuticle and are extensions of the coelom, similar to the branchiae

found in *Branchipolynoe* (Polynoidae) (Hourdez and Jouin-Toulmond 1998). Not all segments bear branchiae and their presence may be restricted to specific body regions or segments. Their appearance is variable, appearing as digitiform, bulbous, filamentous or arborescent projections and species may exhibit more than one form throughout their body. Larger species of *Eupolyodontes* and *Polyodontes* will exhibit well-developed branchiae, while smaller species (*e.g.*, *Euarache*, *Eupanthalis*, *Zachsiella*, *Neopanthalis*, *Panthalis*) may have few to no branchia.

Segments 3-8 in Acoetidae can be considered as transitional segments (Fig. 6C-D). Moving posteriorly from segment 3, the parapodia gradually modify their appearance; the notopodium becomes smaller and less pronounced, while the neuropodium becomes larger, often with the development of neuropodial lobes. If present, capillary notochaetae become shorter and fewer in number. Pettibone (1989) divided the neurochaetae of these segments into three distinct groups (group 1, 2 and 3) based on their position (lower, middle and upper), respectively (Figs. 8-9). The phylogenetic significance of these groups remains to be tested, but recent acoetid descriptions continue to reference these groupings (see Jimi et al. 2019). Neurochaetae of group 1 (lower; *i.e.*, infraacicular) are slender with gently curving tapered tips and large basal spinules, becoming tightly arranged distally; group 2 (middle; *i.e.*, acicular) neurochaetae are stout, acicular with rounded or hooked tips, generally smooth and with aristae; and group 3 (upper; *i.e.*, supraacicular), neurochaetae are lanceolate with spinules, tapering distally (Fig 8B). Upper neurochaetae (group 3) may be completely absent in these segments.

From segment 9 posteriorly, the parapodia go through another major transformation, marking the start of the notopodial feltage chaetae ("spinning glands" (Fig. 6E-F); see below). To accommodate these spinning fibres, the notopodium enlarges to about half the size of the neuropodium, supported by a thin notoaciculum and a stout neuroaciculum. Feltage chaetae may be absent in the posteriormost segments. Internally, the feltage notochaetae appear rope-like or coiled, extending inward towards the middle of the body cavity. The feltage chaetae exit via a slit on the underside of the notopodium. Capillary notochaetae may also be present in some species of *Euarache*, *Eupanthalis*, *Acoetes* and *Polyodontes*. The neurochaetae continue to be identified as the beforementioned three



groups, however, group 3 (upper) neurochaetae are further divided from segment 9 posteriorly into 'type a' and 'type b' (Pettibone 1989). Neurochaetal morphology of the group 3 subdivisions are genera specific (Figs. 8B-C, 9). In general, the appearance of type a (group 3a) are long and stout, resembling a combination of aristate and penicillate, while type b (group 3b) are short and slender. Specifically, type "a" neurochaetae in *Euarche*, *Eupanthalis*, *Neopanthalis* and *Polyodontes* are long and lanceolate, tapering distally to fine tips; in *Zachsiella*, they are long, acicular and aristate with spinules; in *Eupolyodontes* they are long and penicillate with a double brush; in *Panthalis* they are long, penicillate with short rows of spinules subdistally; and in *Acoetes* they abruptly taper to slender tips with long spinules (pseudopenicillate), as well as rows of spinules subdistally. Group 3a neurochaetae emerge from an anterodorsal neuropodial lobe opposite the exit slit for the feltage notochaetae, allowing them to assist in manipulating the feltage fibres. Type "b" neurochaetae are typically shorter, and may be hidden by the notopodium. Their appearance is variable, tapering to sharp tips with whorls of spinules along the shaft. Across acoetids, the middle neurochaetae are all stout and acicular, often aristate or with spinules along the shaft. The lower neurochaetae are numerous, lanceolate, often bearing aristae or other scattered spinules.

External nephridial papillae are absent.

The acoetid body ends with a small pygidium (Fig. 4D), although morphological characterization is lacking from most species as the specimens are often incomplete. In *Acoetes pleei* Audouin & Milne Edwards, 1832, the wide or bulbous anus is terminal, but is dorsally positioned in *Polyodontes vanderloosi*. Anal cirri are present, but are typically not longer than the dorsal cirri of earlier segments.

## **Anatomy**

Given that Acoetidae is one of the smaller families within Aphroditiformia, it is of no surprise that little information exists on their overall anatomy. Claparède (1868) provided the first detailed description of the neurochaetae variation and the presence of unusual

cord-like structure within the notopodia (Figs. 6-9). Eisig (1887) provided great detail of the cord-like structure in *Polyodontes maxillosus* and established the term “spinning glands” and “spinning fibres”. As mentioned below, the only detailed observations on tube construction (for *Panthalis oerstedii*) was provided by Watson (1895) from small aquaria. More recently, Pflugfelder provided the first histological investigations into the ommatophores (Fig. 10), notopodial chaetal sacs and the excretory organs in select species of *Eupolyodontes* and *Polyodontes* (Pflugfelder 1932, 1934). In 1963, Åkesson described the cerebral and internal morphology of the brain in *Panthalis oerstedii* (Åkesson 1963). The only other published observations for Acoetidae were by Storch (1968) on the general segmental musculature in *Panthalis oerstedii*, and by Wolf (1986) on the presence of putative venom glands in piercing jaws across Aphroditiformia.

The most detailed account of the nervous system of an acoetid was given by Åkesson (1963) for *Panthalis oerstedii*, showing a bilobed brain and corpora pedunculata (mushroom bodies) that is similar in architecture found in the aphroditid *Aphrodita aculeata* Linnaeus, 1758, the polynoids *Lepidonotus clava* (Montagu, 1808) and *Harmothoe areolata* (Grube, 1860) and the sigalionids (Örsted, 1845) and *Sthenelais cf. limicola* (Heuer & Loesel 2009; Heuer et al. 2010). In a detailed study, these complex structures are morphologically reminiscent of that of insects and are consistent with their active lifestyle and the important role of the eyes (paired mushroom body neuropils, unpaired midline neuropils and olfactory glomeruli; Heuer and Loesel 2009; Heuer et al. 2010). The large stalked ommatophores of *Panthalis* are partially invaded by the corpora pedunculata, comparable to what was observed in *Polynoe scolopendrina* Savigny, 1822 (Polynoidae; Hanström 1927). The extent of this invasion across other genera with ommatophores is unknown. A large central neuropile is present and is surrounded by large- to medium sized neurons. Five mesodermal strands penetrate the cerebral ganglion, corresponding to the medial antennae and the paired- lateral antennae and palps. Åkesson noted that the variable positions of the prostomial appendages (*i.e.*, lateral antennae, palps and median antenna) complicates their innervation to the brain. Since Åkesson (1963), there have been subsequent evaluations of the nervous system in *Panthalis oerstedii* by Orrhage (Orrhage 1991; Orrhage and Müller 2005), confirming previous accounts while further elucidating the orientation and innervation of palp and antennal nerves in relation to the brain and the circum-oesophageal nerve ring.

Pflugfelder (1932) characterized the fine structure of the eyes (Fig. 10) in *Polyodontes tidemani* Pflugfelder, 1932 and in *Eupolyodontes amboinensis* (as *E. sumatranus*). In his remarks he noted that acoetids possess unusual stalked eyes with proportions unlike those of other annelids. The simple (Fig. 10A) or non-stalked eyes of acoetids are similar to those found in other scale worms, being surrounded by a thin layer of non-pigmented epithelium. The sensory- and supporting cells can be distinguished within the retina and are surrounding the crystalline body and connecting fibrils. The supporting cells are uniquely flask-shaped under the rhabdoms and Pflugfelder noted that these supporting cells provide greater support than those in other scale worms. In comparison, the stalked eyes (Fig. 10B) are quite different from the eyes of other annelids, often so large that they distort the prostomium and its appendages. In the centre of the eye there is an iris-like diaphragm and a pupil clearly visible. This diaphragm in Pflugfelder's illustrations for *Eupolyodontes amboinensis* clearly subdivides the ommatophore into anterior and posterior sections. The anterior refractive body is domed shape above the pupil. Both the cornea and the anterior chamber of the eye are crystal clear. The posterior refractive body (below the diaphragm) makes up the bulk of the ommatophore, with the retina and pigment cells lying distally. Surprisingly, the pedunculate eyes of *Polyodontes* and *Panthalis* are similar to that of *Eupolyodontes*, however, their proportions are more elongate (Fig. 10C). The fine structure of the ommatophores are very similar to the simple eyes, with flask shaped sensory cells and well-defined rhabdoms. A strong optic nerve is present and leads into the central neuropile (Pflugfelder 1932; Åkesson 1963). Åkesson (1963) noted that the second pair of eyes (=simple eyes) are likely rudimentary and non-functional in *Panthalis oerstedii*, with their nerve fibres seemingly not connected. It is unclear if these eyes lack function in all species of *Panthalis* or across other acoetid genera with simple eyes. Surprisingly, if the large ommatophores are damaged in *Panthalis*, they do not regenerate, but are replaced by the smaller rudimentary pair that migrates and forms a misshaped ommatophore with a large transparent cornea and well defined optic nerve (Åkesson 1963).

Storch's (1968) comparative studies on segmental muscles in annelids is the most detailed myoanatomical description for Acoetidae. In general, the musculature appears simplified or less developed than those of non-tubicolous scale worms. Circular muscles are absent as in

other scale worms, but consistency in body wall and parapodial muscles from segment to segment is absent (Storch 1968; Tzetlin et al. 2002; Tzetlin and Filippova 2005). When compared to the myoanatomy of *Aphrodita* (Aphroditidae), *Panthalis oerstedii* lacks several muscle groups from both the body wall (*e.g.*, longitudinal and ventral oblique muscles) and from the parapodia (*e.g.*, acicular muscles). In general, the parapodial musculature is most notably different in acoetids when compared to other scale worms, being modified to accommodate the notopodial chaetal sacs. In turn, these changes have also modified the degree of intestinal caecum within the parapodial space.

There is relatively little known about the excretory organs in Acoetidae. Pflugfelder (1934) remains one of the few studies to examine both the excretory system and the feltage chaetae in detail. In general, the nephridia are extremely small given the large size of acoetids, questioning their overall function. Based on his accounts, the nephridia are closed blindly to the coelom, composed of follicles that contained golden granules that are enveloped in a chitin-like sheath. Pflugfelder (1934) noted that their colour contributes to the coloration of the internal notopodial chaetal sacs, offering up the hypothesis that the two structures are closely tied together. Further studies are needed to characterize what, if any, association exists between these two structures. Excretory granules can also be found throughout the caecum and elsewhere, suggesting that excretion is largely carried out by body epithelium.

As early as 1868, Claparède noted a distinct morphological feature that appeared as a sinuous cord trailing off into the body cavity from the parapodia in *Polyodontes maxillosus*. In a later and more thorough examination, Eisig referred to these unusual structures as “segmented spinning glands”, comprised of bundles of fine golden threads that exited through a notopodial slit (Eisig 1887). Pflugfelder (1934) showed that these fine golden threads were in fact chaetae formed by chaetogenesis, but continued to use the term “spinning gland” even though his histological investigations proved otherwise. Since then, the term “spinning gland” has also been applied to any felt-like covering in species of *Aphrodita* (Aphroditidae), and for species of *Sthenelanelia* (Sigalionidae) (Pettibone 1969; Tilic et al. 2021). In her revision of Acoetidae, Pettibone (1989) explicitly states that this term is a misnomer but its use continues regardless. In an attempt to rectify the prolonged

use of inaccurate terminology, we have instilled the terms ‘feltage chaetae’ and ‘notopodial chaetal sacs’ based on Tillic et al. (2021) for *Sthenelanella* when describing the golden notopodial fibres of Acoetidae. Briefly, the notopodial chaetal sacs of Acoetidae are covered by peritoneum (=coelomic epithelium) and have a metallic sheen with tightly packed golden yellow- to green fibres. On the smaller closed end, loose connective tissue and excretory cells are present, further contributing to the hypothesis that excretion- and notopodial chaetal sacs are interconnected (Pflugfelder 1934). The notopodial chaetal sacs lie nearly parallel to the notopodium when within them, then turn perpendicularly, becoming free within the coelom. The sacs are longer and more prominently coiled in the anterior segments, while being shorter with fewer coils in the posteriormost segments. Pflugfelder (1934) noted internal glandular tubes proximal to the notopodial slit where the feltage chaetae exit, suggesting that secretions enable the feltage chaetae to be separated into individual fibres during tube construction. All acoetids possess notopodial chaetal sacs from segment 9. In the description of *Acoetes jogasimae* (Izuka, 1912) it was noted that feltage chaetae was not observed, but the original drawings show large oocytes that likely obscured them.

Aphroditiformids have remarkable regenerative abilities across their external morphological features (*e.g.*, elytra, dorsal cirri, antenna), but to what effect anterior or posterior ends are capable of regenerating is unknown across the families. In Acoetidae, several specimens have been caught exhibiting posterior regeneration. Since most species are only known by anterior portions, it is largely presumed that acoetids are capable of regenerating an entirely new anterior region after the posterior region retreats within their tubes to regenerate (Pettibone 1989).

## **Reproduction and development**

Reproduction and development in Acoetidae are unknown and largely assumptive from our knowledge of closely related Aphroditiformia. In general, acoetids can be considered gonochoristic with external fertilization. Sexes are separate, as both sperm and large yolky oocytes have been observed within the posterior body cavities (Hartman 1951; Pettibone

1989). Like other scale worms, gametes likely exit the coelom through a ciliated coelomostome and continue out through a narrow ciliated duct (Christie 1982). This reproductive morphology is common among errant annelids.

Larval development in Acoetidae has not yet been described (Rouse and Pleijel 2001). Similar to other Aphroditiformia, acoetids likely have trochophore larvae present in the water column 1-2 days after fertilization. Distinctive structures, such as eyespots or rudimentary appendages needed for familial identification likely develop in the metatrochophore and nectochaete larval stage. Juvenile acoetids were mentioned by Pettibone (1989) for the genera *Acoetes* and *Panthalis*, stating a close resemblance to the adults, but differing in their chaetal morphology and degree of eye development and position.

### **Biology and ecology**

Acoetids have a distribution that is effectively worldwide, common between intertidal zones and 1500 m. Most species are described from warm temperate and tropical regions, with no record from Antarctic waters. Soft sands and mud are preferred substrates, but *Eupanthalis tubifex* is known to inhabit shell gravel and *Polyodontes kuroshio* is described from rocky substrates.

All acoetids inhabit self-constructed tubes (Fig. 4A-B), reaching up to a meter or more in length for larger species (*e.g.*, *Polyodontes lupines*). In *Euarche maculosa* (Treadwell, 1931), the posterior portion of the body is firmly attached to the tube and may explain why most species are only represented by fragments during collection (Willey 1905). Unlike most other annelids, acoetids construct their tubes using feltage chaetae (chitinous silken fibres) and not membranous linings. Each tube is carefully constructed by weaving the feltage chaetae into criss-cross patterns, which they cement together using the surrounding substrate (Pettibone 1989; Jumars et al. 2015). These tubes may have a parchment-like appearance, but are tough and fibrous. Acoetid tubes are slightly larger than the worm, and may be flush with (*e.g.*, *Polyodontes lupinus*) or rise above the sediment (*e.g.*,

*Eupolyodontes batabanoensis*). Tubes are often repaired rather than abandoned. Barnich and Steene (2003) reported that *Polyodontes vanderloosi* repaired a damaged portion of a tube within 24 hours after being removed for *in situ* underwater photography. *Acoetes pleei* has been reported to build Y-shaped tubes, shared between two individuals. Overall tube construction varies between species, and may be open or closed posteriorly. Tubes may exhibit mucus or cobweb-like extensions concealing the entrance, may be with or without a well-defined external collar, may be annulated, branched, narrowed or wider in the middle or posterior portions. Numerous commensal organisms are also often associated within Acoetidae tubes, including entoprocts, gastropods, bivalves and even other scale worms. *Polyodontes lupinus* is often found with the commensal gastropod *Cochliolepis parasitica* Stimpson, 1858, living under their elytra and on their body surface. Only known from these worms, this gastropod feeds off of detritus brought into the tube during respiration and feeding. Nielsen (1964) noted that acoetids are often associated with long-lived commensals capable of generating their own water currents. Sponges, algae, bryozoans or other encrusting organisms may also be present externally on tubes that rise above the sediment surface.

Tube construction itself is an extremely intricate process in Acoetidae. The best *in situ* description of this process is by Watson (1895) on *Panthalis oerstedii* from aquaria. No study has since examined this process for other acoetids, however, their morphology and that of collected tubes suggests the construction process is highly similar for all. In short, Watson (1895) noticed that tube construction (from scratch) begins by weaving their feltage chaetae into what looks like small cobwebs where mud or sediment can be attached. From within, additional layers of feltage chaetae are added parallel to each other, but transverse to the tube. These layers are not consistent for the entire length of the tube and often, no consistent pattern was found along the tube. As the interior dimensions decrease with the added layers, the worm will expand its anterior segments and burst through the anterior portion of the tube. Once burst, the entire process starts over, with the free ends of the internal tube splayed outward. According to Watson (1895), the tubes are a series of hollow truncated cones stacked up one inside the other.

Since acoetid tubes are not secretions, their construction requires both morphological and behavioural modification. Parapodia of segment 2 (buccal segment), so called weaving feet (Watson 1895), are used in conjunction with their buccal cirri in order to manipulate the feltage chaetae and the inswept mud and sediment. As the tube enlarges, the body and elytra will be pressed against the tube for support, allowing the weaving feet, and occasionally dorsal cirri of segment 3, to further assist with construction. Unlike normal parapodial paddling motion, in acoetids, parapodia from segment 2 are brought together near the midline of the body in order to perform the weaving action (Fig. 6B). During this process, the curved chaetae of segment 2 direct the feltage chaetae towards the buccal region. In Acoetidae, segment 9 (Fig. 6E) marks the start of the production and storage of feltage chaetae, and, the beginning of the aristate – penicillate neurochaetae (type a, sensu Pettibone, 1989). Resembling bottlebrushes, these neurochaetae are directed anteriorly and guide the feltage chaetae towards the weaving feet. Watson (1895) noted that the spinules of these brush-shaped neurochaetae appear to open and close when manipulating the feltage chaetae.

Acoetids possess parapodial- and sometimes prostomial branchia (Fig. 7), but the dynamics of respiration or tube ventilation is largely unknown. Water in the tube is likely renewed by carefully orientating their prostomial appendages and their first few segments, directing water flow inwards similar to that of tube dwelling sigalionids (Eibye-Jacobsen et al. 2019). Additionally, respiration is likely further aided by their mutualistic association with commensals capable of generating their own water currents (Pettibone 1989). Watson (1895) observed that the elytra in *Panthalis oerstedii* (in aquaria) do not lie flat, but are held above the body and exhibit a constant rise and fall, indicative of facilitating water exchange for the purpose of respiration. Polynoids also carefully position their elytra in order to direct water posteriorly over their bodies, but circulating water currents are generated by ciliated regions along their parapodia and the surface of their dorsum (Lwebuga-Mukasa 1970). Interestingly, ciliation across the dorsal body surface and along the parapodia is not reported in Acoetidae, suggesting that acoetids rely on other means to generate respirational water currents.



Acoetids are discretely mobile, reluctant to leave their tubes entirely (Jumars et al. 2015). If disturbed, acoetids will retreat within, or, as in the case of *Polyodontes lupinus*, will position themselves head down. Watson (1895) noted that *Panthalis oerstedii* was capable of awkwardly swimming (in aquaria), but to what extent this is utilized in the wild is unknown. Acoetids are strategic ambush (sit and wait) predators that lure prey by protruding the tips of their palps, or, their elongated mouth papillae, from their tube, seizing unsuspecting passers (Fig. 3B). Acoetids grasp or pierce their prey with their beak-like jaws (Fig. 5), then engulf it with their highly expandable pharynx. Using *Polyodontes lupinus* and *Euarche tubifex* (as *Eupanthalis*), Wolf (1986) identified that the piercing jaws of these two acoetids similarly had an internal canal and organ assumed to be a venom gland, but the canal did not open at the tip of the jaws. The venom gland of acoetids is smaller and less developed compared to the size of the animal and to the other scale worm families. The functionality of the venom delivery system requires verification, as well presence of venom glands across all acoetid genera. Occasionally the voraciousness of acoetids is on display, as anterior portions of *Polyodontes maxillosus* have been caught on fishing lines, specifically, an extended pharynx (wider than body) with fluorescent ultramarine-blue granules on the tips and four denticulate jaws. These phosphorescent tips are likely used to attract prey at night, however, it is unknown how many acoetids have this feature (Pettibone 1989).

### **Phylogeny and taxonomy**

The original family designation for Acoetidae was 'Acoetea' by Kinberg (1856), and included species descriptions for *Panthalis oerstedii* and *Acoetes grubei* (Kinberg, 1856). However, Ranzani (1817) for *Polyodontes maxillosa* is the earliest reference to any acoetid. The taxonomic nomenclature of Acoetidae has varied significantly over time, most notably being referred to by 'Acoetinae', 'Polyodontidae' or 'Polyodontinae' (Pettibone 1989). Using a number of morphological characters, Muir (1982) suggested that Acoetidae (as 'Polyodontidae') be treated as a subfamily of Polynoidae (as 'Polyodontinae') given that he found them to only differ by the presence of feltage chaetae (putative synapomorphy). Rouse and Fauchald (1997) using cladistic analyses of morphological characters recovered Acoetidae and Aphroditidae as sister groups due to the shared presence of feltage chaetae.

Eventually, those scale worm groups having only simple chaetae were lumped together in what was referred to as the 'Aphroditoidea', and included Acoetidae, Aphroditidae, Eulepethidae and Polynoidae (Rouse and Pleijel 2001). While all previous classifications are no longer considered valid, it is interesting to note that the once considered Acoetidae synapomorphies are now all considered shared homologous features: ommatophores (with Aphroditidae and Sigalionidae), 'silken' or feltage chaetae (with Aphroditidae and Sigalionidae; Rouse and Fauchald 1997; Tilic et al. 2021) and denticulate jaws (with Iphionidae and Polynoidae; Pettibone (1989)).

Recent phylogenetic analyses across Aphroditiformia (Gonzalez et al. 2018; Zhang et al. 2018) has continued to increase representation across all families, with the exception of Acoetidae, where only a single species continues to be available for genetic comparisons. Currently, this is one of the greatest knowledge gaps that remains in Aphroditiformia, as the lack of additional genetic sequences for Acoetidae prevents any further verification of their monophyly and phylogenetic position with respect to Iphionidae and Polynoidae.

Wiklund et al. (2005) provided the first molecular analyses to include a member of Acoetidae (*i.e.*, *Panthalis oerstedii*). While her dataset was limited, Acoetidae was recovered sister to Polynoidae, rendering 'Aphroditoidea' polyphyletic. More recently in a combined approach using molecular and morphological data, Gonzalez et al. (2018) recovered Acoetidae in a clade with Iphionidae, sister to Polynoidae. While the relationship to Iphionidae was poorly supported by the maximum likelihood analysis, the sister relationship to Polynoidae was highly supported across analyses. Using total evidence approaches (molecular + morphology only terminals), the phylogenetic position of Acoetidae remained stable with the inclusion of *Eupanthalis* and *Polyodontes* by morphology only, (see Gonzalez et al. 2018), with pseudopenicilate neurochaetae as the apomorphy uniting the family. Zhang et al. (2018) generated the first Acoetidae mitochondrial genome for *Panthalis oerstedii*, however, recent phylogenetic investigations using mitochondrial genomes (Zhang et al. 2018; Gonzalez et al. 2021) continue to rely on a single acoetid species. Nevertheless, the implementation of mitogenome analyses continue to recover Acoetidae independent of, and sister to Polynoidae.

## Diagnoses of genera

### ***Acoetes* Audouin & Milne Edwards, 1832**

**Type species:** *Acoetes pleei* Audouin & Milne Edward, 1832

13 species

**Diagnosis:** Acoetids with bulbous, coloured, stalked ommatophores and small pair of sessile lateral eyes (type 3). Median antenna well-developed, with ceratophore positioned near the middle of the prostomium. Lateral antennae ventrally attached on ommatophores. Palps smooth or papillate. Pharynx with up to 19 pairs of papillae, middorsal and midventral papillae may be longer. Jaws with up to 12 lateral teeth. Upper neurochaetae (type a) from segment 9 long, tapering to slender tips abruptly; plumose subdistally and spinous rows basally. Type b neurochaetae short, but not hidden by notopodia. Parapodial branchiae may be present.

### ***Euarche* Ehlers, 1887**

**Type species:** *Euarche tubifex* Ehlers, 1887

5 species

**Diagnosis:** Acoetids with oval or bilobed prostomium (type 1). Two pairs of sessile eyes, may be absent in some species. Median antenna well developed. Lateral antennae anterior, visible. Pharynx with up to 15 pairs of equally sized papillae. Jaws with 8 lateral teeth. Segment 2 with numerous capillary notochaetae. Acicular neurochaetae from segment 3. Upper neurochaetae (type a) from segment 9, long, lanceolate with lateral spinules. Parapodial branchiae absent.

### ***Eupanthalis* McIntosh, 1876**

**Type species:** *Eupanthalis kinbergi* McIntosh, 1876

6 species

**Diagnosis:** Acoetids with oval or bilobed prostomium (type 1). Two pairs of sessile eyes, may be absent in some species. Median antenna absent. Lateral antennae anterior, visible. Pharynx with up to 15 pairs of equally sized papillae. Jaws with 8 lateral teeth. Segment 2

with or without notochaetae. Acicular neurochaetae from segment 3. Upper neurochaetae (type a) from segment 9, long, lanceolate with lateral spinules. Parapodial branchiae absent.

***Eupolyodontes* Buchanan, 1894**

**Type species:** *Eupolyodontes cornishii* Buchanan, 1894

7 species

**Diagnosis:** Acoetids with bilobed prostomium and large, coloured ommatophores (type 2). Median antenna may be absent. Bilobed nuchal organ. Lateral antennae medial to ommatophores. Short palps. May possess prostomial branchiae. Parapodial branchiae present. Pharynx with up to 39 pairs of papillae, middorsal and midventral papillae long. Jaws with up to 17 lateral teeth. Upper neurochaetae (type a) from segment 9 with double brush-shaped tips.

***Neopanthalis* Strelzov, 1968**

**Type species:** *Neopanthalis pelamida* Strelzov, 1968

1 species

**Diagnosis:** Acoetids with bilobed prostomium. Ommatophores enlarged and fused (type 4). Median antenna well developed. Lateral antennae dorsally positioned. Acicular neurochaetae from segment 3. Upper neurochaetae (type a) from segment 9, lanceolate with lateral spinules. Parapodial branchiae absent.

***Panthalis* Kinberg, 1856**

**Type species:** *Panthalis oerstedii* Kinberg, 1856

9 species

**Diagnosis:** Acoetids with bilobed prostomium, ommatophores mostly lacking colour (type 3). Lateral sessile eyes lacking. Well-developed median antenna, ceratophore near middle of prostomium. Lateral antennae attached ventrally on ommatophores. Palps smooth. Pharynx with 19 pairs of papillae, middorsal and midventral papillae may be longer. Jaws with up to 12 lateral teeth. Upper neurochaetae (type a) from segment 9 long, distally plumose. Type b neurochaetae very short, hidden by notopodium. Parapodial branchiae absent.

***Polyodontes* Blainville, 1828**

**Type species:** *Polyodontes maxillosus* (Ranzani, 1817)

16 species

**Diagnosis:** Acoetids with bilobed prostomium and bulbous, coloured, stalked ommatophores (type 3). Lateral pair of sessile eyes present. Well-developed median antenna, ceratophore near middle of prostomium. Lateral antennae attached ventrally on ommatophores. Palps smooth or papillate. Pharynx with 19 pairs of papillae, middorsal and midventral papillae may be longer. Jaws with up to 12 lateral teeth. Upper neurochaetae (type a) from segment 9 long, spinous. Type b neurochaetae shorter than type a, but not completely hidden by notopodia. With or without parapodial branchiae.

### ***Zachsiella* Buzhinskaja, 1982**

**Type species:** *Zachsiella nigromaculata* (Grube, 1878)

1 species

**Diagnosis:** Acoetids with bilobed prostomium and large, coloured ommatophores (type 2). Median antenna well developed. Lateral antennae medial to ommatophores. Parapodial branchia absent. Pharynx with 13 pairs of papillae, middorsal and midventral papillae longer. Jaws with up to 7 lateral teeth. Upper neurochaetae (type a) from segment 9 acicular, spinous, aristate. Without parapodial branchiae.

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## Figures

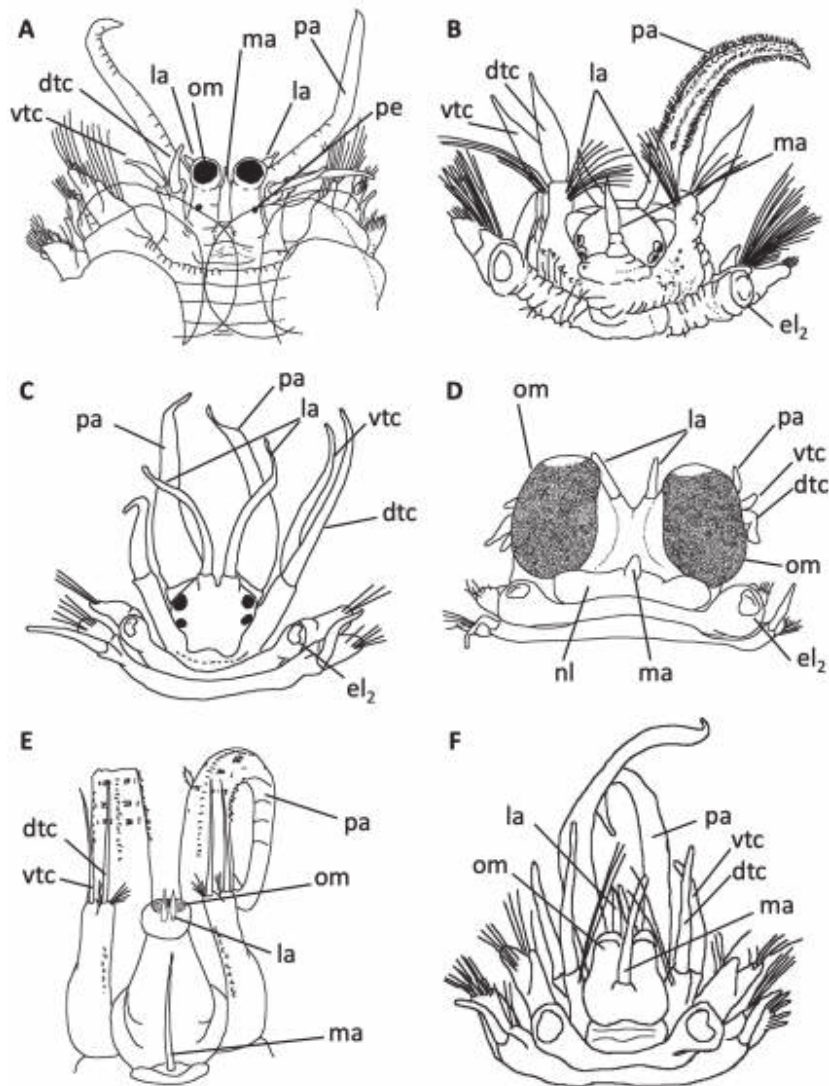


Figure 1: Dorsal view of anterior regions of the different genera of Acoetidae. **A.** *Acoetes jogasimae* (Izuka, 1912). Prostomial type 3. Redrawn after Imajima (1997). **B.** *Euarche tubifex* Ehlers, 1887. Prostomial type 1. Redrawn after Imajima (1997). **C.** *Eupanthalis kinbergi* McInstosh, 1876. Prostomial type 1. Redrawn after Barnich and Fiege (2003). **D.** *Eupolyodontes gulo* (Grube, 1855). Prostomial type 2. Redrawn after Barnich & Fiege (2003). **E.** *Neopanthalis pelamida* Strelzov, 1968. Prostomial type 4. Redrawn after Strelzov (1968). **F.** *Panthalis oerstedii* Kinberg, 1856. Prostomial type 3. Redrawn after Barnich & Fiege (2003). Images not drawn to scale. Abbreviations: dtc, dorsal tentacular cirrus; el<sub>2</sub>, elytophore segment 2; la, lateral antenna; ma, median antenna; nl, nuchal lobe; om, ommatophore; pa, palp; pe, posterior eyes; pr, prostomium; vtc, ventral tentacular cirrus.

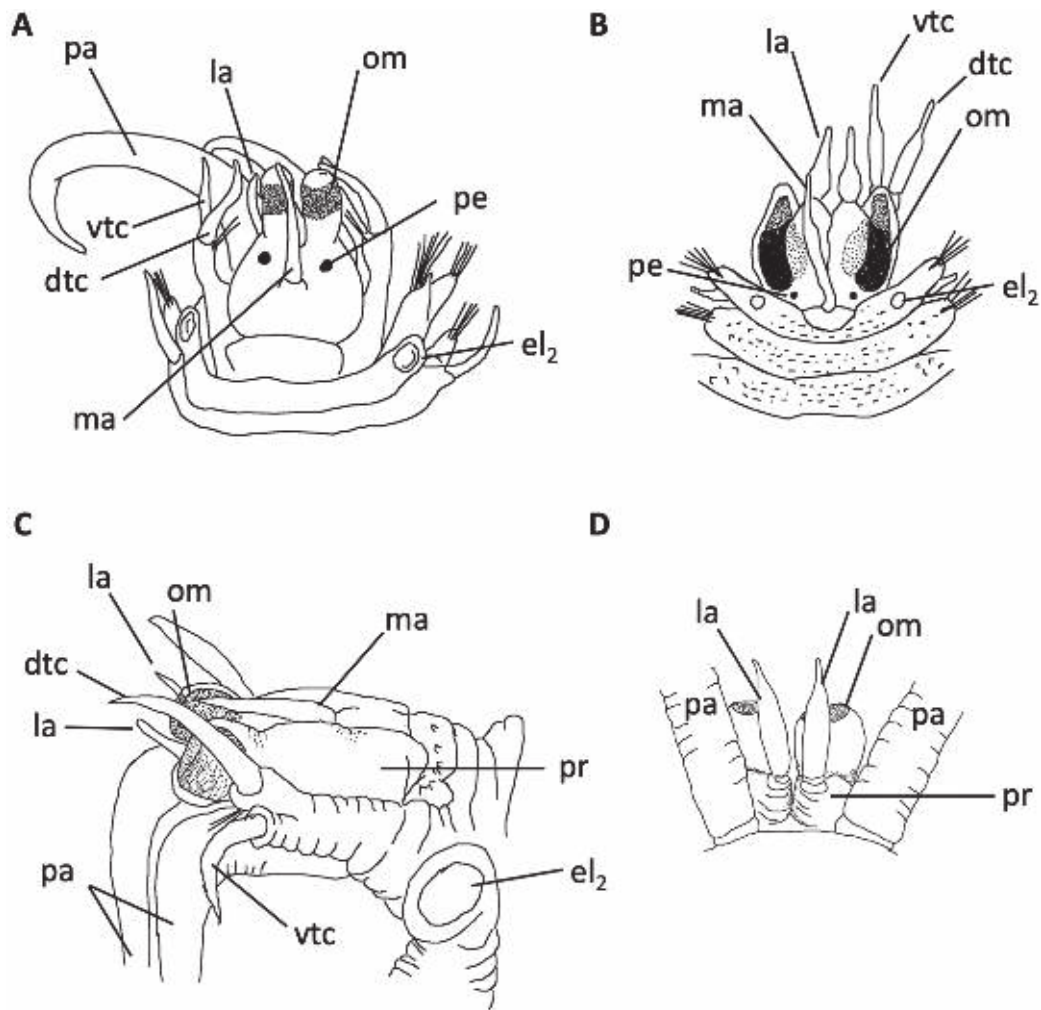


Figure 2: Dorsal view of anterior regions of the different genera of Acoetidae. **A.** *Polyodontes maxillosus* (Ranzani, 1817). Prostomial type 3. Redrawn after Barnich & Fiege (2003). **B.** *Zachsiella nigromaculata* (Grube, 1878). Prostomial type 2. Redrawn after Buzhinskaja (1982). *Acoetes jogasimae* (Izuka, 1912), lateral (**C**) and ventral views (**D**). Redrawn after Imajima (1997). Prostomial type 3. Images not drawn to scale. Abbreviations: dtc, dorsal tentacular cirrus; el<sub>2</sub>, elytophore segment 2; la, lateral antenna; ma, median antenna; om, ommatophore; pa, palp; pe, posterior eyes; pr, prostomium; vtc, ventral tentacular cirrus.

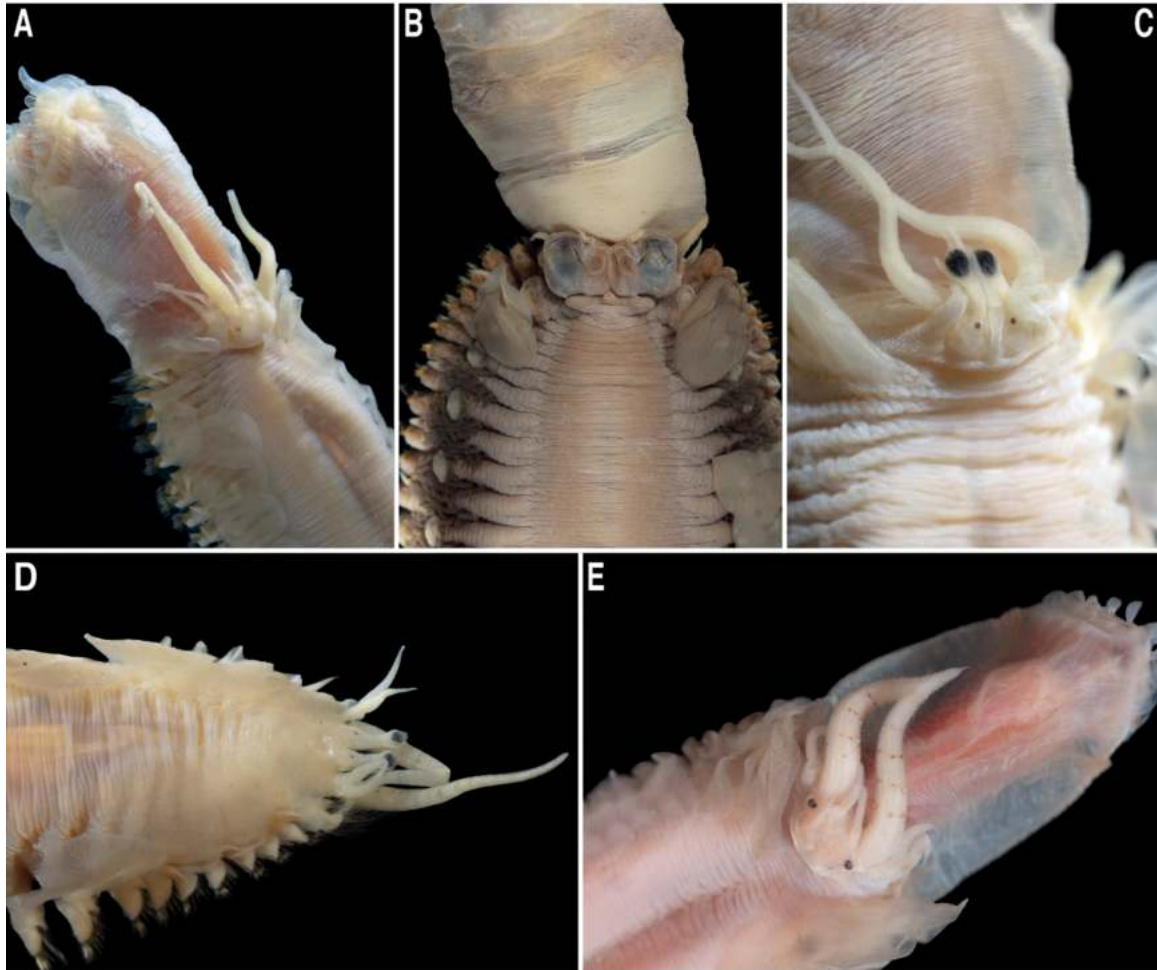


Figure 3: Prostomial and eye variations across Acoetidae. **A.** *Euarche tubifex* Ehlers, 1887 (USNM 71456). Type 1 prostomia. **B.** *Eupolyodontes batabanoensis* Ibarzábal, 1988 (USNM 98809). Type 2 prostomia. **C.** *Polyodontes frons* Hartman, 1939 (USNM 50730). Type 3 prostomia. **D.** *Acoetes melanonota* (Grube, 1876) (USNM 98809). Type 3 prostomia. **E.** *Eupanthalis kinbergi* McIntosh, 1876 (USNM 1184294). Type 1 prostomia.

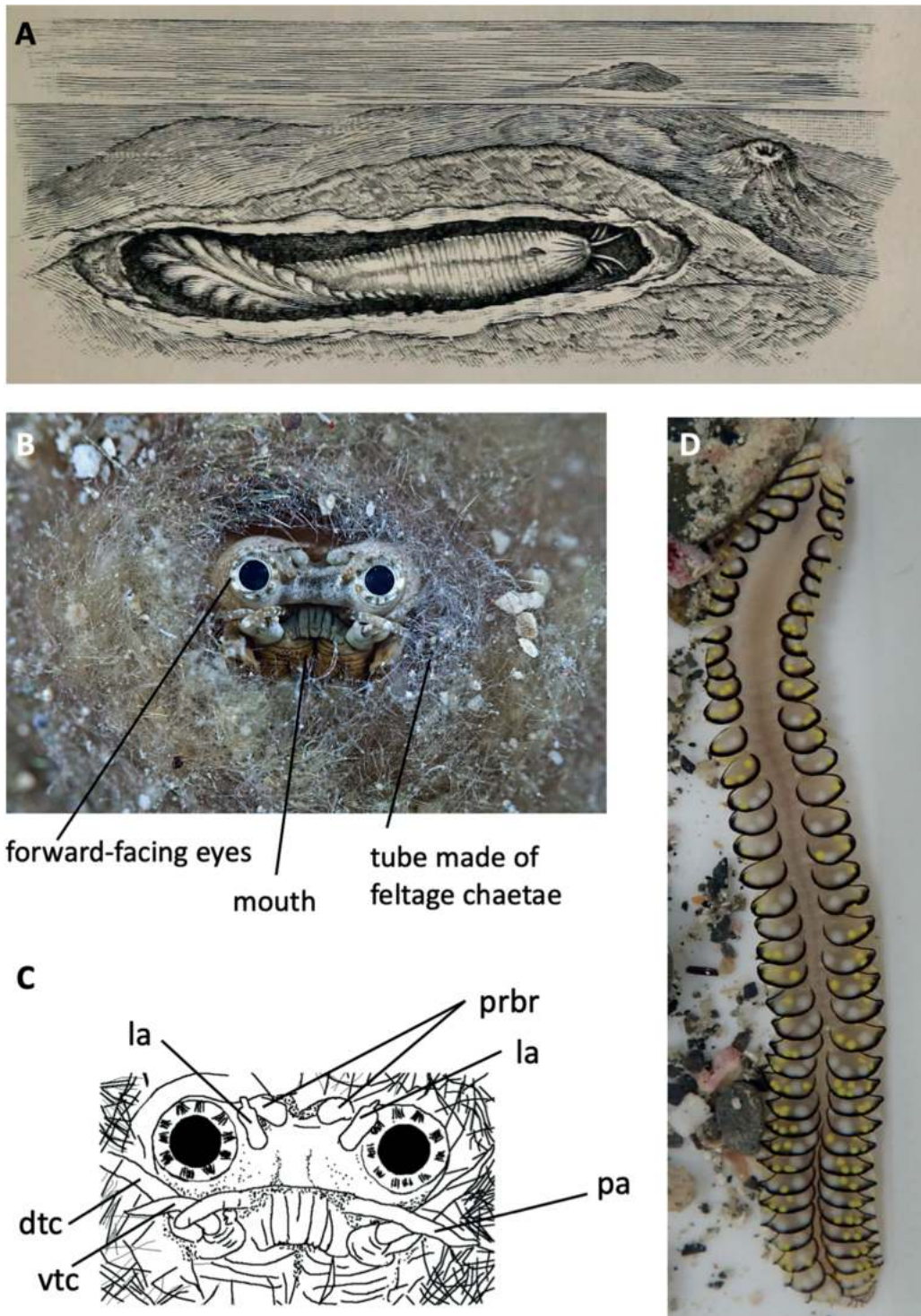


Figure 4: Acoetids in their natural settings. **A.** Drawing of *Panthalis oerstedii* Kinberg, 1856 in its burrow (British Museum (Natural History) 1901). **B.** *Eupolyodontes* sp. at the opening of its tube. Photo by Cedric Paul, with permission. **C.** Annotated drawing of B. **D.** *Polyodontes kuroshio* Jimi, Tomioka, Orita & Kajihara, 2019. Photo by Naoto Jimi, with permission. Images not drawn to scale. Abbreviations: dtc, dorsal tentacular cirrus; la, lateral antenna; pa, palps; prbr, prostomial branchiae; vtc, ventral tentacular cirrus.

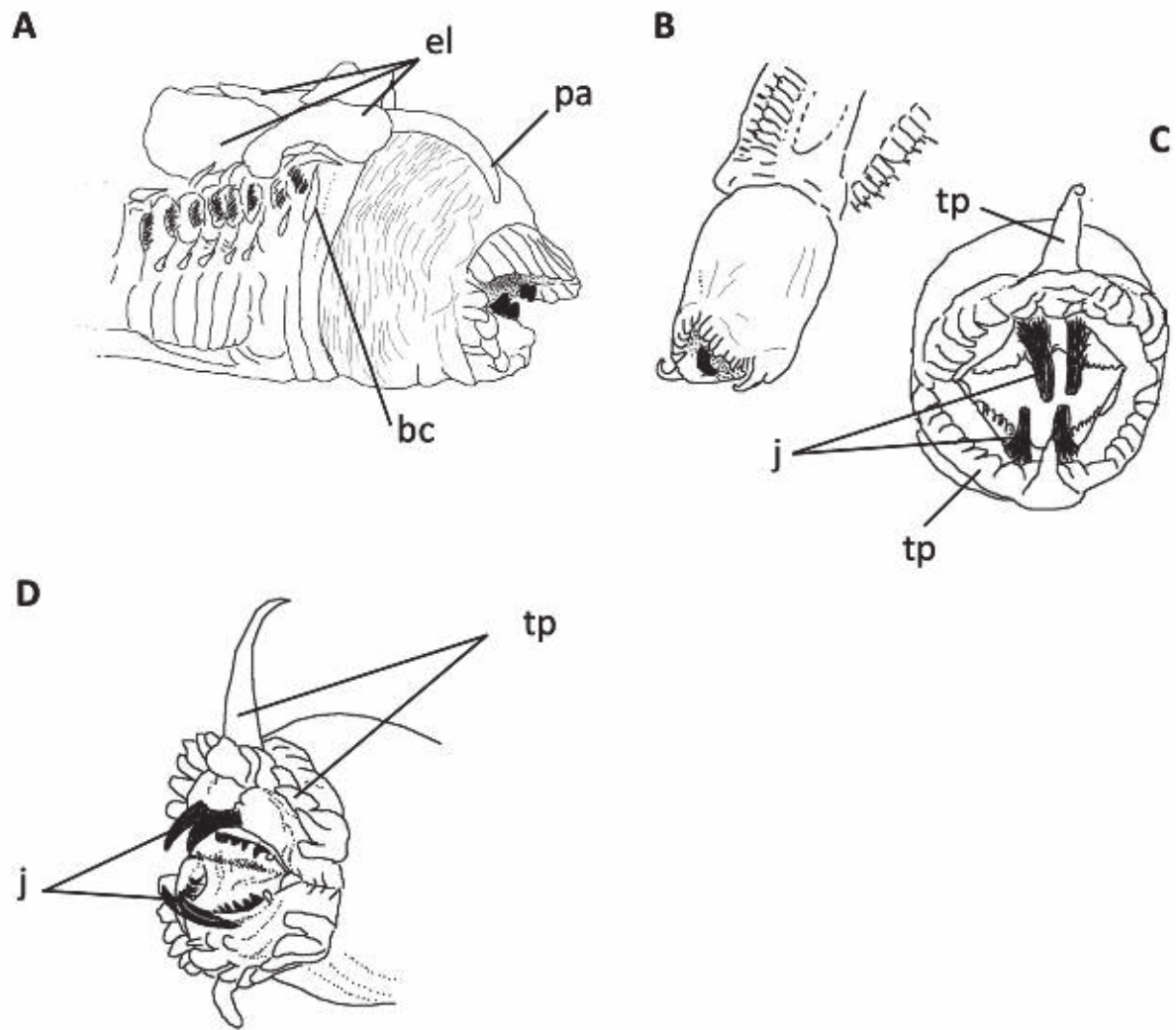


Figure 5: Everted pharynx showing terminal mouth papillae and jaws. **A.** Lateral view of everted pharynx and prostomial appendages in *Euarche rudipalpa* (Amaral & Nonato, 1984). **B-C** Pharynx of *Polyodontes maxillosus* (Ranzani, 1817) in ventral (**B**) and frontal views (**C**). **D.** Terminal mouth papillae and jaws of *Acoetes jogasimae* (Izuka, 1912). Redrawn after Imajima (1997). Images not drawn to scale. Abbreviations: bc, buccal cirrus (segment 2); el, elytra; j, jaw; pa, palp; tp, terminal papillae.

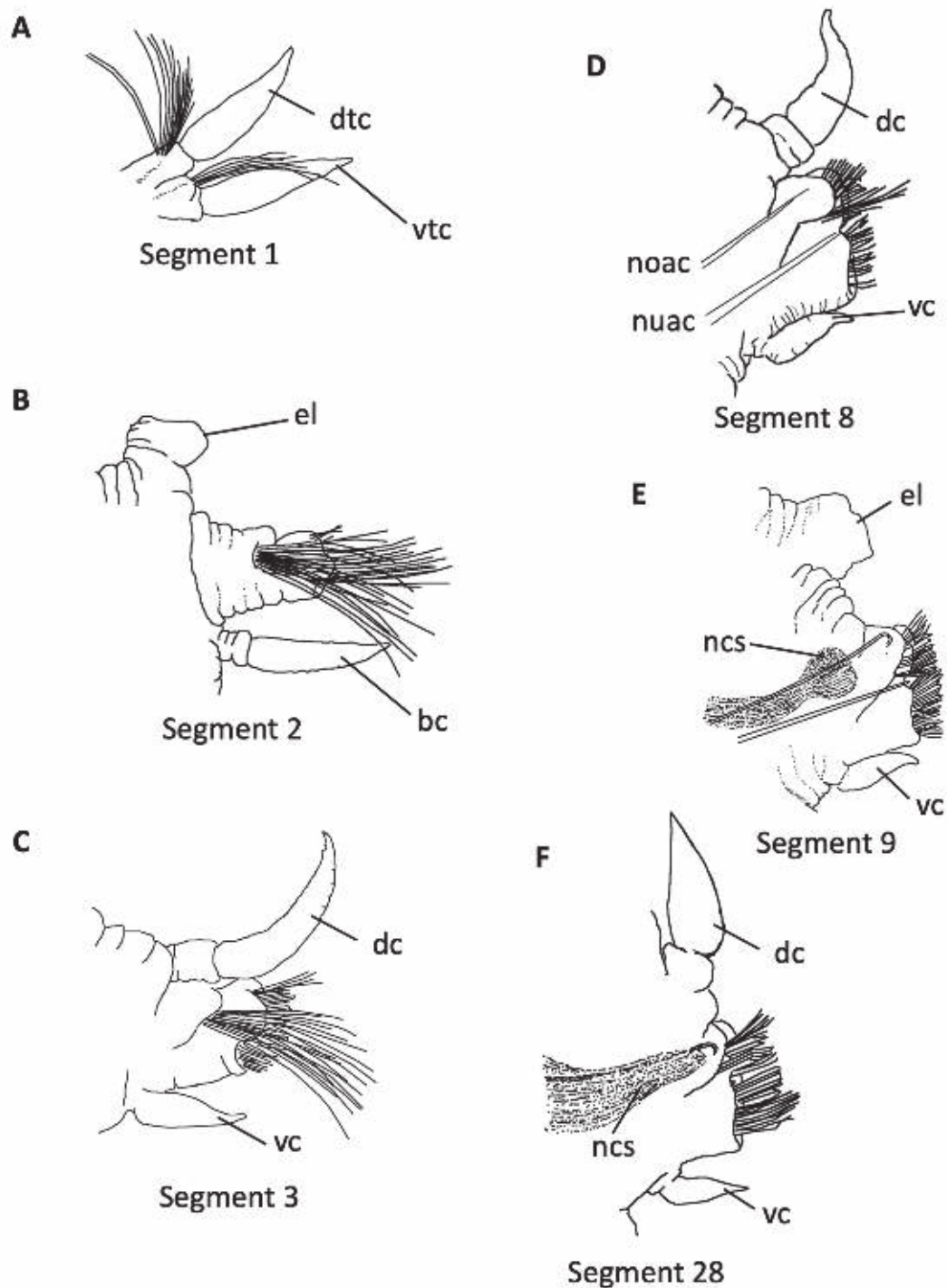


Figure 6: Variation in segment morphology in *Euarche tubifex* Ehlers, 1887. Redrawn after Imajima (1997). **A.** Segment 1, tentacular segment. **B.** Segment 2, buccal segment and first elytragerous segment. **C.** Segment 3, first cirriferous segment. **D.** Segment 8. **E.** Segment 9, first segment with notopodial chaetal sacs. **F.** Segment 28. Images not drawn to scale. Abbreviations: bc, buccal cirrus; dc, dorsal cirrus; dtc, dorsal tentacular cirrus; el, elytraphore; ncs, notopodial chaetal sac; noac, notopodial acicula; nuac, neuropodial acicula; vc, ventral cirrus; vtc, ventral tentacular cirrus.

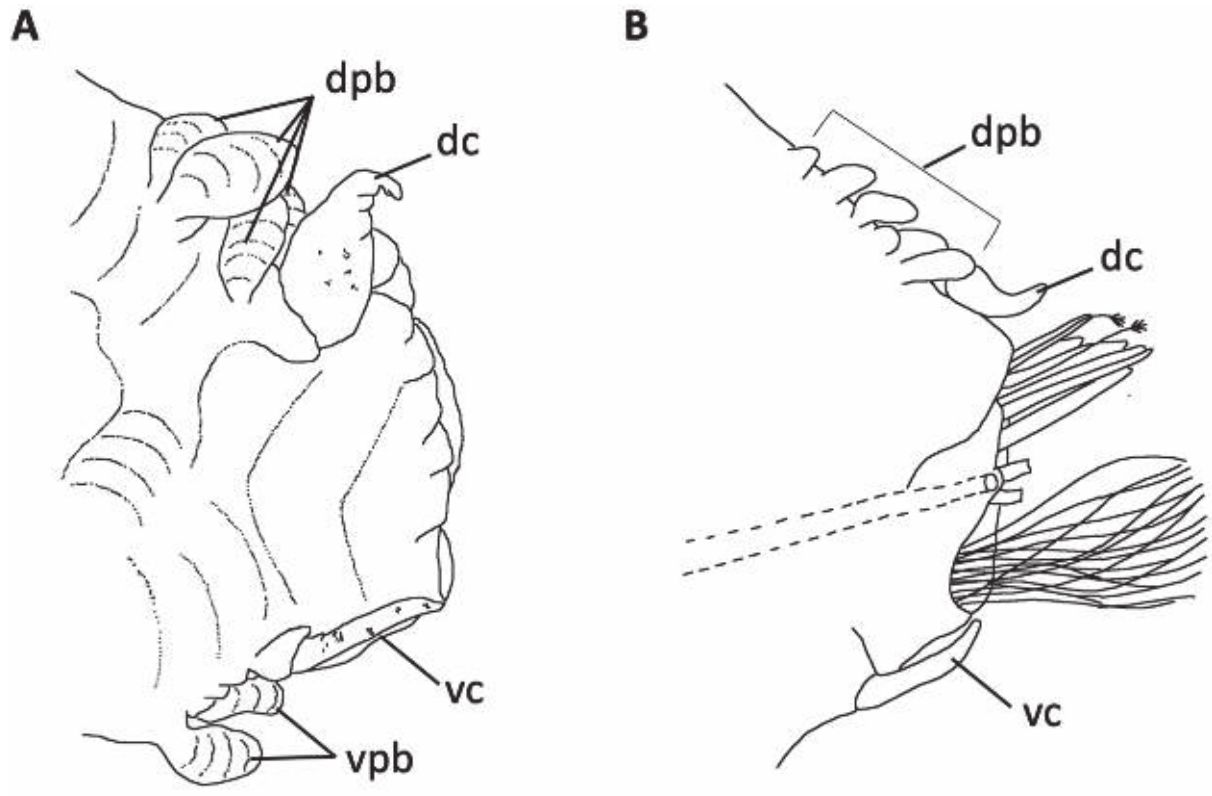


Figure 7: Examples of parapodial branchiae in Acoetidae. **A.** *Polyodontes vanderloosi* Barnich & Steene 2003. Chaetae not shown. Redrawn after Barnich and Steene (2003). **B.** *Eupolyodontes gulo* (Grube, 1855). Redrawn after Barnich & Fiege (2003). Images not drawn to scale. Neuropodial acicula demarked by dashed lines. Abbreviations: dc, dorsal cirrus; dpb, dorsal parapodial branchiae; vc, ventral cirrus; vpb, ventral parapodial branchiae.

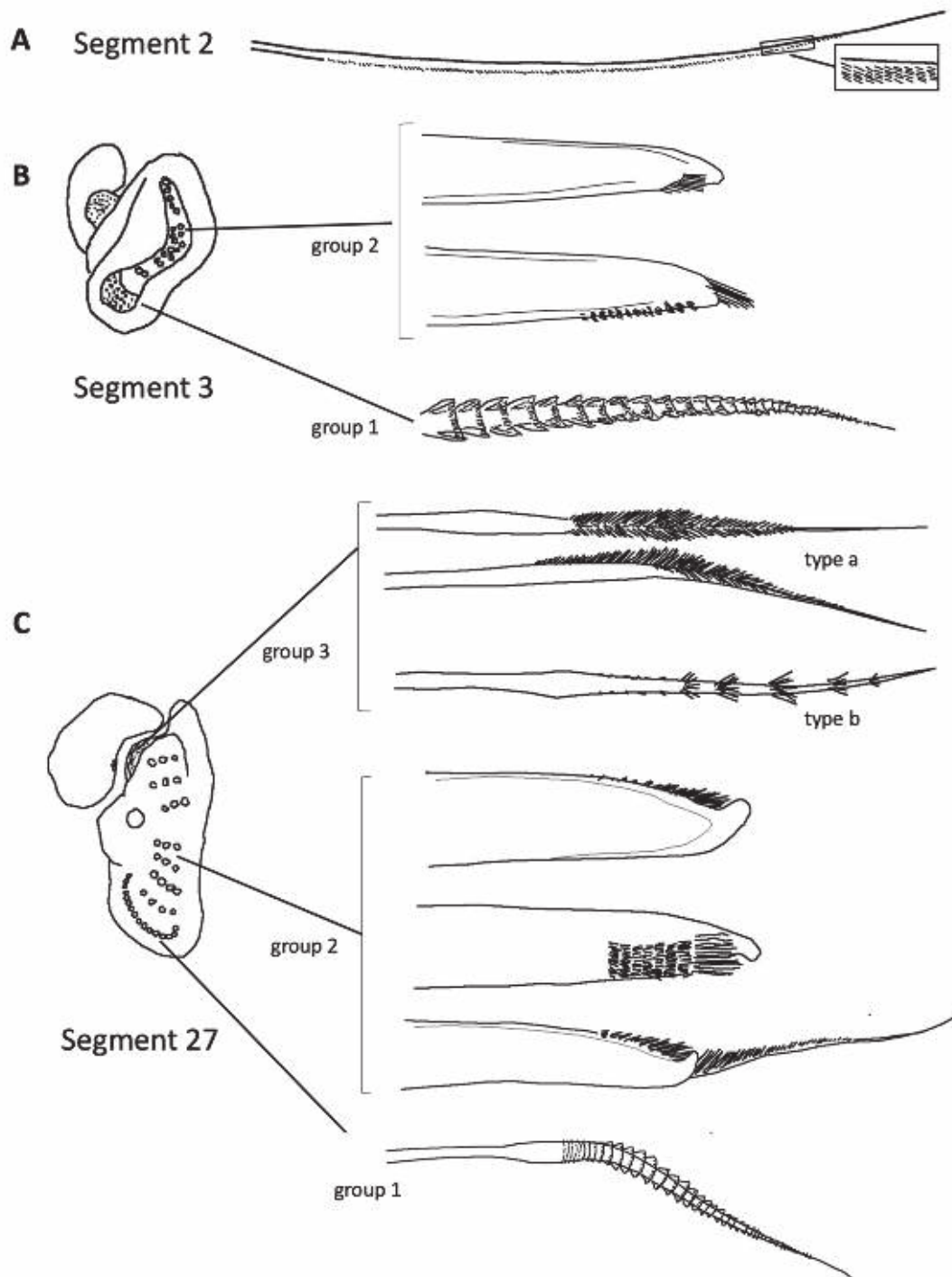


Figure 8: Different chaetal arrangements in *Euarche tubifex* Ehlers, 1887. Chaetal groups, and types, indicated when appropriate. **A.** Segment 2 notochaeta. Detail of distal spinules shown in insert. **B.** Segment 3 neurochaetae with detailed drawings of the middle (group 2) acicular neurochaetae (in bracket) and a single lower (group 1) neurochaeta. **C.** Segment 27 with examples of upper (group 3a and 3b), middle (group 2) and lower (group 1) neurochaeta. Images not drawn to scale. All images redrawn after Imajima (1997).



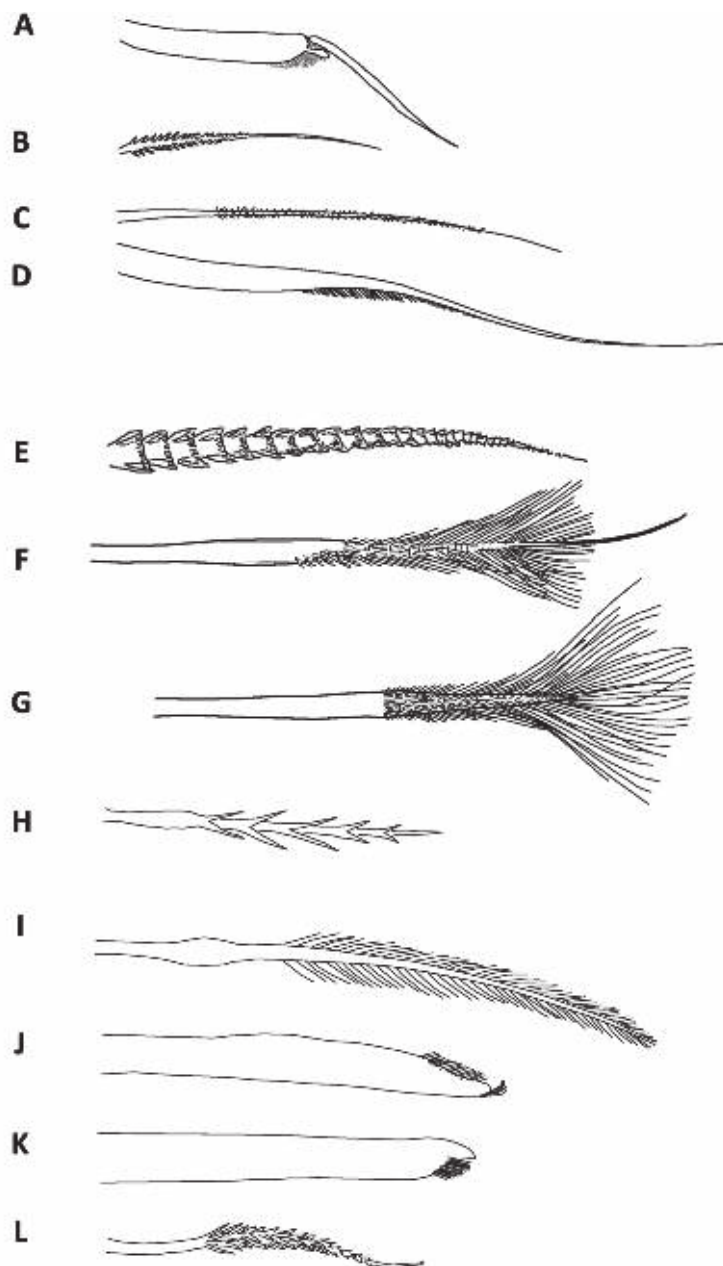


Figure 9: Diversity of chaetal forms across select Acoetidae. **A-D** *Eupanthalis kinbergi* McInstosh, 1876. Aristate acicular neurochaeta from middle of neuropodium (group 2; A), neurochaeta with spines in the lower part (group 1; B) and upper part (group 3b; C and D). Redrawn from Núñez et al. (2015). **E, F** *Acoetes jogasimae* (Izuka, 1912). Segment 9 (group 3; F, G) brush-like neurochaetae. Redrawn after Imajima (1997). **G-L** *Euarche tubifex* Ehlers, 1887. Segment 3 neurochaeta (group 1). Redrawn after Imajima (1997). Capillary with widely separated spines (group 3b; H), tightly set spines in the upper part (group 3b; I), acicular from middle of parapodium (group 2; J, K), and lower part of parapodium (group 1; L). Redrawn from Núñez et al. (2015).

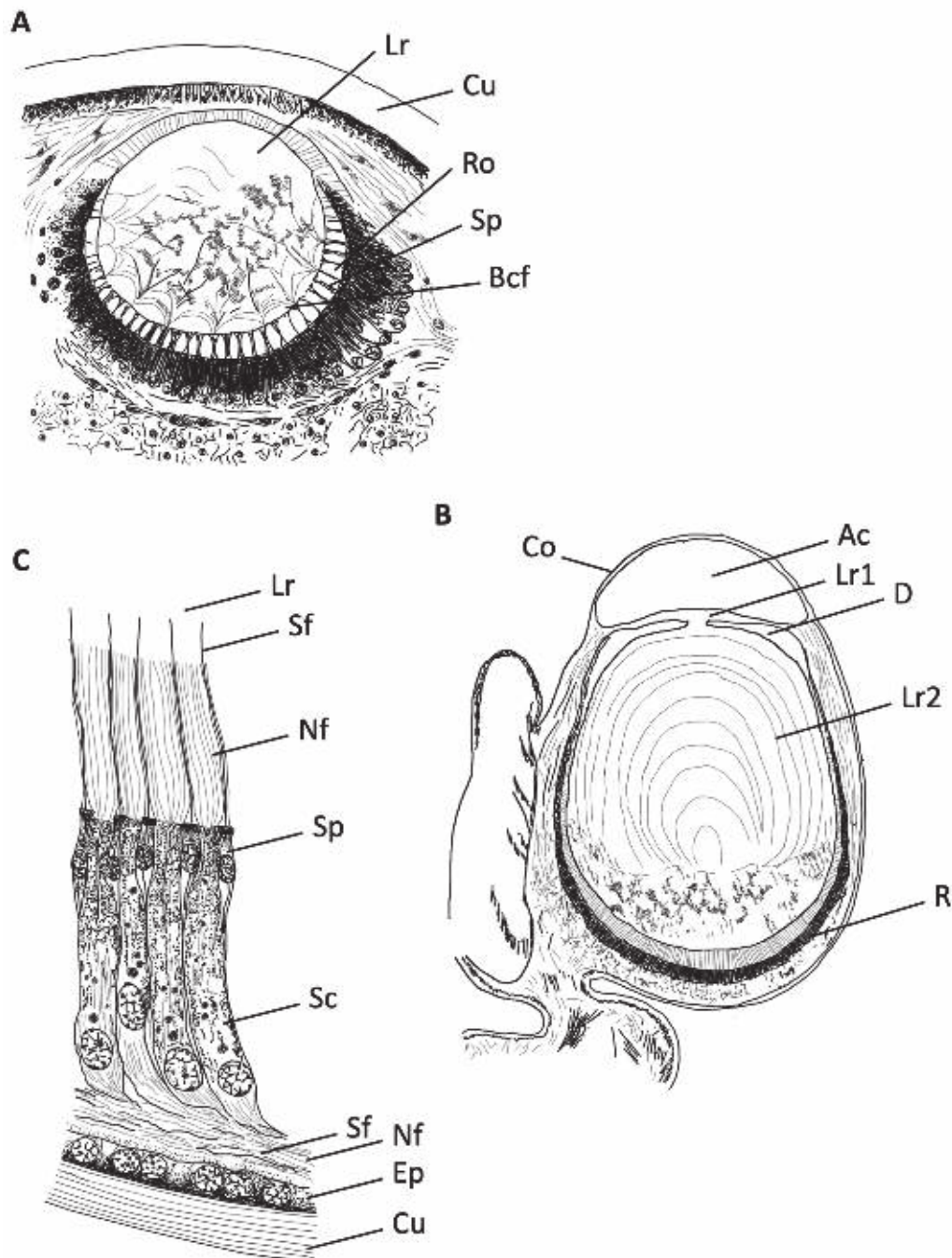


Figure 10: Internal eye morphology of Acoetidae. Redrawn after Pflugfelder, 1932. **A.** Cross section through a sessile eye of *Polyodontes tidemani* Pflugfelder, 1932. **B.** Frontal section through the ommatophore of *Eupolyodontes amboinensis* Malaquin & Dehorne, 1907 (as *Eupolyodontes sumatranus* Pflugfelder, 1932). **C.** Median section through the stalked eye of *Polyodontes tidemani*. Images not drawn to scale. Abbreviations: Ac, anterior chamber; Bcf, bow-shaped connecting fibrils; Co, cornea; Cu, cuticle; D, diaphragm; Ep, epidermis; Lr, light-refractive body; Lr1 and Lr2, anterior and posterior refractive body, respectively; Nf, neurofibrils; R, retina; Ro, rhabdoms; Sc, sensory cell; Sf, support fibres; Sp, support cells.