

Evolution of interstitial Polychaeta (Annelida)

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Abstract

An update of the systematics is given for the eight most important interstitial polychaete families: Diurodrilidae, Nerillidae, Protodrilidae, Protodriloididae, Saccocirridae, Parergodrilidae, Polygordidae and Psammodrilidae. Additional information and new observations are presented for the Diurodrilidae, Nerillidae and Psammodrilidae. Three new supplementary evolutionary hypotheses for these families are here suggested: (1) basal position of Diurodrilidae in Polychaeta, (2) evolution of Nerillidae in mud, and (3) evolution from meio- to macrofaunal forms of Psammodrilidae.

Introduction

Interstitial fauna is a term used for animals capable of moving between sediment particles, quartz grains, and pieces of broken shells or corals, with minimum disturbance of the constituent particles. Mud-dwelling animals are therefore excluded from this classification (Swedmark, 1964; Higgins & Thiel, 1988). The space factor, or size of the interstices, is of great importance for the interstitial species, which are generally small sized (0.3–3 mm), but not necessarily of meiofaunal dimensions (Swedmark, 1964; Higgins & Thiel, 1988). According to Coull & Bell (1979) it is found that in those meiofaunal taxa that have both interstitial and burrowing representatives, the sand fauna tends to be long and slender, whereas the mud fauna is not restricted to a particular morphology and is generally larger. The meiofaunal as well as the interstitial polychaetes are polyphyletic groups of species, which have evolved by many independent lines from various macrofaunal forms (Swedmark, 1964; Westheide, 1971, 1985, 1987, 1988). Many of these are highly derived species evolved by gradual transition from larger to smaller size or by progenesis (maturation in juvenile/larval stage) (Westheide, 1987).

Most of the sediment-inhabiting meiofaunal polychaetes are representatives from macrofauna families, including Acrocirridae, Dorvilleidae, Goniadidae, Hesionidae, Orbiniidae, Paraonidae, Pholoidae, Phyllodocidae, Pisionidae, Questidae, Sabellidae, Sphaerodoridae, Spionidae, and Syllidae. However, several exclusively meiofaunal or interstitial families exist, of which only the eight most important will be treated here. These include the Diurodrilidae, Nerillidae, Parergodrilidae, Polygordidae, Protodrilidae, Protodriloididae, Psammodrilidae and Saccocirridae. Based on a cladistic analysis of morphological data the interstitial taxon Dinophilidae has been included in Dorvilleidae (Eibye-Jacobsen & Kristensen, 1994). It here represents the most reduced forms in a progenetic evolution series leading from large dorvilleids with parapodia, cirri and jaws to small dinophilids without parapodia or jaws. In fact, it is the first time that progenesis has been shown to be the driving force in the annelid evolution. However, a recent cladistic analysis based on molecular data has cast doubt on the monophyly of the Dorvilleidae (Struck et al., 2002b). Yet, additional information is necessary to then clarify the position of the dinophilids and explain the altered evolutionary scenario. Because the dinophilids still

belong to the macrofaunal Dorvilleidae, these are not treated further here. Most of the eight exclusively interstitial families, mentioned above, were formerly classified as archiannelids (defined by Hatschek, 1878), which is now considered an invalid taxon (Westheide, 1985). These families are now believed to be highly derived and most of them to have evolved independently (Fauchald, 1977; Westheide 1985, 1987). However, their phylogenetic position and origin is controversial and the present paper will seek to update the systematics of these families.

Several characteristics have been mentioned for interstitial and former archiannelid polychaetes: small size; complete homonymy; weak segmentation; long, spionid-like primary tentacles (palps); few or no appendages, parapodia, or chaetae; larval characteristics like ventral ciliation (gastrotrich), dorsal ciliary bands and protonephridia; incomplete mesenteries and mesenterial channels; no circular musculature, muscle cells of myoepithelial origin; simple blood vascular system; simple ciliated intestine; simple structure of brain; brain apical; obvious subesophageous ganglion missing; nerve system closely linked to epidermis; ventral nerve cord not segmented; direct development; and novel characters like specialized pharyngeal apparatus; peculiar spermatozoa; special reproductive modes (e.g. internal fertilization) and larvae; and adhesive organs (Hempelmann, 1931; Clark, 1969; Swedmark, 1964; Westheide, 1971, 1984, 1985, 1987, 1990; Bubko, 1973; Orrhage, 1974). Some of these characters, like e.g. protonephridia, which were formerly interpreted as plesiomorphic or larval states, have now been demonstrated to be secondarily reduced or specialized states (Bartolomaeus, 1999).

Many of the interstitial polychaetes have evolved by genetically fixed progenesis (Westheide, 1971, 1987). It is now the general belief that the morphological resemblance of the interstitial polychaetes does not reflect a common ancestor, but convergent adaptations to the environment, small size and progenetic origin (Swedmark, 1964; Westheide, 1971, 1985, 1988). According to Westheide (1987) a progenetic origin is most compelling, when the taxon has great similarity with larval or juvenile stages of a macrofaunal taxon. However, the evolution should not be viewed as totally regressive, as it will often also

involve strongly specialized and novel characters, which are crucial for a successful existence in the interstitial environment (Westheide, 1987). The many apomorphies and problems with scoring absent or reduced characters have made it very difficult to analyze the phylogenetic position of the interstitial families in Polychaeta (Purschke et al., 2000).

The theory of progenesis has been linked rather closely to the size-specific niche of the interstitial environment, indicating that the hard adaptational demands for entering this environment require a one-step specialization to smaller size (Westheide, 1987). Mud-dwelling meiofauna have never been proposed to evolve by progenesis. The four nerillids, *Meganerilla swedmarki* Boaden, 1961, *Nerilla australis* Willis, 1951, *Paranerilla cilioscutata* Worsaae & Kristensen, 2003 and *P. limicola* Jouin & Swedmark, 1965, are among the only examples of mud-dwelling meiofauna polychaetes (Willis, 1951; Jouin & Swedmark, 1965; Saphonov & Tzetlin, 1997; Worsaae & Kristensen, 2003), but mud habitats are not as thoroughly examined for this fauna as the interstitial environment. The possibility that meiofauna polychaetes like Nerillidae could have evolved in mud, either by progenesis or gradual transition to smaller size (miniaturization), is discussed here.

One of the arguments for a progenetic evolution as an alternative to miniaturization is that only few examples of gradual transition of middle-sized species to true small interstitial forms are known (Westheide, 1987). Some of these examples can even be interpreted such that the evolutionary pathway has the opposite direction, from interstitial meiofauna to non-interstitial macrofauna (Westheide, 1987). *Microphthalmus hamosus* Westheide, 1982 is an example of a commensal macrofaunal species, which has evolved from an otherwise interstitial genus (Westheide, 1982). Speciation has led to an increase in body size and number of segments. However, chaetae lost in the previous adaptation of the genus to the interstitial environment were not regained in this species (Westheide, 1982). It was argued that genetic information has been lost and that Dollo's law may affect the evolution from smaller to larger forms (Westheide, 1982). The irreversibility of character reduction as well as the phylogenetic interpretation of macrofaunal

taxa with 'simple' characters has wide implications for our understanding of relationships within Annelida. Evolution from macro- to meiofaunal forms (Swedmark, 1955, 1958; Kristensen & Nørrevang, 1982) and back to larger forms is here discussed in relation to the various coelomic conditions found in especially Psammodrilidae (Fransen, 1980; this paper). Finally, it is discussed whether the family Diurodrilidae may not be a secondarily derived 'pseudocoelomate taxon' of progenetic origin, but instead may occupy a more basal position within the Polychaeta or Annelida.

Results

An update of the systematics of the eight most important interstitial polychaete families is presented in alphabetic order. The dinophilids are not treated here because they belong to the macrofaunal family Dorvilleidae (see Introduction). The genera and number of species (in parenthesis) is summarized and an update on current hypotheses on their phylogenetic position within Polychaeta is presented. Additional information summarizing previous and new results on morphology and distribution is provided for the Diurodrilidae, Nerilidae and Psammodrilidae. This is provided in relevance to the remarks on their evolution, which may not be so simple that they all have evolved from macrofaunal forms by progenesis. Detailed reviews and supplementary information on the interstitial polychaete families can be found in Westheide (1988), Westheide (1990), Beesley et al. (2000), and Rouse & Pleijel (2001).

Diurodrilidae Kristensen & Niilonen, 1982

The family consists of six described species belonging to *Diurodrilus* Remane, 1925 (250–500 μm long). Two undescribed species are known from New Zealand (Riser, 1984) and an undescribed species from Queensland, Australia with dorsal 'cuticular plates' is illustrated by Paxton (2000, fig. 1.64). A detailed description and morphological comparison of the six described species was made by Kristensen & Niilonen (1982) and Villora-Moreno (1996).

Systematics

The genus *Diurodrilus* was originally placed in the Dinophilidae by Remane (1925). Kristensen & Niilonen (1982) demonstrated that this genus deserved family status and erected the Diurodrilidae. The diurodrilids have been proposed to have a resemblance to gnathostomulids (Kristensen & Niilonen, 1982) and it has been hypothesized that psammobiontic 'worms', primarily the Gnathostomulida, are related to Annelida (e.g. Nielsen, 1995). However, Kristensen & Eibye-Jacobsen (1995) totally refuted the idea that Diurodrilidae and Gnathostomulida could be related, but stated that the phylogenetic relationship of the family within the Polychaeta remains unclear. A comparison between Gnathifera, especially *Limnognathia maerski* Kristensen & Funch, 2000 (Micrognathozoa) and Diurodrilidae was made by Kristensen & Funch (2000). Although several striking similarities were found, the overall conclusion was that these were either superficial or have evolved by convergence. Recently, the Diurodrilidae was included in Dorvilleidae (Rouse & Pleijel, 2001) but as these authors stated, they based this alone on superficial similarities of *Apodotrocha* Westheide & Riser, 1983 and *Dinophilus* Schmidt, 1848.

Additional information

Diurodrilids possess a tripartite prostomium, a metastomium (peristomium), 5 trunk segments (weakly segmented) and a pygidium with forked toes (Fig. 1A–D) provided with duo-glands system (adhesive glands) and muscles. Adhesive glands are also found on the prostomium. The oval mouth opening is located ventrally on the metastomium, and surrounded by a cuticular ring. Labial lobes may be present in all species but are so far only observed in the here presented SEM illustrations of *D. minimus* (Fig. 1C). Evidence for the monophyly of the family is the single epidermal cells (ciliophores) located ventrally on head and trunk. The ciliophores carry regularly arranged cilia with very long rootlets (Fig. 2A–B). The prostomium and metastomium (peristomium) are provided with ovoid ciliophores, while the trunk has rectangular ciliophores, forming a discontinuous, midventral band (Figs 1A–B, 2A–B). The trunk ciliophores are the locomotory organs, while the prostomial

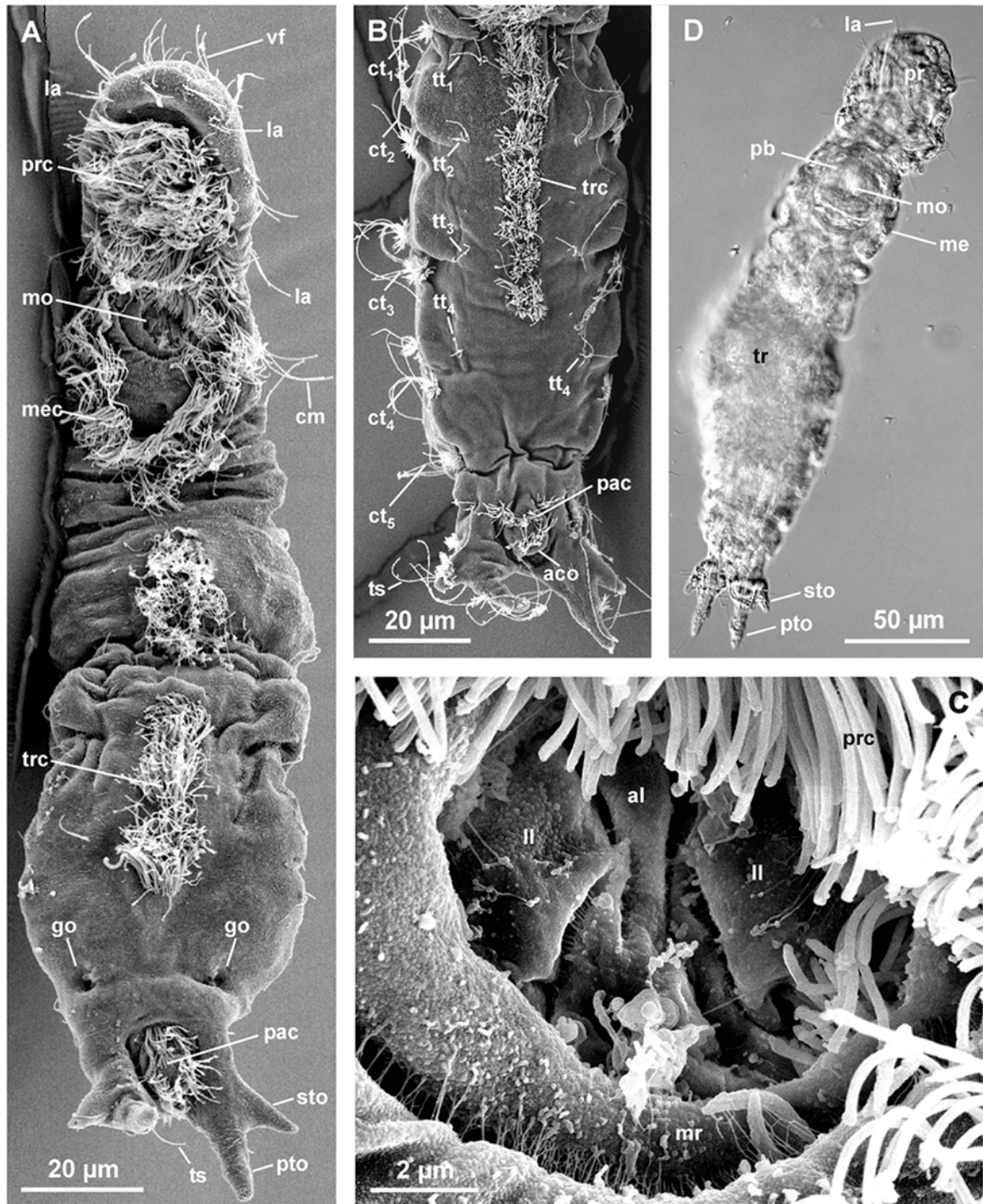


Figure 1. *Diurodrilus minimus* Remane, 1925 from Åero, Denmark. Material relaxed with cocaine, fixed in 2% glutaraldehyde and postfixed in 1% OsO₄. (A–C) Scanning electron micrographs of the ventral ciliation showing the prostomial (prc), metastomial (mec) and trunk ciliophores (trc). The mouth opening (mo) is surrounded by a cuticular mouth ring (mr); the single anterior labial lobe (al) and bifid paired labial lobes (ll) are seen extruded in the mouth opening. Stiff sensory bristles consisting of long adjoined cilia, are present on the prostomium (vf, la), metastomium (cm) and the five trunk segments (ct_{1–5}). The primary (pto) and secondary toes (sto) are provided with a few stiff bristles as well (ts). Not previously observed, ciliary tufts of the trunk (tt_{1–4}) are located ventrally on the first four trunk segments. The preanal cilia field (pac) is found around the short anal cone (aco). Paired male gonopores (go) are located on the fifth trunk segment. (D) Differential interference contrast micrograph of live animal (relaxed with cocaine), showing the prostomium (pr), metastomium (me) with the pharyngeal bulb (pb), and the very weak segmentation of the trunk (tr).

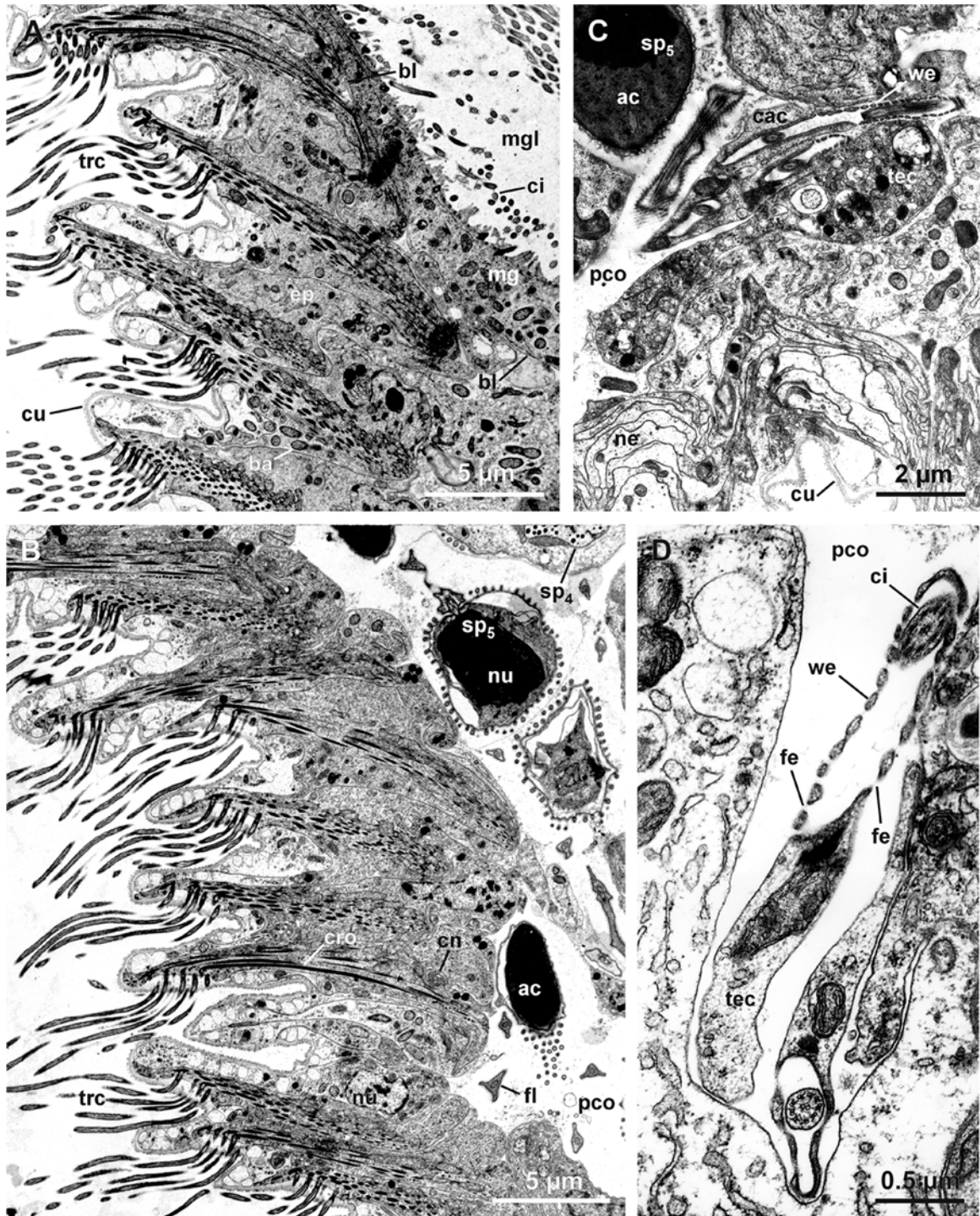


Figure 2. Transmission electron micrographs of *Diurodrilus subterraneus* Remane, 1934 from Ystad, Sweden. Material fixed directly in 1% OsO₄ in 50% seawater adjusted to pH 7.4 with Na cacodylate buffer (see Kristensen & Niilonen, 1982; Kristensen & Eiby-Jacobsen, 1995 for more information). (A–B) Sagittal sections showing trunk ciliophores. (A) ‘Acoelomate’ condition is present in first trunk segment. The epidermis (ep) with the trunk ciliophores (trc) is only separated from the midgut (mg) by two basal laminae (bl). (B) ‘Pseudocoelomate’ condition is present in third and fourth trunk segments. The spermatids (sp₄₋₅) are lying free in the body cavity (pco), which is not surrounded by a peritoneum. (C–D) Cross-sections of the second protonephridium in the third trunk segment. The terminal cells (tec) are monociliated. The weir (we) of the protonephridium has a very thin fenestration lamina (fe) in contact with the pseudocoel (pco). Abbreviations: ac, acrosome; ba, symbiotic bacteria; cac, canal cell; cn, ciliophore nerve; cro, cilia rootlets; cu, cuticle; fl, flagellum; mgl, midgut lumen; ne, ventral cord nerve; nu, nucleus; tec, terminal cell.

ciliophores may be used as a broom to collect food particles. Although the trunk ciliophores may be functional homologous with the midventral ciliary band found in other meiofaunal polychaetes, the ciliary structure and discontinuous distribution in small transverse bands clearly discriminate them (Figs 1A–B, 2A–B). Long sensory bristles (compound cilia) (vf, la) are found dorsally and latero-ventrally on the prostomium (Fig. 1A), and latero-segmentally positioned (cm) on the metastomium (Fig. 1A) and the trunk (ct_{1–5}, Fig. 1B). The forked toes are also provided with tactile bristles (Fig. 1B, ts). Transverse ciliary bands seem to be lacking, except for in the new species from Australia, but the ventral ciliary tufts of the trunk observed on *D. minimus* (Fig. 1B, tt_{1–4}) may be homologous with such ciliary bands. There are no signs of parapodial appendages or chaetae.

Diurodrilids are gonochoristic. The females have paired ovaries that contain one or two large oocytes. The trunk of the males is often found filled with spermatids or spermatozoa lying free in a single large cavity ('pseudocoelom') in the trunk. The spermatozoa are highly specialized with a giant acrosome (Fig. 2B) and the middle piece covered with modified microvilli (mushroom-shaped bodies, see Kristensen & Eibye-Jacobsen, 1995). Males have paired gonopores (go) located on the fifth trunk segment (Fig. 1A).

Two pairs of protonephridia are observed in *D. westheidei* Kristensen & Niilonen, 1982 and *D. subterraneus*. The terminal cell is monociliated and has a weir without basal lamina (Fig. 2C, D), and the very tiny fenestration lamina (fe) functions as the only filter for ultrafiltration of the pseudocoelomic fluid into the protonephridium (Fig. 2D). The cilium from the terminal cell is spiraled several times in the canal cell (Fig. 2C), and it seems that the protonephridia lie in close contact with the germinal cells. Nephridiopores were not observed. Basal laminae are weakly developed or totally lacking between the protonephridia and the germinal cells. The blood vascular system seems to be absent, and the somatic muscles are very tiny. The coelomic condition is unsatisfactorily understood. In the first trunk segment of *D. subterraneus* the ciliophores are in close contact with the cells of the midgut ('acoelomate condition', Fig. 2A). In the other four trunk segments the ciliophores are separated from

the midgut by a large cavity where the spermatozoa and the protonephridia are located ('pseudocoelomate' condition, Fig. 2B).

Remarks on evolution

The Diurodrilidae do not possess any larval characters (besides small size) and have no close resemblance to any present macrofaunal families, which are two criteria for recognizing a pro-genetic origin. The ventral band of trunk ciliophores is not interpreted as a larval feature but as a unique specialization. The 'acoelomate/pseudocoelomate' condition and various morphological specializations cannot be used as evidence for a secondary miniaturization or that this exclusive meiofaunal family should have evolved from a macrofaunal form by progenesis. Pro-genetic origins of other meiofaunal taxa like the gnathostomulids, micrognathozoans and rotifers from juvenile eucoelomate Spiralia during the 'Cambrian explosion' is even an improbable explanation for their 'acoelomate/pseudocoelomate' condition. Although no phylogenetic justification exists, it has been well argued by Bartolomaeus & Ax (1992) that 'acoelomate' condition and lack of larval state are plesiomorphic character states in the Bilateria. However, the variability of coelomic conditions throughout the animal kingdom (see Bartolomaeus, 1993) indicates that the 'acoelomate', 'pseudocoelomate' or 'eucoelomate' condition should be used with caution analyzing phylogenetic relationships. Ciliophores are found in both *Neotenotrocha sterreri* Eibye-Jacobsen & Kristensen, 1994 (Dorvilleidae) and *Limmognathia maerski* (Micrognathozoa), but they differ in several aspects and are more developed in *Diurodrilus* (see Eibye-Jacobsen & Kristensen, 1994; Kristensen & Funch, 2000). Nuchal organs, characteristic for polychaetes, have never been found in Diurodrilidae. The findings of gonopores above the pygidium in this study (Fig. 1A) contradicts the idea that the anal cone in diurodrilids should be homologous with the copulatory organ in *Dinophilus* (see Rouse & Pleijel, 2001). The other similarities with dorvilleids pointed out by Rouse & Pleijel (2001) are superficial and do not provide evidence for a relationship within the Dorvilleidae. It is there-

fore at present not possible to eliminate that the Diurodrilidae could have branched off very early within the Polychaeta. The new data on the protonephridia and the body cavity condition of *Diurodrilus subterraneus* (Fig. 2) may indicate that diurodrilids are in fact primary small interstitial annelids, but it remains an unproven alternative to the current comprehension of a progenetic origin of the family. Additional morphological studies in eLSM and TEM, and in particular molecular data are strongly needed for small aberrant families like the Diurodrilidae.

Nerillidae Levinsen, 1883

Nerillidae is the largest meiofauna family in Polychaeta with 48 species in 17 genera (generally, 300 μm –2 mm in length): *Afronerilla* Faubel, 1978 (1 species), *Akessonella* Tzetlin & Larionov, 1988 (1), *Aristonerilla* Müller, 2002 (1), *Bathychaetus* Faubel, 1978 (1), *Leptonerilla* Westheide & Purschke, 1996 (2), *Megonerilla* Boaden, 1961 (3), *Mesonerilla* Remane, 1949 (9), *Micronerilla* Jouin, 1970 (1), *Nerilla* Schmidt, 1848 (12), *Nerillidium* Remane, 1925 (9), *Nerillidopsis* Jouin, 1966 (1), *Paranerilla* Jouin & Swedmark, 1965 (2), *Psammoriedlia* Kirsteuer, 1966 (1), *Thalassochaetus* Ax, 1954 (1), *Trochonerilla* Tzetlin & Saphonov, 1992 (1), *Troglochaetus Delachaux*, 1921 (1), and *Xenonerilla* Müller, Bernhard & Jouin, 2001 (1). Previous studies on the systematics and morphology of Nerillidae have been made by Swedmark (1959), Jouin (1967, 1968, 1970a, 1971), Schmidt & Westheide (1977), Westheide (1990) and Müller et al. (2001).

Systematics

In the earlier literature the nerillids have been placed along with nereids and syllids (e.g. Schmidt, 1848; Quatrefages, 1866). The family was later on classified as archiannelids, and various relationships within this group have been proposed (e.g. Beauchamp, 1910; Goodrich, 1912). The pharyngeal apparatus has been shown to have some similarities with that of protodrilids (Purschke, 1985). However, great structural differences exist as well and the resemblances are most likely a matter of convergence (Purschke & Jouin, 1988). Rouse & Fauchald (1997) place them in Aciculata

as incertae sedis, which is followed by Rouse & Pleijel (2001). Their superficial resemblance to juvenile onuphids, studied by Hsieh & Simon (1987) is pointed out by Westheide & Purschke (1996). This resemblance, as well as their otherwise meiofaunal characteristics, may point to a progenetic origin of the family (Westheide, 1990; Westheide & Purschke, 1996). Based on morphological studies, Rouse & Pleijel (2001) suggest a close affinity to *Aberranta* Hartman, 1965.

Westheide & Purschke (1996) proposed a regressive evolutionary pathway within Nerillidae, with *Leptonerilla* positioned most basally in the family. *Leptonerilla diplocirrata* Westheide & Purschke, 1996, *L. prospera* Sterrer & Iliffe, 1982 and *Mesonerilla diatomeophaga* Núñez, 1997 in Núñez et al. 1997 all have the following combination of character states: compound chaetae and maximum number of segments (9) and appendages among nerillids (3 antennae, 2 palps, 2 pygidial cirri, double parapodial cirri). *Mesonerilla diatomeophaga* should according to the definitions of *Leptonerilla* by Westheide & Purschke (1996) be reassigned to this genus. The presented character states were believed to represent the plesiomorphic conditions of the family (Westheide & Purschke, 1996). However, the hypothesis was not based on cladistic analyses, which are necessary to verify the basal position of *Leptonerilla* within the family, as well as the evolution of characters. Some of the character states presented may also prove to behave more homoplastic than predicted by Westheide & Purschke (1996).

Additional information

Nerillids are nearly all marine and distributed worldwide from the intertidal to abyssal depths (3660 m – see Worsaae & Kristensen, 2003). Nerillidae have generally been characterized as an interstitial polychaete family as several species are described from either the interstitial sandy habitat or shell gravel. The gravel (with or without shells) containing nerillids is sometimes ‘dirty’, holding mud, although the content of silt in coarse interstitial habitats is generally not reported. When the very large interstices of the gravel contain deposits of silt it may in fact not represent a true interstitial environment. Many nerillid species are actually found outside the

interstitial environment: *Nerilla australis*, *Paranerilla cilioscutata* and *P. limicola* are described from mud bottoms (Willis, 1951; Jouin & Swedmark, 1965; Worsaae & Kristensen, 2003) and *Meganerilla swedmarki* has occasionally been found in mud (Saphonov & Tzetlin, 1997; personal observations of animals at 100–250 m depth in mud at Iqpik, Disko, West Greenland); *Leptonerilla prospera* is found in caves with fine silt (Sterrer & Iliffe, 1982); *Bathychaetus heptapous* Faubel, 1978 in mud with sand (Faubel, 1978); *Nerilla* spp. in detritus sand, organic debris, green algae and macrophytes (for review see Gelder, 1974); *Xenonerilla bactericola* Müller, Bernhard & Jouin-Toulmond, 2001 in bacterial mats of the Santa Barbara Basin (Müller et al., 2001); *Troglochaetus beranecki* Delachaux, 1921 in freshwater caves and pebbles in rivers (see review in Morselli et al., 1995); *Leptonerilla diatomeophaga* (Núñez, 1997 in Núñez et al. 1997) in caves with diatom carpets on lapilli (Núñez et al., 1997); and as mentioned several species have been found in ‘dirty’ gravel with or without shells e.g. *Aristonerilla brevis* (Saphonov & Tzetlin, 1997), *Meganerilla swedmarki*, *Mesonerilla armoricana* Swedmark, 1959, *M. fagei* Swedmark, 1959, *M. roscovita* Lévi, 1953, *Nerilla* spp., *Nerillidium troglochaetoides* Remane, 1925, *Thalassochaetus palpifoliaceus* Ax, 1954 and *Trochonerilla mobilis* Tzetlin & Saphonov, 1992 (Ax, 1954; Boaden, 1961; Gelder, 1974; Saphonov & Tzetlin, 1997; and personal observations on habitats of *A. brevis*, *Mesonerilla* spp., *N. troglochaetoides*. and *T. mobilis*). Many nerillid descriptions only give a poor habitat report, and the few observations of live animals generally do not describe behavior from the natural habitat but from sieved or decanted material. However, if a well-supported phylogeny of the family Nerillidae existed, it would be interesting to map the different nerillid habitats on the tree and then trace and analyze the evolutionary scenario.

Most nerillids have direct development, sometimes including brooding. They would only be able to spread from one locality to another and from the interstitial environment to other habitats by migration, dispersal of the sediment or continental drift. However, the obligate mud-dwelling *Paranerilla limicola* is found to have indirect development with a pelagic trochophore larva, which is

more easily spread by currents over larger distances to different habitats (Jouin & Swedmark, 1965). It would be interesting to know whether the plesiomorphic condition in nerillids is indirect development, which could indicate a non-interstitial origin of the family.

The freshwater nerillid *Troglochaetus beranecki* Delachaux, 1921 has been reported from many localities around central Europe (Germany, France, Italy) as well as from the Colorado Rocky Mountains (e.g. Delachaux, 1921; Pennak, 1971). According to Pennak (1971) the species most likely originated before the continental drift was well under way, which would explain its existence on continents on each side of the Atlantic, and he predicts that the species will be found in many other parts of North America. Nerillids are known from all continents except the Antarctic, and this wide geographical distribution as well as the diversity in habitats may very well reflect an old history of the family.

Remarks on evolution

Nerillids may have evolved in the interstitial habitat and secondarily spread to non-interstitial habitats. However, the opposite evolutionary history cannot be rejected based on current knowledge of their distribution.

Westheide (1987) considered different evolutionary pathways of meiofauna in the interstitial environment and the selective forces supporting them. The induction of progenesis was linked closely to the interstitial habitat, which possessed so extraordinary adaptational demands, that a one-step adaptation in size would be necessary to enter this habitat (Westheide, 1987). However, some of these evolutionary pathways, including progenesis, may also be applicable to the muddy environment.

The highest concentration of meiofauna in mud has generally been found in the upper one centimeter of the bottom (Coull & Bell, 1979). *Paranerilla cilioscutata*, *P. limicola*, *Meganerilla swedmarki* from Disko, West Greenland, *M. swedmarki* from the White Sea and *Nerilla australis*, all have been found in mud (Willis, 1951; Saphonov & Tzetlin, 1997; Worsaae & Kristensen, 2003, unpublished observations). The three first of which were more specifically found in the sedi-

ment–water interface, which may be a size-specific niche for meiofauna organisms. This flocculent layer contains a higher concentration of small sized food particles compared to the underlying layers of the mud due to suspension and resuspension of less heavy particles. Furthermore, the layer is well oxygenated, thereby allowing respiratory exchanges of animals living there and facilitating a higher production of bacteria and algae. The meiofauna has therefore access to higher concentrations of oxygen and appropriate food items in this layer. In the interface, small organisms would be less exposed than larger motile organisms to selective predation. In some areas, the lower part of the sediment may be anoxic thereby limiting the meiofauna to the upper oxygen-rich layers. The uppermost part of the sediment–water interface may also be so loose that only small organisms using ciliary motion could move around without costly use of the musculature in actual swimming.

The flocculent layer of the sediment–water interface of muddy habitats may therefore function as a size-related niche, comparable to the size-specific niche of the interstices in the interstitial environment. The specific size limitations are dependent on the depth and density of the muddy flocculent layer. These factors are defined by local current conditions and the composition of sediment particles, which are the same abiotic parameters that define the space available in the interstitial environment (Swedmark, 1964). In lower parts of the mud bottom with less organic material and oxygen, the expenditure/use analysis for motile deposit-feeding macrofauna may be negative. The same may apply to existence above the bottom, where the current is higher. Energetically expensive burrowing or swimming is then only worthwhile when a great deal of food is available and small distances have to be covered. Thus, a selection pressure may exist in or above mud bottoms for a decrease in size down to dimensions that allow an exploration of the sediment–water interface.

In a very thin or loose flocculent layer a pro-genetic evolution would be advantageous in providing a one-step speciation to a small size. If the interface is more extensive or particle dense, middle-sized animals may be able to explore some of the same advantages of this environment, and a

miniaturization by gradual decrease in size is also possible.

Besides a reduction in size a well-developed ciliary covering may be particularly advantageous when entering the niche of the sediment–water interface of the muddy environment. Adhesive organs, as found on many interstitial forms would not be useful. It is more important to have the ability to move on or in the flocculent layer as well as to sink into the mud during current and other turbulent influence to avoid dispersal to the water column. *Paranerilla cilioscutata* and *P. limicola* possess a distinct dense dorsal ciliation (Fig. 3A, C) making them capable of not only gliding ‘epibenthically’ on top of the flocculent layer (by help of the ventral ciliation) but also entering the mud. The animal burrows into the flocculent layer by transporting mud particles across the dorsal surface by help of the very dense dorsal ciliation (Jouin & Swedmark, 1965; Worsaae & Kristensen, 2003). No information is given on the motility of *Nerilla australis*; however, Willis (1951) describes it with thin dorsal transverse ciliary bands. Although far from as dense in their distribution, they may have some resemblance to the dorsal ciliation found in *Paranerilla*. *Meganerilla swedmarki* almost lacks a dorsal ciliation (Fig. 3B) and cannot burrow, but it is capable of gliding on the sediment surface. When doing so, it generates a thick mucus-string from the posterior end of the midventral ciliary band, attaching it to the uppermost flocculent layer (personal observations). Indirect development, which is found in the obligate mud-dwelling *P. limicola* (Jouin & Swedmark, 1965), would provide a possible way of spreading and of decreasing intraspecific competition, when living outside the interstitial environment. Jouin & Swedmark (1965) argued that the large number of relatively small eggs found in the facultative mud-dwelling *Meganerilla swedmarki* by Boaden (1961) might also indicate an indirect development.

Meganerilla swedmarki is a facultative mud-dweller (Saphonov & Tzetlin, 1997; personal observations of animals from West Greenland) and does not seem as well adapted morphologically to the muddy habitat as the obligate mud-dwelling *Paranerilla* species. It therefore seems possible that more nerillids may be facultative mud-dwellers. Although *Nerilla*, *Paranerilla* and *Meganerilla* have a very different body shape,

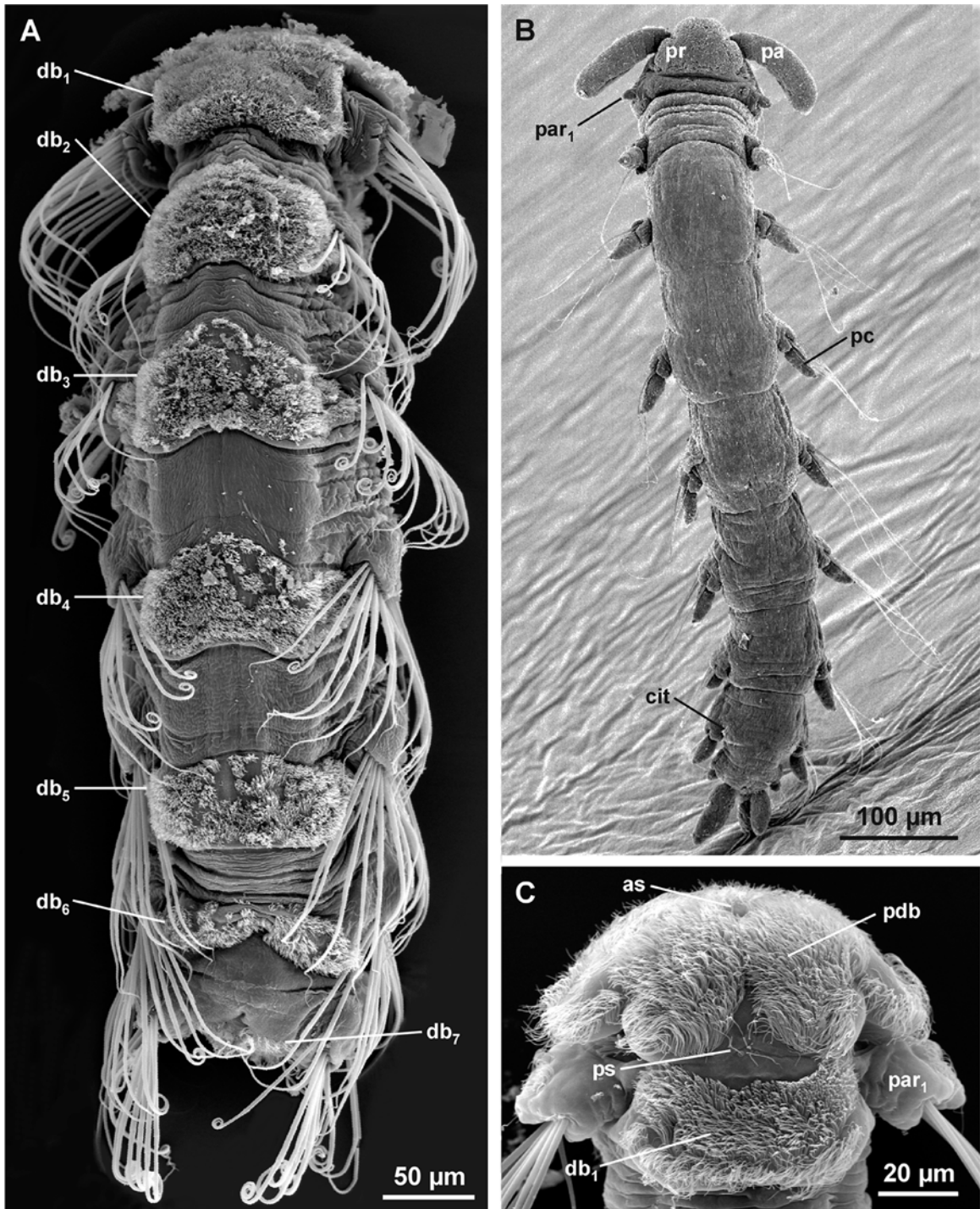


Figure 3. Scanning electron micrographs of *Paranerilla cilioscutata* Worsaae & Kristensen, 2003, *P. limicola* Jouin & Swedmark, 1965 and *Meganerilla* cf. *swedmarki* Boaden, 1961 (see Worsaae & Kristensen, 2003 for details on fixation). (A) Dorsal view of *Paranerilla cilioscutata* from North East Greenland, showing dorsal ciliary plates on segment 1–7 (db_{1-7}). (C) Close-up of *Paranerilla limicola* from Kristineberg, Sweden, showing dense ciliation on prostomium with prostomial ciliary plate (pdb) and on segment 1 with dorsal ciliary plate (db_1). Parapodia of segment 1 (par_1) and two groups of sensory cilia are present: anterior sensory cilia (as) and posterior sensory cilia (ps). (B) Dorsal view of *Meganerilla* cf. *swedmarki* from Disko, West Greenland, showing sparsely ciliated dorsal surface only with parapodial ciliary tufts (cit). Abbreviations: pr, prostomium; pa, palp; pc, parapodial cirri.

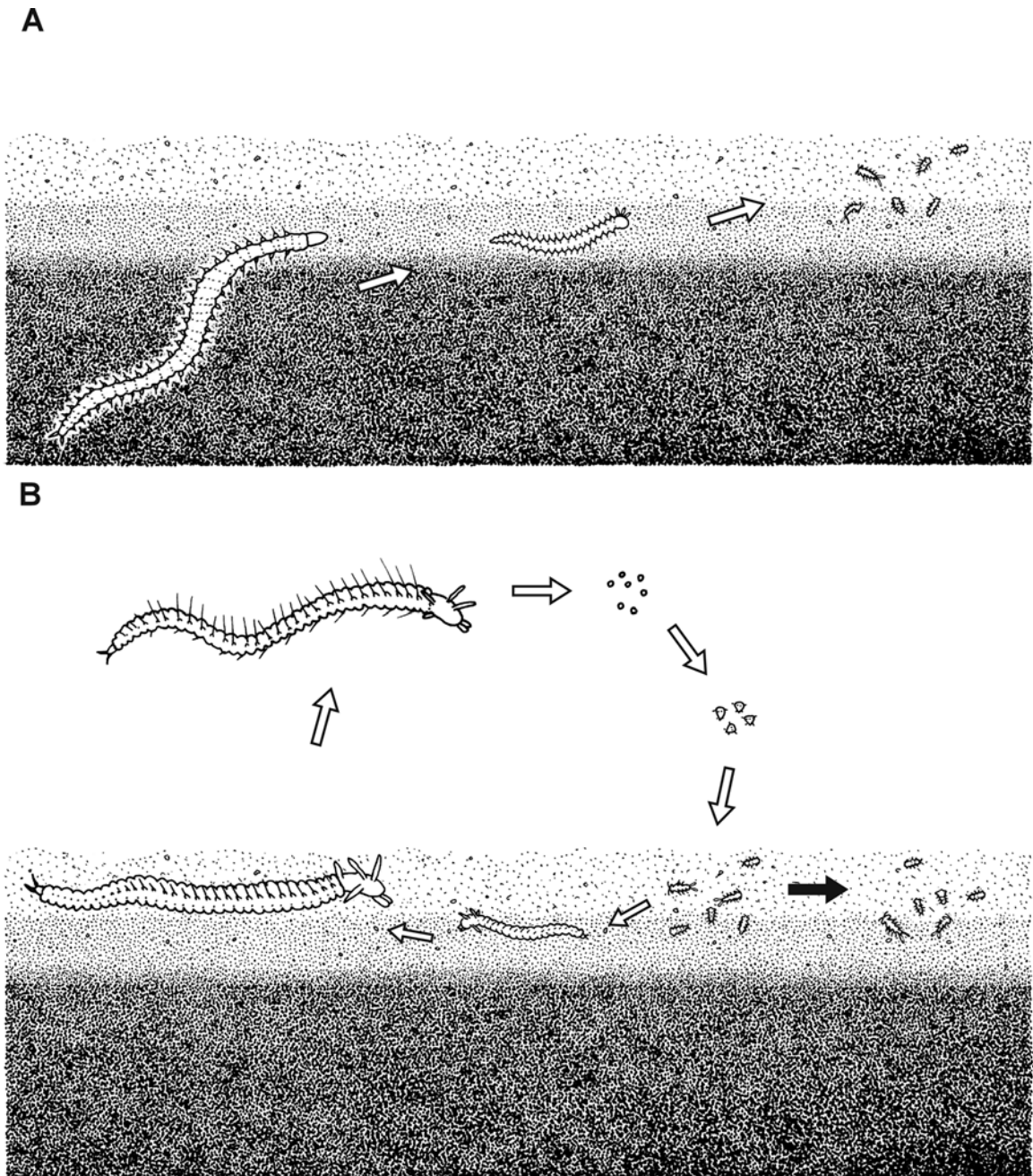


Figure 4. Hypothetical evolutionary pathways in muddy habitats (following the schemes presented by Westheide, 1987). (A) Regressive evolution, by gradual decrease in size from endopsammic macrofaunal form (in lower mud layers) to meiofaunal form in the mud interface (flocculent layer). (B) Example of progenetic origin (black arrow) of present meiofauna in the mud interface (flocculent layer) from a temporary meiofaunal juvenile stage of an epibenthic macrofauna organism with a pelago-benthic lifecycle.

they are all relatively large and robust compared to the interstitial nerillids (e.g. most species of *Nerillidium*). This is in accordance with the generally larger size of the mud-dwelling meiofauna (Coull

& Bell, 1979). According to Coull & Bell (1979) the sand fauna tends to be long and slender, whereas the mud fauna is not restricted to a particular morphology. Compared to most other interstitial

polychaetes, the nerillids possess many appendages and long chaetae and are not particularly slender, however, they are relatively small.

Based on these arguments, it is at present not possible to reject the idea that the nerillids could have evolved in mud – either by a gradual transition in size (Fig. 4A) or by progenesis (Fig. 4B). However, more sampling in muddy habitats as well as phylogenetic analyses are needed to clarify their evolution.

Parergodrilidae Reisinger, 1925

Two species in two genera are described in the family (0.7–2.6 mm long): *Parergodrilus* Reisinger, 1925 (1) and *Stygocapitella* Knöllner, 1934 (1). The latter taxon may contain several species according to Schmidt & Westheide (2000).

Systematics

The family was described as ‘archiannelids’ (Reisinger, 1925), and has since then been characterized as oligochaetes (Meyer, 1927), capitellids (in the description of *Stygocapitella* Knöllner, 1934), related to nerillids (Reisinger, 1960), to ctenodrilids (Fauchald, 1977), and to *Hrabeiella* Pizl & Chalupsky, 1984. Rouse & Fauchald (1997) placed the family as incertae sedis in Polychaeta. Although the family shares many similarities with clitellates and the terrestrial *Hrabeiella*, most of these have been explained by convergent evolution and recent morphological studies regard them as polychaetes (Rota, 1998; Purschke, 1999; Purschke et al., 2000). Two cladistic analyses based on molecular data of 18S rDNA support the independent evolution of Parergodrilidae and Clitellata (Rota et al., 2001; Struck et al., 2002a). Struck et al. (2002a) also found a relationship of *Stygocapitella subterranea* Knöllner, 1934 (although weakly supported) with a cluster comprising the polychaetes *Scoloplos armiger* (O.F. Müller, 1776), *Questa paucibranchiata* Giere & Erseus, 1998 and sometimes *Magelona mirabilis* (Johnston, 1865).

Polygordiidae Czerniavsky, 1881

The family consists of one genus, *Polygordius* Schneider, 1868 with 15 nominal species (1–10 cm long). The validity of *Chaetogordius canaliculatus*

Moore, 1904 described from fragmentary material was questioned by Hermans (1969) and the species (and genus) was considered invalid by Westheide (1990). A revision of *Polygordius* was made by Rota & Carchini (1999).

Systematics

Early literature placed the family near the Opheliidae (e.g. McIntosh, 1875), and later on in the ‘archiannelids’ together with *Protodrilus* Hatschek, 1880 and closely related to *Saccocirrus* Bobretzky, 1871 (e.g. Marion & Bobretzky, 1875; Hatschek, 1878, 1893). Hatschek (1893) suggested that opheliids (classified with the Spiomorpha) were derived from saccocirrids that in their turn had evolved from polygordiids. This hypothesis has been rejected, and the family is generally believed to be highly derived within the polychaetes. According to Westheide (1990), *Polygordius* is a rather isolated genus with no close affinity to Protodrilida. However, the relationship to Spiomorpha was indirectly supported by Rouse & Fauchald (1997), who placed the family as incertae sedis in Canalipalpata, partly by assuming that the palps are grooved, which they are not. A sister group within the Opheliidae has been reconsidered, based on similarities in the structure of cuticle, musculature and locomotion as well as by rejecting the interpretation of grooved palps (Hermans, 1969; Rouse & Pleijel, 2001). According to Westheide (1990), these unproven similarities with Opheliidae might as well reflect convergent adaptations to a life in coarse gravel sediments. In a recent cladistic analysis based on molecular data (18S rDNA) a species of *Polygordius* tends to clade with *Saccocirrus papillocercus* Bobretzky, 1871 (Struck et al., 2002a). Although more genes and taxa need to be examined, molecular systematics seems an obvious way to gather more information on the phylogenetic position of this morphologically indistinct family.

Protodrilidae Czerniavsky, 1881

The family consists of 31 species in two genera (2–15 mm long): *Parentodrilus* Jouin, 1992 (1 species) and *Protodrilus* Hatschek, 1880 (30). Detailed morphological studies and revisions of *Protodrilus*

have been published by Pierantoni (1908), Jägersten (1952), Jouin (1970b), and von Nordheim (1989) and of *Parenterodrilus* by Jouin (1979, 1992).

Systematics

The Protodrilidae were originally considered to be archiannelids by Hatschek (1893). Morphological studies by Purschke & Jouin (1988) supported the definition of three families (Protodrilidae, Protodriloididae and Saccocirridae) and their inclusion in the monophyletic order Protodrilida. Within this order, the Saccocirridae was suggested to form a clade with the Protodrilidae, and with the Protodriloididae, as their closest relative. The order Protodrilida may be a sister group to Spionida (Purschke & Jouin, 1988). This view supported the close relationship to Spionida proposed by Orrhage (1974), who found similarities in the nervous system and the development of the palps, especially those of Apistobranchidae. A progenetic origin of these families was indicated by Westheide (1985). The three families were placed as incertae sedis in Canalipalpata by Rouse & Fauchald (1997) and Rouse & Pleijel (2001); in the latter they are grouped as an order.

Additional information

The ultrastructure of protodrilids is generally well investigated – especially the gutless species *Parenterodrilus taenioides* (Jouin, 1979) (see Jouin, 1992). A cross section of *Protodrilus* sp. from Portugal will serve to illustrate the main characters and coelomic conditions for an anterior trunk segment (Fig. 5). The epidermal cells are covered with a well-developed cuticle. Single stiff sensory cilia (se) surrounded by microvilli penetrate the cuticle. The continuous median ventral band of locomotory cilia is always present. It is formed by two clusters of epidermal cells. The cilia rootlets of the locomotory cilia are relatively short, however, an offshoot of the cell with ciliary rootlets extends into a neighboring cell (icr). The two intraepidermal nerve cords are in close contact with the median ventral ciliary band. True ganglia were not observed, but the nerve cord neuropil may be surrounded by clusters of glial cells. Protodrilids are true coelomates with a body cavity along each side (Fig. 5, eco) crossed by oblique muscles, but the peritoneal layer is partially incomplete, e.g. the

coelomic space is lined by the peritoneum and by large longitudinal muscles (lmu) arranged in distinct segmental blocks separated from the epidermis by a thin basal lamina. The oblique muscles lack basal laminae. Circular muscles seem to be absent. The ventral blood vessel (vbv) is surrounded by the midventral basal laminae. The midgut cells are densely ciliated.

The Protodrilidae is an example of a clearly ‘eucoelomate’ interstitial family, which may have evolved by progenesis. A progenetic origin and/or interstitial habits do therefore not necessarily involve a reduction of the coelom.

Protodriloididae Purschke & Jouin, 1988

The family was erected based on species formerly assigned to Protodrilidae and consists of two species in the genus *Protodriloides* Jouin, 1966 (up to 13 mm long). Detailed morphological studies were made by Jouin (1966) and Purschke & Jouin (1988).

Systematics

The family differs morphologically from Protodrilidae, by, e.g., the presence of tentacles appearing as anterior extensions of the prostomium and lacking a central canal; external fertilization, aflagellate spermatozoa, large yolky eggs laid in ‘cocones’, direct development of benthic larvae; and presence of chaetae in *Protodriloides chaetifer* (Remane, 1926) (Jouin, 1966, 1978–1979; Westheide, 1990). For the phylogenetic position in Polychaeta, see above (Protodrilidae, *Systematics*).

Saccocirridae Czerniavsky, 1881

The family consists of 18 nominal species belonging to *Saccocirrus* Bobretzky, 1871 (length up to 3 cm). Detailed morphological studies were provided by Jouin & Rao (1987) and Purschke & Jouin (1988), and the most recent revision is given by Brown (1981).

Systematics

The family is thought to be closely related to Protodrilidae (Purschke & Jouin, 1988). It shows some resemblance to Protodrilidae in, e.g., the tentacle morphology and pharyngeal apparatus.

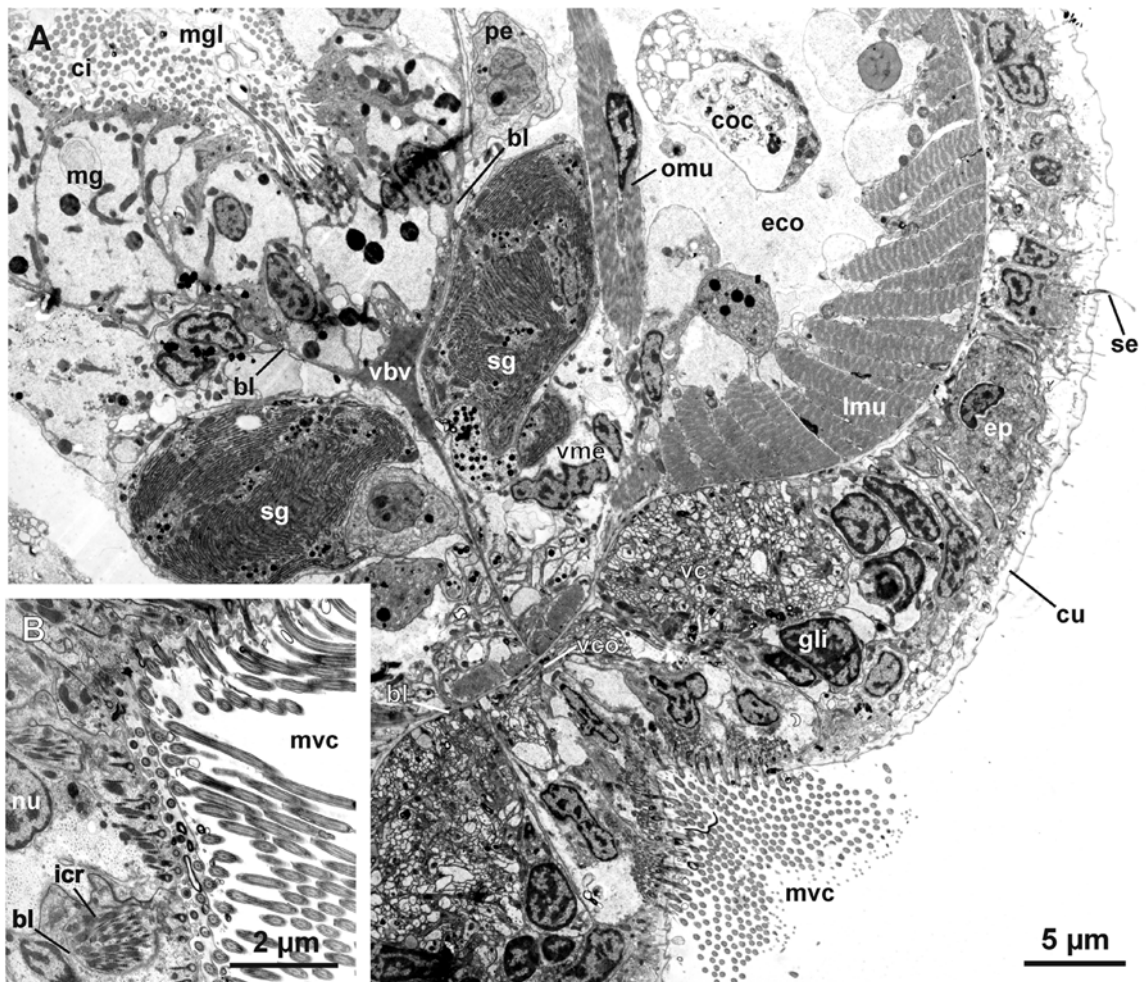


Figure 5. Transmission electron micrographs of *Protodrilus* sp. from Valle de Lama, Portugal. Material fixed in modified trialdehyde and postfixed in 1% OsO₄ (see Lake, 1973 about fixation). Ultrathin sections of Epon-embedded material stained in 3.5% uranyl acetate at 60 °C and in lead citrate at 20 °C. (A) Ventral cross section of anterior trunk segment showing 'eucoelomate' condition (eco), ciliated midgut cells (mg), salivary glands (sg), and the midventral ciliary band (mvc) covered by the intraepithelial ventral nerve cords (vc) with a ventral commissure (vco). (B) Close-up of the midventral ciliary band. The cells that contain ciliary rootlets (icr) are surrounded by a basal lamina (bl). Abbreviations: ci, cilia in midgut; coc, coelomocyte; cu, cuticle; ep, epidermis; gli, glial cell; lmu, longitudinal muscle; mgl, midgut lumen; nu, nucleus; omu, oblique muscle; pe, peritoneal cell; se, sensory cell with stiff cilium; vbv, ventral blood vessel; vme, ventral mesentery.

Other characteristics of the family are, e.g., the presence of various types of chaetae, parapodial stumps, and a complicated reproductive system. For the phylogenetic position of the family, see above (Protodrilidae, *Systematics*).

Psammodrilidae Swedmark, 1952

The family consists of three described species in two genera (1–8 mm long): *Psammodrilus* Swed-

mark, 1952 (2 species) and *Psammodriloides* Swedmark, 1958 (1).

Systematics

Whereas there is little doubt that Psammodrilidae must be placed systematically within the Polychaeta, their relationship to any particular polychaete family is much more doubtful. The only clue so far seems to be the fine structure of the abdominal uncini. As already pointed out by Swedmark

(1958), uncini with barbules are present only in Arenicolidae and Maldanidae. Recently, the family was regarded as the sister group of Arenicolidae and Maldanidae, based on detailed ultrastructural studies of these uncini (Meyer & Bartolomaeus, 1997). Rouse & Fauchald (1997) placed it as incertae sedis in Polychaeta.

Additional information

Only *Psammodriloidea fauveli* Swedmark, 1958 is a true interstitial species (up to 1 mm long), and it is possible that this species evolved by progenesis from a macrofaunal psammodriliid. However, several morphological data presented here point towards an alternative evolutionary scenario.

TEM-investigations of both *Psammodrillus balanoglossoides* and *P. aedificator* have shown unique cavities in the prostomium (the paired lateral and paired median cavities, see Swedmark, 1958), which are true coeloms with a peritoneum (Fig. 6). Furthermore, the peristomium (buccal region) of these species has a distinct segment-like collar region. The prostomial coeloms and the collar region are not found in juveniles, in the interstitial *P. fauveli*, or any other polychaetes. However, it seems that all psammodriliids have the two 'diaphragma sacs' (coeloms) in the anterior region described by Swedmark (1958, fig. 8). The ultrastructure of the collar region is unique within the polychaetes. The epidermis of the collar consists of hexagonally arranged microvillar cells, and totally lack cilia and cuticle (Fig. 7). The epidermal cells interdigitate and form ducts in the intercellular space. Especially the collar cells of *P. balanoglossoides* are basally strongly infolded, as is often seen in osmoregulatory cells (Fig. 7B). Kristensen & Nørrevang (1982) suggested that the collar cells are secretory, but they did not mention that the collar might secrete the mucous that glues the sand grains together in the tube or 'house' of the two species of *Psammodrillus*. Alternatively, the abundant and extensive microvilli of the collar region may represent an absorptive surface of small dissolved molecules in seawater.

Below the epidermal cells, the collar is bordered by two muscular diaphragms. These are believed to function as a suctorial pharynx (Westheide, 1990). In *P. balanoglossoides* the epidermal cells are separated from the muscular diaphragms by a very thick basement membrane

with collagen fibres (Fig. 7B). In *P. aedificator* the muscular diaphragms are compact and 'acoelomate' (Fig. 7A, see also Kristensen & Nørrevang, 1982). The border between the epidermal cells and the muscle cells consists only of a sandwich-like structure (two thin basal laminae), and the muscle cells attach directly to the basal lamina. Interstitial and juvenile psammodriliids lacking a collar region also totally lack muscular diaphragms.

The coelomic situation in the thorax and abdomen is very different in the three described species. In *P. balanoglossoides* the longitudinal muscles (lmu, Fig. 8A) form large sacs (coeloms) in the thorax. The animal is a true 'eucoelomate'. In *P. aedificator* the coelomic situation of the thorax is quite different. The animal is 'acoelomate', as the giant endoderm gut cells and the coelenchyme cells (Fig. 8B) fill up most of the thorax and abdomen and a true coelom, i.e. a body cavity lined by a continuous mesodermal epithelium, seems to be absent (see also Kristensen & Nørrevang, 1982, fig. 13). The longitudinal muscles and other muscles are diminutive, except from the muscles moving the three first pair of aciculae. Especially in the abdomen, the muscles are very tiny, the epidermis is very thin, and in the mid-dorsal sulcus the large midgut cells are in near contact with the environment (see Kristensen & Nørrevang, 1982, fig. 13). The endoderm gut cells may have a chordoid function. Most of the cytoplasm consists of a homogeneous granular matrix. The same kind of parenchymatic cells (endodermal) with a chordoid function are observed in plathyhelminthes and in gnathostomulids, e.g. *Rastrognathia* (see fig. 6 in Kristensen & Nørrevang, 1977).

The metanephridial system of *P. balanoglossoides* is well-developed with a ciliated and microvillar funnel (mef) and a metanephridial duct (med) passing through the longitudinal muscles as a pore is observed in the sixth segment using TEM (Fig. 8A), but additional metanephridia may be present in other abdominal segments. The metanephridial funnel opens into a true coelom lined with peritoneum. The metanephridia of *P. aedificator* (Fig. 8B) contain only 7–9 cilia and the whole metanephridial system seems to be less developed.

Very little is known about the coelomic condition in the interstitial *Psammodriloidea fauveli*, but

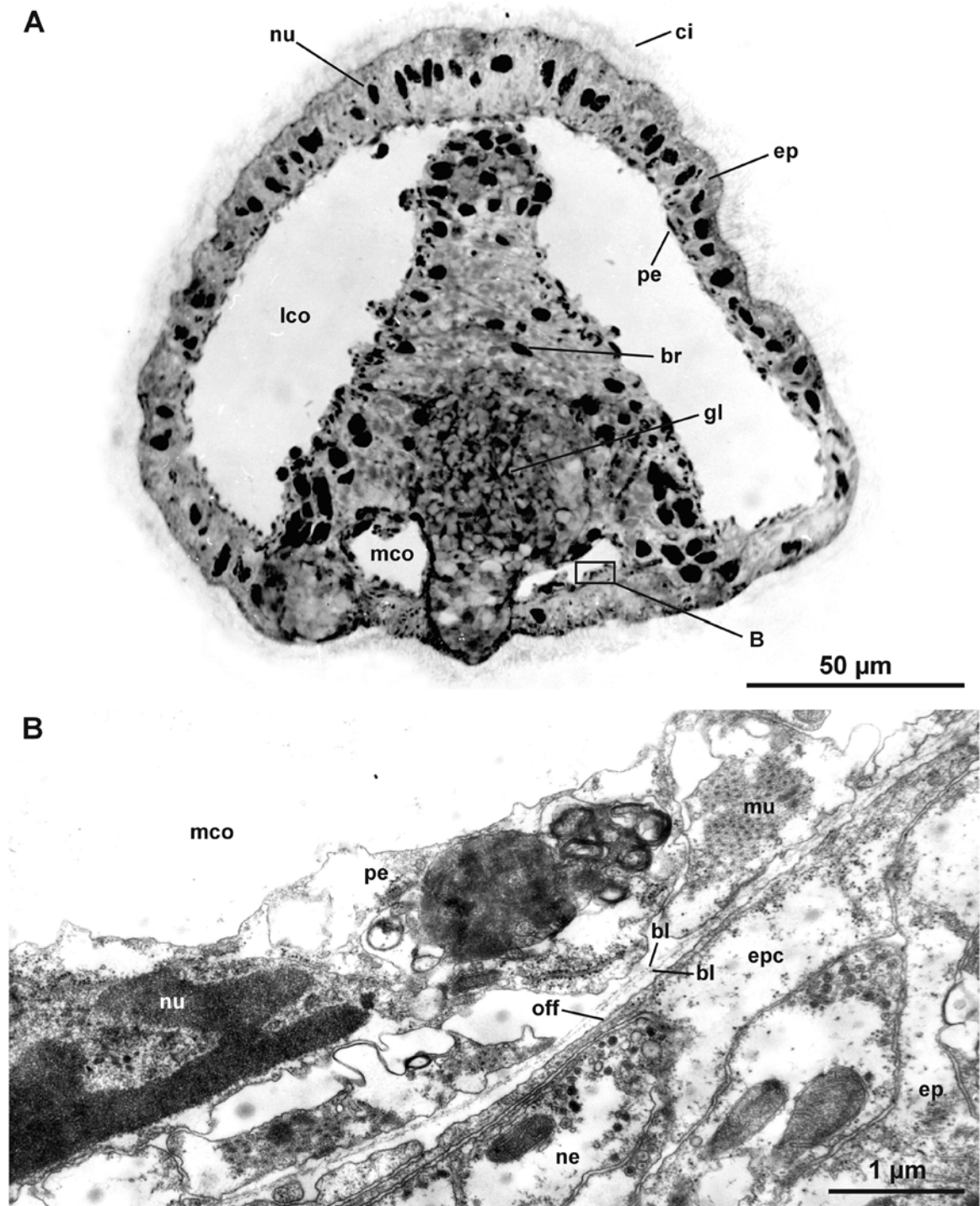


Figure 6. *Psammodrillus balanoglossoides* Swedmark, 1952 from Helsingør, Denmark. Material fixed in modified trialdehyde and postfixed in 1% OsO₄. (see Kristensen & Nørrevang, 1982). (A) Light microscope micrograph of semi-thin cross section (1 μ m) stained with toluidine blue and examined with DIC-technique. The section is located through the prostomium with the two large lateral coeloms (lco) and the two smaller median coeloms (mco). The very thin peritoneum (pe) covers the cavities of both coeloms. (B) Transmission electron micrograph of median coelom (mco). The coelom cavity is covered by peritoneal cells (pe) and some myoepithelial cells (mu). The epidermal cell (epc) has many cellular offshoots (off) in close contact with the epidermal basal lamina. Abbreviations: br, brain; ci, cilia covering the entire surface of the prostomium; ep, epidermis; gl, gland in close contact with the brain; ne, nerve process; nu, nucleus.

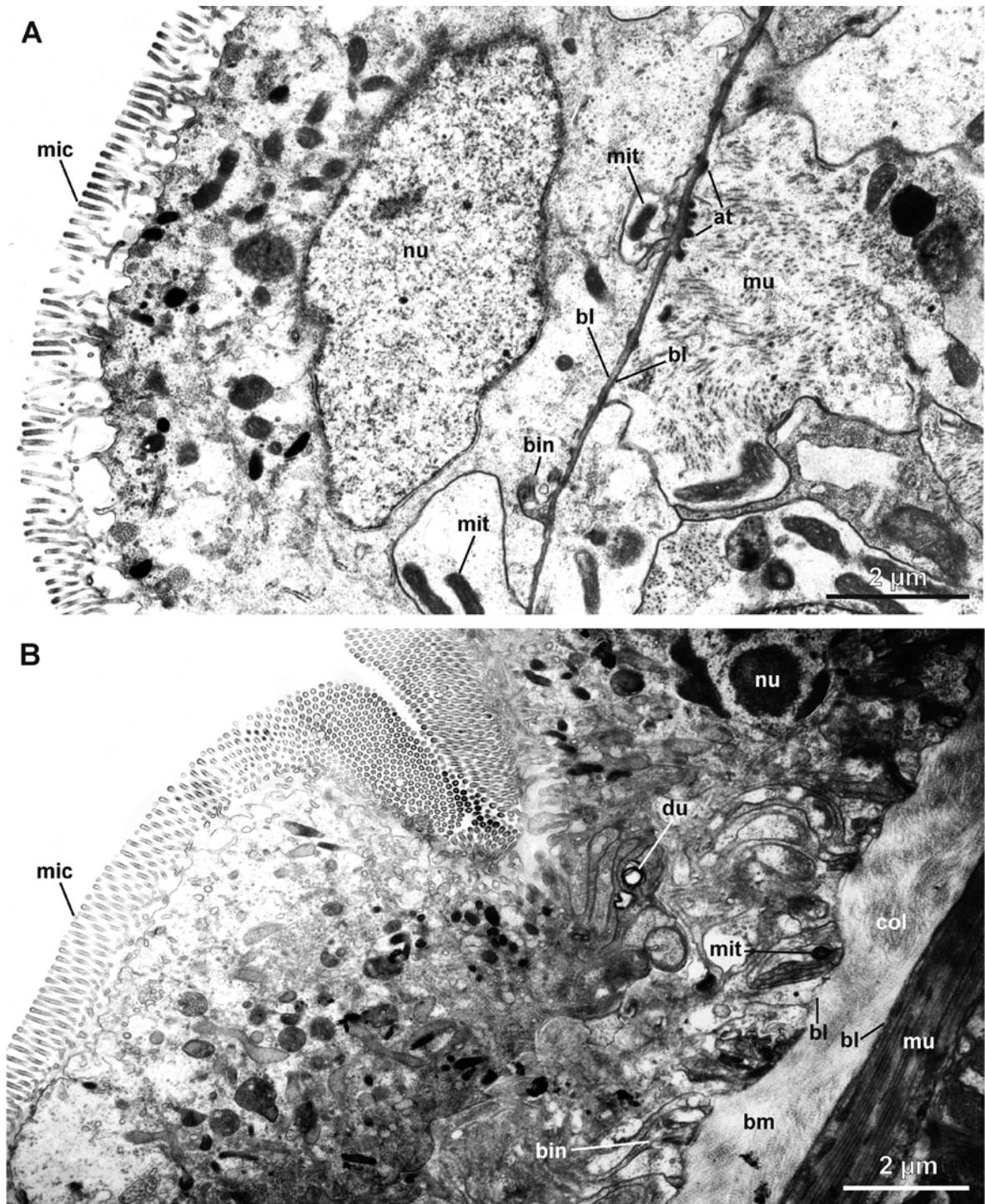


Figure 7. Transmission electron micrographs of the collar region of Psammodrillidae. For information on fixation and techniques see Kristensen & Nørrevang (1982). (A) *Psammodrillus aedificator* Kristensen & Nørrevang, 1982 from Disko Island, Greenland fixed directly in 1% OsO₄. Two closely opposed basal laminae (bl) present and few basal infoldings (bin) of the epidermal cells. No coelomic cavity present. (B) *Psammodrillus balanoglossoides* from Denmark. The two basal laminae form a true basement membrane (bm) with collagen fibers (col). The basal infoldings of the epidermal cells form a labyrinth with ducts (du). Abbreviations: at, muscle attachment; mi, microvilli of collar cell; mit, mitochondrion; mu, muscle; nu, nucleus.

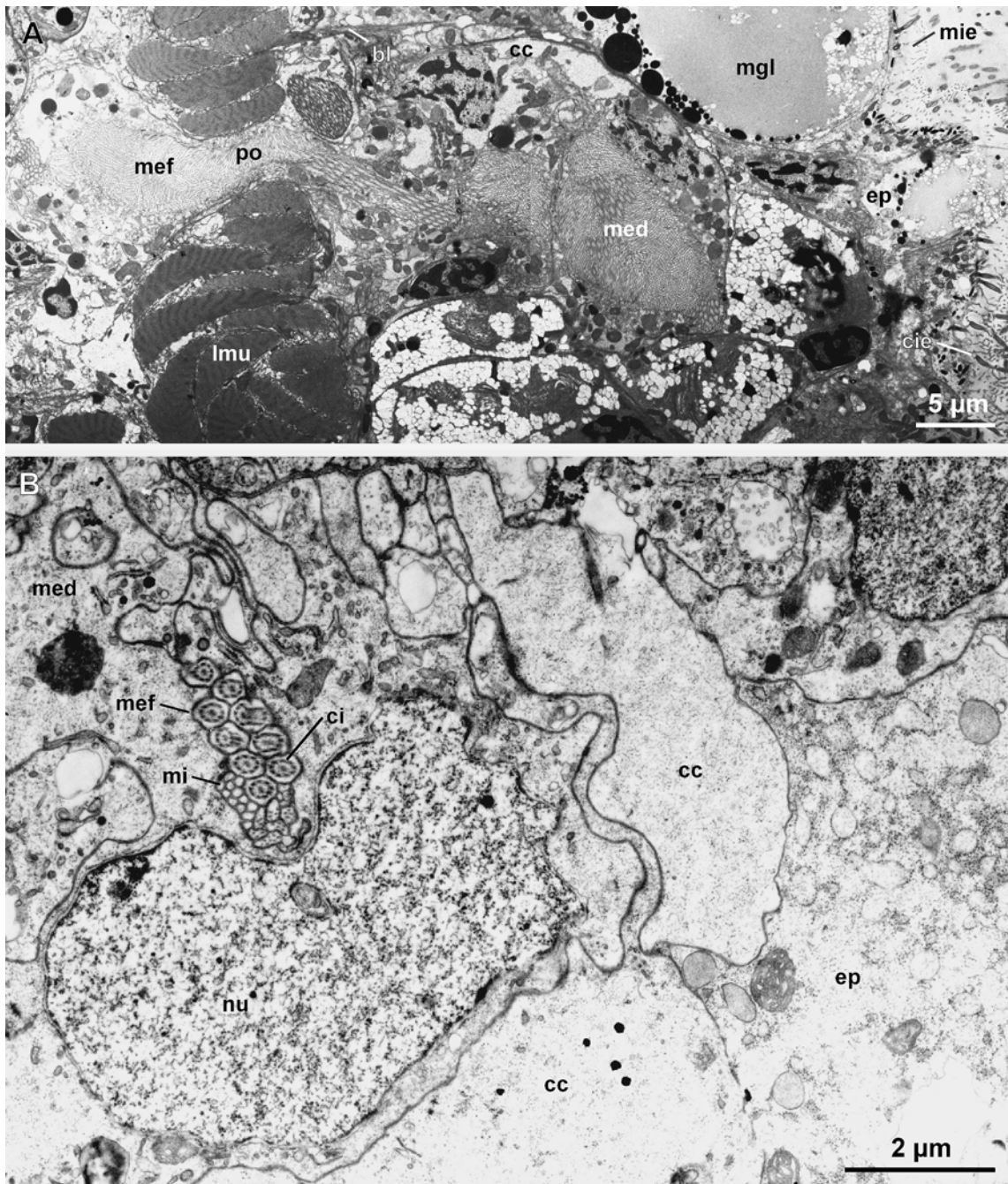


Figure 8. Transmission electron micrographs of the metanephridial system of Psammodrilidae. (A) *Psammodrilus balanoglossoides* from Denmark. A well-developed metanephridial system from the thorax region with a ciliated and microvillar funnel (mef) and a metanephridial duct (med) passing through longitudinal muscles (lmu) as a pore (po). (B) *Psammodrilus aedificator* from Greenland. A weakly developed metanephridial system from the thorax region with few cilia (ci) and microvilli (mi) surrounded by coelenchyme cell (cc). Abbreviations: bl, basal lamina; cie, cilia of epidermis; ep, epidermis; mie, microvilli of epidermis; mgl, mucous gland of epidermis; nu, nucleus.

Fransen (1980) published some information on an undescribed species of *Psammodriloides* from USA. The animal is 'acoelomate' and the metanephridia are weakly developed. What is very interesting is that the compactness of the trunk is formed by large coelenchyme cells and not by the endoderm cells as in *P. aedificator*.

Remarks on evolution

The conclusion of the TEM-investigations of the psammodrilids is that the 'acoelomate' *P. aedificator* is not an intermediate form between *P. balanoglossoides* and *Psammodriloides fauveli*, where *P. fauveli* should have evolved by progenesis from a larger form. *Psammodrilus aedificator* may instead have evolved from a line of interstitial psammodrilids and secondarily have become larger. This may explain the nearly 'acoelomate' condition, less complex metanephridia, and the minor length of the 6 pairs of cirri with aciculae in this species. Except for the lack of cilia on the collar (Fig. 7) and in the middorsal sulcus of the trunk, all of the Psammodrilidae have an almost uniform and completely ciliated epidermis which counterpart is found only among the Lobatocerebrida (see Rieger, 1980); however, the latter taxon has a true cuticle, a character lacking in Psammodrilidae. The well-developed ciliation (see Fig. 6A) of psammodrilids (including the larger species) may indicate that the whole family has evolved from an interstitial ancestor. Further phylogenetic analyses, preferably with additional new taxa, are needed to explain the evolution within the Psammodrilidae and prove whether *Psammodrilus* is a paraphyletic genus or *Psammodrilus balanoglossoides* descended from an interstitial ancestor as well. If the last scenario is followed to its extreme, the whole family may have evolved by progenesis.

Conclusion

The many examples of meiofauna representatives from macrofauna polychaete families can most easily be explained by progenetic evolution. These examples are found in all major clades in the phylogeny of polychaetes, thus it must be assumed that progenesis is a common evolutionary pathway. This pathway may also apply to many of

the exclusively meiofaunal families. However, it is very difficult to prove a progenetic origin phylogenetically (and reject a primary meiofaunal form) by morphological data alone, since the lack of characters and many specializations make it difficult to compare these taxa with macrofaunal polychaetes. Although several hypotheses on the evolution of meiofauna polychaetes have been presented here, cladistic analyses have generally failed to substantiate the phylogenetic position of meiofaunal families within Polychaeta and explain their evolution. Techniques like SEM, TEM and cLSM can still provide important comparative information on the external and especially internal morphology (see, e.g., Müller & Westheide, 2002; this paper). Time consuming studies of animals in culture could provide comparative information on, e.g., ontogeny, reproduction and common parasites (see, e.g., Åkesson, 1977). However, molecular studies may seem the most obvious solution for gathering additional comparative characters of the 'simple' looking meiofauna taxa. However, as in morphological studies, the genes used at present in molecular systematics seldom provide convincing information on the more basal splits in the evolution of polychaetes and new genes may have to be considered (see, e.g., Struck et al., 2002a).

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