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Phylogeny of basal descendants of cocoon-forming annelids (Clitellata)

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Abstract: Molecular analyses have been unsuccessful in placing the clitellates among annelids. Available morphological characters are ordered into congruent transformation series according to Hennigian principles. Orbiniidae is chosen as the outgroup. I propose the following phylogeny [number of apomorphies within brackets]: (Clitellata *sensu lato* [6] (Questidae [6] + Apodadrilida, new [2] (Parergodrilidae [3] (*Stygocapitella* [3] + *Parergodrilus* [4]) + Oligochaeta [7] (Aphanoneura [2] (Aeolosomatidae [2] + Potamodrilidae [3]) + Dorsopharyngea, new [7] (Hrabeiellidae, new [6] + Euclitellata [5]))). Worms with ring-like clitella surrounding the body almost completely are herein renamed Euclitellata. Clitellata is expanded to include all annelids that, in addition to producing cocoons, have sperm receptacles and a restricted number of gonads. Oligochaeta is established as a valid clade for the hermaphroditic annelids bearing few or no chaetae. Questidae, Parergodrilidae, and *Hrabeiella* belong to Clitellata. Terrestrial “polychaetes”, such as *Parergodrilus* and *Hrabeiella*, are actually clitellates. *Hrabeiella* is the sister group of Euclitellata, despite a secondary loss of spermathecae and clitellum. Aphanoneura belong to Oligochaeta.

Key words: Euclitellata, Questidae, phylogenetic systematics, plesiomorphic noise, a priori character polarization, methodological bias

Introduction

Annelid phylogeny is one of the largest unresolved problems within Metazoa Haeckel, 1874 (Almeida and Christoffersen, 2001; Almeida et al., 2003; Jenner, 2004; Bartolomaeus et al., 2005; Zrzavý et al., 2009). There is now growing consensus that Polychaeta Sars, 1863 represents a paraphyletic group (McHugh, 1997; Westheide, 1997a, 1997b; Rouse and Fauchald, 1998). For example, Purschke (1999, 2002a) remarks that the Clitellata Michaelsen, 1919 are highly derived annelids. Thus a basal position for Clitellata as the sister group of the Polychaeta (Rouse and Fauchald, 1995, 1997) can be ruled out.

The previous conclusions that Annelida Lamarck, 1803 and Articulata Cuvier, 1812 are also paraphyletic and should be replaced by a much more inclusive clade Metameria Christoffersen and Araújo-de-Almeida, 1994 (Almeida and Christoffersen, 2001; Almeida et al., 2003) have still not been accepted. The implications of these views are that not only Echiurida Baltzer, 1931 and Pogonophora Ivanov, 1949 are descendants of annelid ancestors, but larger groups such as Ecdysozoa Aguinaldo et al., 1997 and Deuterostomata Huxley, 1874 are also descended from annelid-like marine ancestors. This phylogeny implies that Polychaeta, Annelida, and Articulata are

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paraphyletic groups, and contrasts with the recent consensus derived largely from molecular data that divides the Bilateria Metschnikoff, 1881 into 2 main clades, Lophotrochozoa Aguinaldo et al., 1997 and Ecdysozoa (Philippe et al., 2009). This consensus assumes that Lophotrochozoa is also monophyletic, despite the evidence compiled by Almeida et al. (2003) against such an assumption, which in our opinion is not adequately supported by morphological data.

Rouse and Fauchald (1997) first proposed the monophyly of Polychaeta based on the presence of nuchal organs, but now admit that another possibility is that Clitellata have lost a number of morphological features that would help identify their sister group among the polychaetes (Rouse and Pleijel, 2003: 178; Rouse et al., 2008).

The monophyly of the Clitellata is well supported by morphology (Purschke et al., 1993; Rouse, 1998; Nielsen, 2001; Jenner, 2006; Martin et al., 2008), sperm ultrastructure (Ferraguti, 2000), molecular data (McHugh, 1997; Kojima, 1998; Siddall et al., 2001; Erséus and Källersjö, 2004), and total evidence (Marotta et al., 2008). On the other hand, their historical origins from particular polychaete outgroups are still unresolved (Brinkhurst and Nemeč, 1987; Eibye-Jacobsen and Nielsen, 1996; Rouse and Fauchald, 1997; McHugh, 1997, 2000; Westheide, 1997a; Purschke, 1997, 1999; Westheide et al., 1999; Purschke et al., 2000). Martin (2001) found that the placement of Clitellata among polychaetes could not be resolved on the basis of available sequences of 18S rRNA. Struck and Purschke (2005) attribute the poor resolution among different taxa of Annelida by previous molecular approaches (e.g., Rota et al., 2001; Struck et al., 2002; Bleidorn et al., 2003) to a supposed 'explosive radiation' and to speciation events having occurred in the distant past, about 500 MYA. They share with other molecular phylogeneticists (Borchiellini et al., 1998; Hausdorf, 2000) the hope that with an increasing number of molecular data the resolution of the signal in the data will become high enough to resolve such basal nodes (Struck and Purschke, 2005). There is a general belief that molecular data are the most reliable source of phylogenetic inference (Struck, 2006).

On the other hand, Westheide et al. (1999) have shown that different assessments of absent features

have led to conflicting hypotheses about phylogenetic relationships in Annelida. Choice of method clearly influences phylogenetic resolution.

Recent attempts to resolve the origin or internal phylogeny of the Clitellata are based on comparative evolutionary morphology, with characters weighted mainly by functional considerations (Westheide, 1997a; Purschke, 1999), numerical cladistics of morphological characters (Rouse and Fauchald, 1997), molecular phylogeny (Rousset et al., 2007), and a total evidence approach (Marotta et al., 2008).

In this paper, I use a classical Hennigian approach to reconstruct a phylogenetic hypothesis for the origin of clitellates from marine polychaetes, based on morphological characters. My aim is to demonstrate that method, rather than insufficiency of data, has been responsible for previous ambiguities in establishing a satisfactory history of the conquest of continental habitats by the lineage of cocoon-forming metameric metazoans.

Materials and methods

Morphological characters available in the literature are ordered by hand into transformation series and tested qualitatively by reciprocal illumination for congruence with evolutionary transformations of other characters (Hennig, 1966; Amorim, 1997). As a methodological side issue of this paper, I hope to demonstrate that, under a qualitative Hennigian approach to phylogenetic reconstruction of morphological characters, it is by no means necessary to use available computer software packages and now routinely used for quantitative analyses of molecular data and for assessments of total evidence.

I used Orbiniidae Hartman, 1942 as the outgroup for the phylogenetic analysis of the Clitellata. Orbiniid monophyly is well supported by morphological data (Fauchald and Rouse, 1997; Rouse and Fauchald, 1997; Bleidorn et al., 2009), although molecular inferences of orbiniid phylogenies (Bleidorn, 2005; Struck et al., 2008; Bleidorn et al., 2009) are incongruent with morphology (Solis-Weiss and Fauchald, 1989; Blake, 2000). The phylogenetic position of Orbiniidae within Annelida is considered unresolved (Wilkins and Purschke, 2009).

Results

Phylogenetic reconstruction

The morphological characters successfully interpreted in a phylogenetic context are used to construct the phylogeny of Figure 1.

Phylogenetic system

Clitellata Michaelsen, 1919, *sensu lato*

Questidae Hartman, 1966

Apodadrilida, new

Parergodrilidae Reisinger, 1925

Stygocapitella Knöllner, 1934

Parergodrilus Reisinger, 1925

Oligochaeta Grube, 1850, emended

Aphanoneura Vejdovský, 1884

Aeolosomatidae Levinsen, 1884

Potamodrilidae Bunke, 1967

Dorsopharyngea, new

Hrabeiellidae, new family

Euclitellata Jamieson, 1983a

Systematic considerations

Clitellata Michaelsen, 1919, *sensu lato*

Synonym. Apoclitellata Almeida et al. (2003).

Etymology and taxon concept. This taxon has never been used formally to include the variety of annelids considered herein, although Almeida and Christoffersen (2001), Almeida et al. (2003), and Garraffoni and Amorim (2003) identify the Questidae as more closely related to Clitellata than to other polychaetes. Clitellata *sensu lato* refers to all taxa descended from ancestors in which a glandular pad of clitellar cells adjacent to the female pores evolved from glandular areas first surrounding each pore independently, and then coalescing into a single glandular area that gradually surrounded the body wall in a partial or full ring-like fashion, extending over one to several segments in length and, in advanced evolutionary stages, becoming several layers thick. The descriptive name clitellum will be used for all those epithelial structures hypothesized to be homologous to the fully developed, multilayered, or “true” clitella of euclitellates. Previously, the incomplete ventral glandular areas of questids,

parergodrilids, and aphanoneurans were considered to represent convergent adaptations to continental environments. With the hypothesis that all cocoon-forming glandular epithelia are homologous to the multilayered ring-like clitella of euclitellates, Clitellata becomes a convenient name, especially considering that this name was originally meant to be more inclusive than Oligochaeta (Erséus, 2005).

Diagnostic apomorphies (Figure 1, node a). (1) mature females with a more or less strongly papillated glandular epidermis one cell thick, forming a pad adjacent to female pores (Giere and Erséus, 1998: 346); these glands were referred to as a clitellum for questids by Giere and Riser (1981) and Jamieson and Webb (1984), because they produce cocoons for the deposition of eggs (Jamieson, 1983b: 179); (2) Gonads limited to few (originally 1-2) segments (Giere and Riser, 1981); (3) sperm receptacles or spermathecae in females for the storage of sperm (Jamieson, 1983b); (4) in males sperm matures in sperm sacs or seminal vesicles (supposedly reduced secondarily in a few groups) (Giere and Riser, 1981); (5) parapodia vestigial in basal lineage, with loss of supporting aciculae, and fully lacking in more advanced clades; (6) sperm filiform (Rota and Lupeti, 1997: 608).

Further diagnostic characters. Paired prostomial appendages absent (Fauchald and Rouse, 1997). Development direct.

Included taxa. Questidae and Apodadrilida, new.

General references. None for this enlarged concept of Clitellata.

Reference phylogenies. Almeida and Christoffersen (2001); Almeida et al. (2003); Garraffoni and Amorim (2003).

Further comments. I first considered giving a new name for these clitellates (based on the incipient clitellum or on the presence of cocoons). The name Apoclitellata Almeida et al. (2003) was even proposed for Questidae + Clitellata. However, I am now convinced that expanding the concept of the name Clitellata, based on a perfectly plausible homology such as the clitellum and totally in line with Jamieson's (1983a) suggestion of restricting the concept of the “true” clitellates (leeches, microdriles, and megadrile earthworms) to the Euclitellata Jamieson, 1983a, will cause less confusion and should gain quicker support. The homology of the ventral clitellar pads

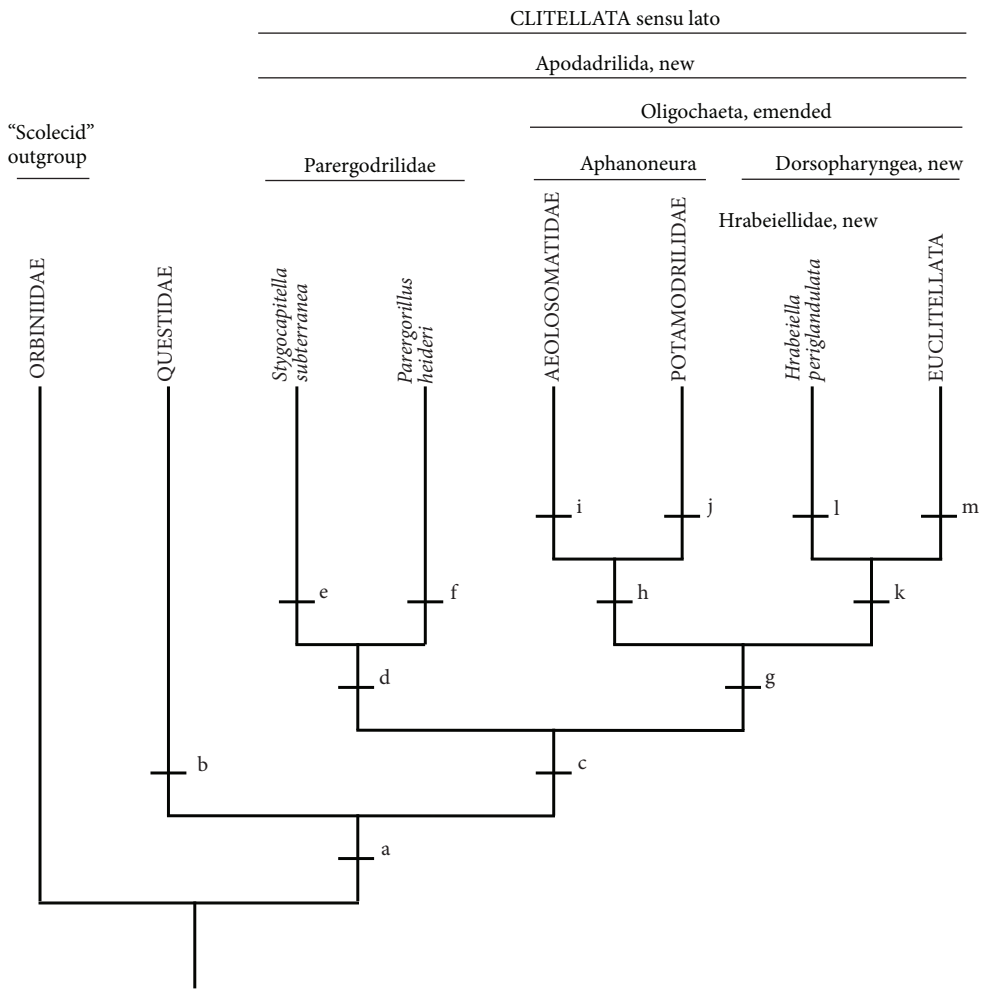


Figure 1. Phylogeny of Clitellata sensu lato. The polychate family Orbiniidae is used as an outgroup. Characters for each node are obtained from published species descriptions. They are organized into logical but hypothetical transformation series. Objective character states defining a clade are present in all descendant species in either unmodified or further evolved states.

of Questidae with the ring-like clitella of Euclitellata is indicated by criteria of position (associated with the female pores) and of function (production of cocoons).

Chapman (1965: 190) describes the formation of cocoon jellies from the terminal glandular portions of the nephridia of the female in the orbiniid *Scoloplos armiger* O. F. Müller, 1776. In clitellates the female pores, which may be derived from nephridia, supposedly become surrounded by glandular pads of such cocoon-secreting ectodermal cells. Only in the Euclitellata does a ring-like clitellum become fully formed. Within the Euclitellata this

full-ringed clitellum continues to evolve, becoming multistratified in Crassicitellata Jamieson, 1988, and saddle-shaped in the megadrile earthworms (Jamieson et al., 2002), these evolutionary advances representing additional apomorphic states within subordinate clades of clitellates.

Purschke (1999) confirmed the presence of a complex of gland cells behind the ovaries in both *Parergodrilus heideri* and *Stygocapitella subterranea* Knöllner, 1934 (both taxa belong to the Parergodrilidae), and noted that these glands consist of 2 types of cells that probably produce the

egg capsules. Purschke and Jördens (2007: 295) note that the clitellate-like cocoons of Parergodrilidae may have arisen by gonochorism from the glandular genital ducts and jelly egg masses of orbiniids. The same reasoning applies to the Questidae.

By referring to the traditional Clitellata as Euclitellata, Jamieson (1983a) implied that the concept of Clitellata should be broadened. However, he did not attempt to establish the limits of this broader concept of Clitellata.

Neither a clitellum nor spermathecae have so far been detected in *Hrabeiella periglandulata* Pižl & Chalupský, 1984. Because *Hrabeiella* Pižl and Chalupský, 1984 shares other important apomorphies with the Euclitellata, the absence of these 2 structures is herein interpreted as secondary reduction.

No evidence for the monophyly of “Scolecida” Rouse and Fauchald, 1997, which include the Questidae, has been found (Bleidorn et al., 2003: 279). The latter authors noted that orbiniids appear paraphyletic with regards to *Questa* Hartman, 1966. It now appears that Orbiniidae Hartman, 1942 are paraphyletic in relation to the entire clitellate lineage.

In all Clitellata *sensu lato* development is direct and there are no paired sensory appendages on the head. However, with a more precise establishment of the outgroups of Clitellata among the Orbiniidae, the generality of these 2 characters will probably be extended to include some of the “scolecoid polychaetes”.

Filiform flagellate introsperm is observed not only in euclitellates and questids, but also in several other marine interstitial “polychaetes” with complex modes of sperm transfer and internal fertilization (Franzén, 1970, 1977; Olive, 1983; Rouse and Jamieson, 1987; Jamieson and Rouse, 1989; Rota and Lupetti, 1997). Purschke and Fursman (2005) established the presence of introsperm also for the Parergodrilidae and for *Hrabeiella periglandulata*. Because the interstitial polychaetes mentioned above (questids, parergodrilids, and hrabeiellids) are herein included in the clitellates, the generality of introsperm can now be established for the Clitellata.

Questidae Hartman, 1966

Diagnostic apomorphies (Figure 1, node b). (1) mature males with a dorsal fold (cup) in segments

13-14 or 13-15, where a pair of male gonopores open (Giere and Erséus, 1998: 358); (2) complex genital organs, including a single unpaired sperm receptacle or spermatheca (duplicated in *Q. trifurcata* Hobson, 1970) with dorsal opening(s) in intersegment 5/6 (Giere and Erséus, 1998: 358); (3) a pair of intestinal caeca extending anteriorly at transition from esophagus to intestine, and set off from intestine by sphincters (Giere and Erséus, 1998: 358, fig. 2F); (4) a lateral organ (Von Nordheim, 1991) (ciliated pit of sensory function?) (Giere and Erséus, 1998: 346) is present medially between notopodial and neuropodial chaetal bundles in all segments (Jamieson and Webb, 1984: 26, fig. 4; Giere and Erséus, 1998: 346; Purschke and Hausen, 2007); (5) last segment before pygidium without chaetae (Giere and Erséus, 1998: 346); (6) pygidium forms a dorso-ventral cleft into which the terminal anus opens (Giere and Erséus, 1998: 346).

Further diagnostic characters. Up to 10 cm long, with 45-60 segments (Giere and Erséus, 1998: 346). Segments often with secondary annulations, anteriorly with 2-3 annuli, in median body region often with 7-8 annuli, number decreasing posteriorly (Giere and Erséus, 1998: 346). Chaetae include: a), long, serrated capillary or hair-like chaetae; b, short, stout, bifid, compound crotchets or hooks; and c, 1-2 trifurcate chaetae on notopodial bundles of segments 2-7 in *Q. trifurcata* Hobson, 1970).

Included taxa. *Questa* Hartman, 1966 (with 10 species).

General references. Hobson (1970); Giere and Riser (1981); Jamieson and Webb (1984); Taylor and Gathof (1984); Fauchald and Rouse (1997); Giere et al. (2007).

Reference phylogenies. Giere and Erséus (1998); Garraffoni and Amorim (2003).

Further comments. Known as ‘oligochaetoid polychaetes’, and prompting comparisons with marine oligochaetes (Hobson, 1970). However, these animals would more appropriately be called polychaetoid clitellates, because they are more closely related to the remaining clitellates than to other polychaetes.

The questids, like Orbiniidae and Parergodrilidae, have gonoducts that show glandular parts, the eggs being deposited in egg capsules or cocoons (Eisig,

1914; Giere and Riser, 1981; Purschke, 1999; Glasby, 2000; Rouse and Pleijel, 2001; Purschke and Jördens, 2007). Egg capsules may have developed more than once in polychaetes (Chapman, 1965; Giere and Riser, 1981; Jamieson, 1983a; Jamieson and Webb, 1984). For example, the nereidid *Namalycastis indica* (Southern, 1921) has larvae in cocoons (Rungandhan, 1943; Glasby, 1999), but it is also possible that clitellates developed from an extended lineage beginning with such cocoon-forming precursors. It is not to be expected that the “true” clitellum of continental euclitellates appeared full fledged, particularly if such convenient precursors for producing egg shells from their oviducts are already known in marine polychaetes, such as orbiniids, and other scolecidids, such as maldanids (Day, 1967), and even more basal nereidids (Glasby, 1999).

Giere and Riser (1981) and Jamieson and Webb (1984) demonstrated that questids are gonochoristic, which excludes this group from the hermaphroditic oligochaetes. Jamieson and Webb (1984) also found that the sperm lack the unique structures found in euclitellates. Jamieson and Webb (1984) discussed a series of possible autapomorphies for the family based on the ultrastructure of the sperm, which need to be further considered on the basis of comparative spermiogenesis.

Fauchald (1977) includes the Questidae, together with Orbiniidae and Paraonidae Cerruti, 1909, in the order Orbiniida. He comments that it is quite possible that the family should be considered among the oligochaetes, although this possibility was precluded by Jamieson and Webb (1984), who did not find sperm apomorphies of questids with either oligochaetes or euclitellates.

Giere and Erséus (1998) suggest that the complexities seen in the reproductive system of questids, including a clitellum, spermathecae and reduction of gonads to few segments, represent convergences with oligochaetes. Characters leading previous authors to consider questids as polychaetes, such as the presence of nuchal organs, lateral organs, a ventral buccal pad, and the prostomial position of the supraesophageal ganglia (Giere and Riser, 1981; Jamieson and Webb, 1984; Westheide, 1997a) are all plesiomorphic characters at this level of analysis. Consequently, there is no longer any need to avoid

terms such as a clitellum for questids (cf. Giere and Erséus, 1998).

The pairs of dorsal appendages (1 pair per segment) confined to the posterior segments (absent only in *Questa trifurcata*), mostly assigned as branchiae, would seem to represent plesiomorphic retentions of typically polychaete body appendages associated with the parapodia. One to multiple pairs of pygidial (anal) cirri may be present (absent only in *Questa trifurcata*) (Jamieson and Webb, 1984; Giere and Erséus, 1998). The absences of both branchiae and pygidial cirri in *Q. trifurcata* represent secondary reductions, according to the cladistic analysis of Giere and Erséus (1998).

The possession of vestigial parapodia (tiny humps), among other characters, precludes the questids from belonging to the Apodadrilida, new (see below).

Questids are almost cosmopolitan in distribution and have even been found in the Pacific deep sea (Wilson and Hessler, 1987), but they are predominant in the shallow sublittoral and low intertidal sediments (Giere and Erséus, 1998), which is consistent with the present scenario of an interstitial marine group originating the freshwater and terrestrial euclitellates.

Apodadrilida, new

Etymology and taxon concept. The taxon name refers to the complete loss of body appendages (parapodia).

Diagnostic apomorphies (Figure 1, node c). (1) complete loss of parapodia and associated appendages (cirri, branchiae, etc.); (2) nuchal organs mostly or entirely internal (Purschke and Hessling, 2002), being completely absent in Parergodrilidae and Euclitellata.

Included taxa. Parergodrilidae + Oligochaeta, emended.

Further comments. Similarities of *Stygocapitella subterranea* with either *Hrabeiella periglandulata* or [Eu]clitellata have been previously interpreted as representing convergent evolutionary events due to similar biology and habitats (Rota, 1998; Purschke, 1999, 2002b, 2005; Rouse and Pleijel, 2001; Purschke and Jördens, 2007). These similarities are interpreted

herein as synapomorphic for *Hrabeiella* + Euclitellata or for Apodadrilida.

Parergodrilidae Reisinger, 1925

Synonyms. Stygocapitellidae Karling, 1958.

Diagnostic apomorphies (Figure 1, node d). Sperm with (1) persistence of a considerable amount of cytoplasm proximal to the axoneme, (2) an unusually high number of mitochondria, and (3) an annular constriction of the cell membrane below the mitochondria (Purschke and Fursman, 2005: 146).

Further recognition characters. Chaetae present in single fascicles, with only 2 bundles per segment, each with 1 or a few chaetae (Fauchald, 1977: 20).

Included taxa. *Parergodrilus* Reisinger, 1925 + *Stygocapitella* Knöllner, 1934.

General references. Karling (1958); Reisinger (1960); Purschke (1986, 1987); Rouse and Fauchald (1997).

Further comments. Included in order Ctenodrilida (Fauchald, 1977) and transferred to Scolecida by Rouse and Fauchald (1997). All previous attempts failed to resolve the phylogenetic position of Parergodrilidae on the basis of morphological characters (Purschke, 1999, 2002b; Rouse and Pleijel, 2001; Purschke and Jördens, 2007).

Stygocapitella Knöllner, 1934

Diagnostic apomorphies (Figure 1, node e). (1) Capillary chaetae present along body (in addition to specialized winged and forked chaetae in *Stygocapitella*) (Rouse and Fauchald, 1997: 196); (2) intestine strongly coiled; (3) sperm length 320 µm, which is among the longest spermatozoa known for annelids (Purschke and Fursman, 2005: 146).

Further recognition characters. Nephridia are present along the body, but gonoduts are restricted in distribution (Rouse and Fauchald, 1997: 109).

Included taxon. *Stygocapitella subterranea* Knöllner, 1934.

General references. Knöllner (1934); Riser (1980); Hobson and Banse (1981); Purschke (1986, 1987, 1999, 2005).

Further comments. Populations of *Stygocapitella subterranea* from North America (Riser, 1984) have been shown to be genetically, and probably

specifically, distinct (Schmidt and Westheide, 2000). Those from New Zealand and Australia (Riser, 1984; Hartmann-Schröder, 1996) are also likely to be distinct (Worsfold, 2006).

Parergodrilus Reisinger, 1925

Diagnostic apomorphies (Figure 1, node f). (1) Nuchal organs absent (Purschke, 1986: 13); (2) nephridia restricted in distribution to second and third chaetigers (Reisinger, 1960; Rota, 1997: 92, fig. 3); (3) enlarged copulatory chaetae present in chaetiger 10 (Purschke, 2002b: 125); (4) terrestrial habitat derived from a marine interstitial environment (Graefe, 1977: 25).

Further diagnostic characters. Small worms comprising 8-9 chaetigerous segments and worms not longer than 1 mm (Rota, 1998: 76). Chaetae paired and distally simple-pointed (Fauchald and Rouse, 1997: 109).

Included taxa. *Parergodrilus heideri* Reisinger, 1925.

General references. Reisinger (1925, 1929, 1960); Fauvel (1927); Meyer (1927); Karling (1958); Graefe (1977); Purschke (1987, 2002b); Chalupský (1992); Rota (1997, 1998); Rota et al. (2001).

Further comments. The absence of nuchal organs is interpreted as a secondary loss, convergent with Euclitellata.

In *Parergodrilus* the brain is confined to the prostomium according to Rota (1997). If the brain actually extends into the following achaetigerous segment (or peristomium), as observed by Purschke (1999), this position will represent a convergence with the similar condition in Dorsopharyngea.

Oligochaeta Grube, 1850, emended

Etymology and taxon concept. The traditional concept of the Oligochaeta excludes the Hirudinea. However, there is now ample evidence and consensus that Hirudinea form a monophyletic taxon together with the remaining traditional oligochaetes (Purschke et al., 1993; Brinkhurst, 1994; Siddall and Burreson, 1996; Ferraguti and Erséus, 1999; Martin et al., 2008). I refer to this restricted clade that includes the traditional Oligochaeta and Hirudinea as Euclitellata. Herein the name Oligochaeta is expanded to refer to the clade that includes Euclitellata, *Hrabeiella*, and

Aphanoneura Vejdovský, 1884. As the descriptive name implies, all species belonging to the clade Oligochaeta have few or no chaetae.

Diagnostic apomorphies (Figure 1, node g). (1) hermaphroditism (monoecism); (2) chaetae few (4 or less bundles per segment, although secondarily modified genital chaetae occur in many tubificids and the number of chaetal bundles is greatly increased in perichaetine earthworms) and simple (2 or less types, although some groups may present several secondary modifications); (3) nephrostome in metanephridia, with unique mantle cell of mesodermal (septal) origin in the funnel (Bunke, 1994, 1998, 2000, 2003a, 2003b; Struck and Purschke, 2005: 291; Bartolomaeus and Quast, 2005: 161); (4) continental habitat, originally limnetic (Timm, 1981); (5) prostomium and peristomium fused into single unit (Fauchald and Rouse, 1997); (6) sperm with acrosome tube (Jamieson, 1983b: 179); (7) photoreceptors consisting of single type of cell, the phaosomes (Purschke, 2003a: 102; Suschenko and Purschke, 2009).

Included taxa. Aphanoneura + Dorsopharyngea, new.

General references. Vejdovský (1884); Beddard (1895); Michaelsen (1900); Stephenson (1930); Brinkhurst and Jamieson (1971); Reynolds and Cook (1976, 1981, 1989, 1993).

Reference phylogenies. Jamieson (1971, 1980, 1983c); Timm (1981); Siddall and Burreson (1996).

Further comments. Oligochaetes in the sense delimited herein are thought to have derived from a common freshwater ancestor (Timm, 1981), although Purschke (1999) refers to a terrestrial origin. This suggests that a marine lifestyle in oligochaetes is a secondary acquisition that has occurred several times independently in the evolution of clitellates (Rousset et al., 2008).

The phylogenetic relation between Aphanoneura and [Eu]clitellata, as suggested by Timm (1981) and Brinkhurst and Nemeč (1987) is supported by a very strong apomorphy, hermaphroditism. The results of 2 molecular studies reveal that Aeolosomatidae Levinsen, 1884 are closely related to [Eu]clitellata (Moon et al., 1996; Winnepenninckx et al., 1998).

Although Jamieson (1981) originally established the sperm acrosome tube as restricted to the euclitellates, Gluzman de Pascar (1997) found this character also in *Aeolosoma marcusii* Van der Land, 1971, and so it now seems reasonable to consider the presence of an acrosome tube a further apomorphy for Oligochaeta.

Bartolomaeus et al. (2005), following Goodrich (1945), use the absence of mixonephridia to distinguish clitellates from polychaetes (including questids).

Aphanoneura Vejdovský, 1884

Diagnostic apomorphies (Figure 1, node h). (1) ventral pad of cilia on prostomium, which has an evident locomotory function (Bunke, 1988) and may also be involved in feeding (Jennings and Gelder, 1969; Gelder and Uglow, 1973; Hessling and Purschke, 2000); (2) progenesis, with reduction of sexual phenomena (Bunke, 1986).

Further diagnostic characters. Presence of simple sigmoid or hair-like chaetae (Purschke and Hessling, 2002: 19). Specimens present mostly in limnetic habitats. Position of nervous system intra- or basiepidermal (Stolte, 1969; Purschke, 1993; Hessling and Purschke, 2000).

Included taxa. Aeolosomatidae + Potamodrilidae.

General references. Vejdovský (1884); Benham (1890); Beddard (1901); Michaelsen (1900); Brinkhurst (1982); Brinkhurst and Wetzel (1984).

Reference phylogeny. Moon et al. (1996).

Further comments. The Aeolosomatidae (together with the Potamodrilidae) have variously been considered as a subtaxon of the 'Oligochaeta', as the sister group of the Clitellata or as a group with no close affinity to the [Eu]clitellata (Hessling and Purschke, 2000). This taxon has been either included in Clitellata *sensu stricto* (=Euclitellata) (Bunke, 1967) or considered the sister group of [Eu]clitellata (Bunke, 1985), a relationship later to be rejected by Bunke (1986) on the basis of sperm ultrastructure. The cladistic analysis by Rouse and Fauchald (1997) suggested that they fall into Polychaeta, though admittedly their placement in this group could not be resolved. Based on sequences of 18S rDNA, Moon et al. (1996) suggested a sister-group relationship

between Aphanoneura and [Eu]clitellata. They were excluded from [Eu]clitellata by Michaelsen (1930), Stephenson (1930), Bunke (1967), and Brinkhurst and Jamieson (1971). The presence of nuchal organs and a ventral pharyngeal pouch in both Aeolosomatidae and Potamodrilidae clearly confirms their exclusion from the [Eu]clitellata (Brinkhurst and Jamieson, 1971; Timm, 1981; Bunke, 1985, 1986; Brinkhurst and Nemeč, 1987; Rouse and Fauchald, 1997; Purschke and Hessling, 2002).

Glasby and Timm (2008) included the “enigmatic” Aphanoneura among the polychaetes. Struck and Purschke (2005) provide molecular evidence for a sister group relationship between Aeolosomatidae and Potamodrilidae, but they also “confirmed the polychaete nature” of Aphanoneura from gene sequences. On the other hand, Bunke (1994) notes that morphological synapomorphies of Aeolosomatidae with any non-clitellate annelid group have not been established.

Purschke et al. (2000) classify the ciliated pads found on the ventral side of the prostomium in Aeolosomatidae (and, by implication, Potamodrilidae) as kinocilia.

Aeolosomatidae Levinsen, 1884

Synonyms. Schizoneura P. J. Schmidt, 1897.

Diagnostic apomorphies (Figure 1, node h). (1) epidermal cells usually colored; (2) seminal receptacles reduced to mostly epidermal formations (Marotta et al., 2003: 123).

Further recognition characters. Capillaries usually ornamented (Fauchald and Rouse, 1997: 90), although in some species, such as *Aeolosoma travancorensis* Aiyer, 1926 and *A. tenebrum* Vejdovský, 1880, short and forked chaetae, possible polychaete atavisms, occur in addition to the capillary chaetae.

Included taxa. *Aeolosoma* Ehrenberg, 1831 (contains about 41 species), *Rheomorpha* Ruttner-Kolisko, 1955 (with 1 species) and *Hystricosoma* Michaelsen, 1926 (with 1 species inquirenda).

General references. Beddard (1895); Michaelsen (1900); Marcus (1944); Ax and Bunke (1967); Bunke (1967, 1988); Van der Land (1971); Brinkhurst (1971, 1982); Hrabě (1981); Rouse and Fauchald (1997); Gluzman de Pasciar (1997); Purschke and Hessling (2002).

Reference phylogeny. Ax and Bunke (1967).

Further comments. Aeolosomatidae are cosmopolitan meiofaunal Annelida characterized by small size and almost exclusively asexual reproduction (Marescalchi et al., 2008). Aeolosomatidae reproduce predominantly by paratomy (Bunke, 1986).

Aeolosomatids are known to alternate sexual and asexual generations, in a way remarkably similar to some naids. The asexual generation in aeolosomatids is characterized by paratomic buddings (Hämmerling, 1924). The sexual generation appears before winter or drought and individuals survive by diapausing cocoons (Timm, 1984). The process of cyst-formation in *Aeolosoma hemphrichi* Ehrenberg, 1831 has been described by Herlant-Meewis (1950). It would be interesting to know if the epidermal cells forming the cysts of aphanoneurans are the same as the cells forming egg-cocoons in other clitellates.

A peculiar feature of this group is that an indefinite number of male gonads occur both in front and behind the female ovaries (Bunke, 1986).

Bunke (1986) noted that the cushion of glandular skin restricted to the ventral side and surrounding the female pore might consistently be interpreted as even a reduced or a foreshadowed clitellum.

Marcus (1944) is of the opinion that Aeolosomatidae belong definitively to the Oligochaeta. He observed shallow epidermal depressions that he referred to as spermathecae. Marotta et al. (2003) show that the seminal receptacles are less reduced in *Aeolosoma singulare* Semernoi, 1982, a species that contains worms having a larger body size. In this species, the seminal receptacles penetrate the muscular layers and end deep inside the coelomic cavity.

Although the group is predominant in freshwater, a single marine species has been described (Westheide and Bunke, 1970).

Potamodrilidae Bunke, 1967

Diagnostic apomorphies (Figure 1, node j). (1) With 7 trunk segments (Lasserre, 1971: 73); (2) Epidermal glands produce an adhesive secretion (Lasserre, 1971: 73); (3) Female gonads in segment 5 and male gonads in segment 6 (Bunke, 1967; Lasserre, 1971: 73; Fauchald and Rouse, 1997: 113).

Further recognition characters. All chaetae capillary (Fauchald and Rouse, 1997: 113). Metanephridia present in segments 1 and 2 (Fauchald and Rouse, 1997: 113). Circumoesophageal connectives with dorsal and ventral roots (Purschke and Hessling, 2002: 31), a plesiomorphic condition relative to Dorsopharyngea. Multicellular ciliary sensory organ in brain (Purschke and Hessling, 2002: 24) (also known in *Hrabeiella* and *Aeolosoma*) (Purschke and Müller, 1996; Purschke, 2000; Purschke and Hessling, 2002: 32).

Included taxa. *Potamodrilus* Lastochkin, 1935 (1 species).

General references. Bunke (1967, 1986); Lasserre (1971); Rouse and Fauchald (1997); Purschke and Hessling (2002).

Further comments. Bunke (1967) stated that the clitellum of *Potamodrilus* is homologous to the clitellum of the remaining Oligochaeta. However, Brinkhurst (1971) remarks that the clitellum of *Potamodrilus* resembles a copulatory gland similar to those found in addition to the clitellum of other genera.

Dorsopharyngea, new

Etymology and taxon concept. Although *Hrabeiella* shares strong synapomorphies with Euclitellata, this sister-group relationship has not been unambiguously established before, apparently because a clitellum and spermathecae have so far not been found in *Hrabeiella periglandulata*.

Diagnostic apomorphies (Figure 1, node 1). (1) pharyngeal pad positioned dorsally (Purschke, 2003b); (2) brain positioned behind the prostomium (Jördens et al., 2004: 278); (3) anterior-ventral and single circumoesophageal connectives in adult (Jördens et al., 2004: 278; M. C. M. Müller, 2006: 127); (4) ganglia not well defined in ventral nerve chord; (5) subepidermal position of nervous system (Jördens et al., 2004: 278); (6) epidermis without kinocilia (Purschke et al., 2000: 119).

Included taxa. *Hrabeiella* + Euclitellata.

Further comments. A dorsally muscularized pharynx was previously considered an apomorphy of the traditional oligochaetes or clitellates (Cook, 1971; Brinkhurst and Nemeč, 1987; Jamieson, 1992; Purschke and Tzetzlin, 1996). However, Jördens et al. (2004) indicate that ultrastructural investigations of

this organ in *Hrabeiella periglandulata* revealed a close structural correspondence, providing strong evidence for homology of these organs rather than assuming convergent evolution.

Several specializations of the central nervous system were previously thought to represent [eu]clitellate apomorphies, but are now considered to represent shared synapomorphies of *Hrabeiella periglandulata* and [Eu]clitellata (Jördens et al., 2004): a) A brain displaced into one or the following segments during ontogeny, perhaps an adaptation to burrowing, has been previously considered a[n] [eu]clitellate apomorphy (Bullock, 1965; Orrhage, 1995; Purschke, 1997; Rouse and Fauchald, 1997; Westheide, 1997a; Westheide et al., 1999; Hessling and Westheide, 1999); b) lateral trunks of ventral nerve cord completely fused into one midventral chord with only an internal commissural pathway (Purschke and Hessling, 2002); c) nervous system within muscle layers in the coelomic cavity (not subepidermal) (Bullock, 1965; Stolte, 1969; Brinkhurst and Jamieson, 1971: 195; Purschke and Hessling, 2002: 30); d) ventral ganglia not well defined (Bullock, 1965; Orrhage, 1995; Purschke, 1997; Rouse and Fauchald, 1997; Hessling and Westheide, 1999).

In one of the phylogenetic trees based on molecular data *Hrabeiella periglandulata* appears as the sister group of Clitellata (Struck and Purschke, 2005: 287, fig. 1). This position also receives support from previous morphological and molecular data (Purschke, 2003b; Jördens et al., 2004).

Purschke (2003b) notes that absence of a typical clitellum, different structure and position of the genital organs, different ultrastructure of the spermatozoa and chaetae, as well as the presence of nuchal organs, although internal and highly modified, precluded inclusion of *H. periglandulata* within [Eu]clitellata. Consequently, convergent evolution of the clitellate-like features in these groups due to similar selection pressure was generally assumed. However, the above author noted that a dorsally positioned pharynx is so far only known for [Eu]clitellata, and he found several synapomorphies in the structure of the dorsal pharynx shared by *Hrabeiella periglandulata* and *Enchytraeus minutus* Nielsen and Christensen, 1961, making a sister group relationship of *H. periglandulata* and [Eu]clitellata conceivable. This

hypothesis is supported by molecular data, by the structure of the cerebral sense organs, and the central nervous system, making the clade Dorsopharyngea strongly supported, despite the secondary absences of a clitellum and sperm receptacles in *Hrabeiella*.

Hrabeiellidae, new

Etymology and taxon concept. *Adenodrilus punctulatus* Graefe, 1975 (nom. nud.) was considered as a new family of terrestrial polychaetes (Graefe, 1977: 25). I formalize this new family as Hrabeiellidae. Subsequently, *Adenodrilus punctulatus* Graefe, 1977 has been synonymized with *Hrabeiella periglandulata* by Rota et al. (2001). The genus name was also preoccupied by a haplotaxid, *Adenodrilus* Čekanovskaja, 1959.

Diagnostic apomorphies (Figure 1, node l). (1) body densely covered by cuticular glands, distributed in 4 transversal rows in each segment (Pižl and Chalupský, 1984), (2) chaetae shovel-shaped (Pižl & Chalupský, 1984), also described as ‘ice-cream spoon’-like (Rota, 1998: 78); (3) clitellum or any cushion of glands around female pore absent (Pižl and Chalupský, 1984); (4) 4 pairs of lobes or oesophageal glands anteriorly (Pižl and Chalupský, 1984; Rota, 1998: 78, figs 11, 12); (5) spermatheca absent (Rota, 1998: 81); (6) terrestrial habitat probably derived from a freshwater environment.

Further recognition characters. Worms 1.5-2 mm long and with 15 chaetigerous segments (Rota, 1998: 76).

Included taxa: *Hrabeiella* Pižl and Chalupský, 1984 (monotypic for *Hrabeiella periglandulata* Pižl and Chalupský, 1984).

General references. Pižl and Chalupský (1984); Rota (1998); Jans and Römbke (1989); Rota et al. (2001); Rota and Lupetti (1997); Purschke (1999, 2000, 2002b).

Further comments. The epidermal glands of *Hrabeiella* do not appear to be directly involved in reproduction (Rota, 1998); Graefe (1977) noted the hermaphroditism of *Hrabeiella* and dorsal pharyngeal apparatus, but dismissed these as deviating features convergent with oligochaetes.

The absence of a clitellum in *Hrabeiella* is herein interpreted as a secondary reduction. No eggs or

cocoons have ever been encountered on the surface of the culture plates (Rota and Lupetti, 1997). These authors also note that the egg of *Hrabeiella* seems to be provided with an unusually viscous yolk.

Spermathecae (a clitellate *sensu lato* apomorphy) have not been observed in *Hrabeiella periglandulata* (Pižl and Chalupský, 1984). Their absence has been confirmed by Rota (1998), and so this absence is considered to represent a secondary loss and consequently another apomorphy of this group.

Euclitellata Jamieson, 1983

Synonyms. Clitellata Michaelsen, *sensu stricto* (Clitellata of most previous authors).

Etymology and taxon concept. Jamieson (1983a) introduced the term Euclitellata for the old class Clitellata (Oligochaeta, Hirudinea, and Branchiobdellida), or the clade with female pores pre- or intraclitellar in position. These taxa were ordinarily grouped within the Clitellata, but Jamieson (1983a) anticipated that the latter term might have to be expanded to groups ordinarily considered to belong to the polychaetes. I have herein followed his recommendation to use the name Euclitellata, mainly because the clitellar structures can be hypothesized to be homologous rather than having evolved repeatedly within the annelids (cf. Jamieson and Webb, 1984).

Diagnostic apomorphies (Figure 1, node m). (1) clitellum completely surrounding body, at least in basal lineages; (2) mitochondria interpolated in sperm (Rouse and Fauchald, 1995); (3) loss of chemosensory nuchal organs (Rouse and Fauchald, 1995; Purschke and Hessling, 2002: 32); (4) female pores pre- or intraclitellar (Jamieson, 1983a; Jamieson and Webb, 1984: 32); (5) body with a complete layer of longitudinal muscle fibers (Purschke and Müller, 2006); (6) penial bulbs, which are completely absent in *Hrabeiella* (Pižl and Chalupský, 1984: 293), surround the male pores.

Further recognition characters. Hooked chaetae with ligaments lacking (Stephenson, 1930: 8; Cook, 1971: 12).

Included taxa. Capilloventridae Hartman and Loden, 1984; Phreodrilidae Beddard, 1891; Naididae Ehrenberg, 1828; Propappidae Coates, 1986; Haplotaxidae Michaelsen, 1900; Enchytraeidae Vejdovský, 1879; Crassiclitellata Jamieson, 1988;

Acanthobdellida Grube, 1851; Branchiobdellida Holt, 1965; Hirudinea Lamarck, 1818; and Lumbriculidae Vejdovský, 1884.

General references. Euclitellata: Jamieson (1983a); Rota and Lupeti (1997); Ferraguti (2000). Clitellata: Livanow (1931); Michaelsen (1928, 1934); Brinkhurst and Gelder (1989); Brinkhurst and Jamieson (1971); Lasserre (1975); Ferraguti (1982, 1984); Manum et al. (1991); Omodeo (1998); Dohle (1999); Ferraguti and Erséus (1999); Brinkhurst (1999); Erséus (1999); Hessling and Westheide (1999); Erséus et al. (2000); Purschke et al. (2000).

Reference phylogenies. Clitellata: Timm (1987); Brinkhurst (1994); Kojima (1998); Purschke (1999); McHugh (2000); Martin et al. (2000); Martin (2001); Erséus (2005).

Further comments. The absence of nuchal organs is convergent with *Parergodrilus*.

Siddall et al. (2001) proposed synonymizing the paraphyletic Oligochaeta under Clitellata auct. I take the alternative stance of redefining Oligochaeta so as to retain its descriptive content and to expand its included taxa. This previously paraphyletic taxon thus becomes a monophyletic clade. The Clitellata of most previous authors are here referred to as Euclitellata.

Gills and branchiae in some naidids, phreodrilids, and glossoscolecids do not correspond to any of the forms of gills discussed for polychaetes by Rouse and Fauchald (1997).

Discussion

Discussion of phylogeny

Brief evolutionary scenario for the origin of Clitellata. From jelly-mass and cocoon forming orbiniids sprang a lineage of clitellates with ventral glandular pads of epithelial cells associated with the female pores and responsible for the formation of egg-bearing cocoons, with spermathecae in females and usually with seminal vesicles in males (although this feature is not universal in clitellates, many of which have spermatozoa swimming freely in the body cavity), gonads restricted to a few segments, and appendages reduced. In the Apodadrilida the parapodia and all associated appendages became completely lost, while the nuchal organs became

mostly internal. *Parergodrilus* successfully invaded moist land directly from marine interstitial forms resembling *Stygocapitella* and lost its nuchal organs completely. The Oligochaeta became hermaphroditic, reduced their chaetae as in Parergodrilidae, and successfully conquered limnic and, subsequently, terrestrial environments. In Dorsopharyngea there is a dorsal pharyngeal pump, the nervous system became condensed, and the brain lies behind the prostomium. *Hrabeiella* invaded land, apparently losing its spermathecae and clitellum. Finally, a clitellum completely surrounding the body developed in Euclitellata (although with further secondary modifications), the nuchal organs were completely lost, and a body layer of longitudinal muscle fibers became well developed. In the subsequent evolution of the euclitellates land was further conquered several times, by Monogastridae, Enchytraeidae, *Rhyacodrilus falciformis* Bretscher, 1901, by the earthworms, and by some of the leeches.

“Clitellate apomorphies”. Purschke (1999) provides an impressive list of 20 diagnostic characters of the Clitellata, based on Jamieson (1992), Purschke et al. (1993), Westheide and Müller (1996), Omodeo (1998), and Westheide (1997a). One problem with this list is that apomorphic similarities are not always clearly separated from plesiomorphic similarities. Another problem is that, although many of the characters represent true apomorphies, they have not all appeared simultaneously at a single time and at the same evolutionary level, but have appeared gradually along an extended period in the history of clitellates, from marine metameric worms (“polychaetes” and “annelids”) to euclitellates.

Transformation series. Cocoon-forming glands evolved much before ring-shaped clitella (Euclitellata). Within euclitellates, the annular clitellum has later become multilayered in Crassiclitellata, and saddle-shaped in many terrestrial megadriles and other groups of oligochaetes. Rouse and Fauchald (1997), for example, do not code epithelial glands surrounding the female pores of questids as the same homologous character as the annular clitellum. Giere and Erséus (1998) explicitly recommend not referring to the glandular epithelial cocoon-producing cells of questids as a clitellum. However, Sayers et al. (2009) recently noted that the cocoon-producing cell types

identified for the leech *Theromyzon tessulatum* O. F. Müller, 1774 may well have functional analogues throughout the Annelida.

Phylogenetic order of apomorphies. Hermaphroditism (in Oligochaeta) evolved only after sexual characters became restricted to a limited number of segments (in Clitellata). Similarly, dorsal pharyngeal bulbs (in Dorsopharyngea) evolved much later than the conquest of continental environments (in Apodadrilida).

The new phylogenetic tree of the Clitellata. When the distinct generalities of the “clitellate” apomorphic characters are established, the system of the Clitellata unfolds as a consequence, and many supposed shared convergences are seen to represent true synapomorphies (although some convergences remain, such as those associated with the independent conquest of continental soils, first by *Parergodrilus heideri* and *Hrabeiella periglandulata*, and then more ubiquitously by Euclitellata. Some morphological reversals also occur, such as the apparent loss of a clitellum and of spermathecae in *Hrabeiella*.

Phylogenetic tree topology. Twenty-seven morphological characters that normally appear in discussions of the origin of clitellates from polychaetes are grouped into 5 successive clades along the main clitellate lineage: Clitellata (6 apomorphies), Apodadrilida (2), Oligochaeta (7), Dorsopharyngea (7), and Euclitellata (5).

Previous typological biases. When these apomorphic similarities are used as key characters for the recognition on an idealistic taxon Clitellata, and when the corresponding 27 plesiomorphic similarities are used to recognize a similarly essentialistic taxon Polychaeta, where does one pigeon-hole the “aberrant”, “enigmatic” and “problematical” questids, parergodrilids, aphanoneurans and *Hrabeiella*? Questidae becomes most polychaete-like, because this group shares 21 plesiomorphic similarities with the polychaetes (they are plesiomorphic regarding the apomorphies appearing in Apodadrilida, Oligochaeta, Dorsopharyngea, and Euclitellata). On the other hand, Questidae shares only 6 apomorphic similarities with the Apodadrilida (the Clitellata apomorphies). Similarly, while the Parergodrilidae share 2 apomorphic similarities with Oligochaeta, they share 19 plesiomorphic similarities with polychaetes

(7 becoming apomorphic in Oligochaeta, 7 in Dorsopharyngea, and 5 in Euclitellata). Aphanoneura are still clearly more polychaete-like than clitellate-like (7 apomorphic similarities shared with Dorsopharyngea, but 12 plesiomorphic similarities still shared with polychaetes). Finally, *Hrabeiella*, herein hypothesized to represent the sister group of the Euclitellata, becomes of “problematic standing”, from a perspective of overall resemblance, because it shares 7 apomorphic similarities with Euclitellata, and 5 plesiomorphic similarities with polychaetes (those characters that become apomorphic for Euclitellata). Overall similarity alone would place *Hrabeiella* as a “clitellate”. However, this taxon also happens to lack 2 “key” characters of this typological clitellate concept, the clitellum proper and spermathecae (characters herein hypothesized to have been secondarily reduced). Under the typological biases characterized above, Questidae, Parergodrilidae, and Aphanoneura are definitively more polychaete-like, while *Hrabeiella* is at least as much polychaete-like (5 plesiomorphic similarities and 2 reversal similarities) as clitellate-like (7 apomorphic similarities). Would this not explain the gut-feeling of so many previous authorities that these 4 groups should be considered “oligochaetoid polychaetes”?

Questids. Rouse and Fauchald (1997), Bartolomaeus et al. (2005), and Zrzavý et al. (2009) find close relationships of questids with orbiniids and paranoids. Under the present phylogenetic framework, these relations would seem to be a consequence of shared plesiomorphies. These authors also note the clitellate similarities of questids, revealed by the presence of clitellar material, the gonads limited to a few segments, and in the resemblance of the bifid crochets to the chaetae of certain clitellates (Fauchald and Rouse, 1997). These represent apomorphies indicative of true phylogenetic relationships. Consequently, the opinions of Giere and Erséus (1998) that the character specializations of the reproductive organs such as prostate glands, sperm receptacles, and incomplete clitella are convergent characters for questids and [eu]clitellates must be reconsidered.

Questidae and Parergodrilidae. Struck et al. (2002), Bleidorn et al. (2003), and Bleidorn (2005) state that molecular studies clearly speak in favor

of a phylogenetic placement of Parergodrilidae as sister of a clade comprising Orbiniidae and Questidae. Maybe the molecular analysis, conducted with no consideration of evolutionary polarities of molecular sequences, illustrates yet another example of groupings apparently based on plesiomorphic similarities.

Questidae, Parergodrilidae, and Aphanoneura. Rouse and Fauchald (1995) placed Questidae within the scolecid polychaetes. Rouse and Fauchald (1997) later suggested that Parergodrilidae, Aeolosomatidae, and Potamodrilidae can also be clustered with the scolecid polychaetes, although their exact placements remained uncertain. Polychaeta were recognized mainly for the presence of nuchal organs. However, when this character is accepted as plesiomorphic for Clitellata, clitellates become “polychaetes” that have gradually lost not only nuchal organs, but also several other characters such as parapodia, branchiae, chaetae, and primary larvae.

“Terrestrial polychaetes”. *Parergodrilus heideri* and *Hrabeiella periglandulata* were excluded from Clitellata in the previous accounts for not having some of the key character similarities with clitellates, and were included in the “Polychaeta” for their overall resemblance to polychaetes. The fewer characters shared with [Eu]clitellata were interpreted as convergences (Erséus and Rota, 1998; Rota, 1998; Purschke, 1999, 2000). However, when only apomorphic resemblances are accepted as a basis for inferring shared ancestry, then such epithets as ‘enigmatic’ or ‘aberrant’ to describe *Hrabeiella* and *Parergodrilus* (Rota, 1998; Rota et al., 2001) no longer seem necessary. Their positions in the phylogenetic system of the clitellates become firmly established with available morphological data alone. Rather than referring to parergodrilid polychaetes and terrestrial polychaetes (e.g., Des Châtelliers et al., 2009), we must now assume the obvious: they not only share features with oligochaetes, but in actuality are clitellates.

Hrabeiella and Aphanoneura. Struck and Purschke (2005) remark that there seems to be an unresolved conflict between molecular and morphological data sets, and thus clitellate characters found in Aeolosomatidae are more probably convergently evolved than due to common ancestry.

Rota et al. (2001) and Zrzavý et al. (2009) find that *Hrabeiella periglandulata* groups as a sister taxon to Aphanoneura, although with weak support. In reality, it appears that this placement may be due to plesiomorphic similarities.

The discovery of a high degree of correspondence in the structure of the foregut in *Hrabeiella periglandulata* and *Enchytraeus minutus* Nielsen & Christensen, 1961, extending to details in the ultrastructural level led Purschke (2003b) to question whether these correspondences can still be explained as convergently evolved. Even though such correspondence extends to characters of the central nervous system (Purschke, 1999, 2000, 2002b), he concluded that the position of *H. periglandulata* within the Annelida is unknown and cannot be defined at the present time, and that a proposed sister group relationship to Clitellata is of no help in clarifying its systematic position (Purschke, 2003b). Clearly, the failure to recognize a definite sister group relationship between *Hrabeiella* and [Eu]clitellata is not due to lack of information, but on not clearly distinguishing signaling apomorphic characters from plesiomorphic non-informative phylogenetic noise. Rather than considering *Hrabeiella periglandulata* the only non-clitellate annelid to possess a dorsal pharynx (Jamieson, 1992; Rota, 1998; Purschke, 1999, 2002a, 2003b; Tzetlin and Purschke, 2005), this character may be considered to represent strong evidence for the sister-group relationship between *Hrabeiella* and Euclitellata, and from which we may infer that the clitellum has become secondarily reduced in the Hrabeiellidae.

Other continental polychaetes

Glasby et al. (2009) have listed an impressive 197 species, 78 genera, and 26 families of non-marine Polychaeta of the world, of which 7 species are terrestrial. Of these, the 27 species of freshwater Aeolosomatidae, the 2 species of terrestrial Parergodrilidae, and the terrestrial *Hrabeiella periglandulata* have been removed in this paper from the polychaetes to the Clitellata *sensu lato*.

This still leaves 167 non-marine polychaetes, of which 4 are terrestrial species of Oriental Nereididae: *Namalycastis terrestris* (Pflugfelder, 1933), *Neanthes belewanensis* Pflugfelder, 1933, *N. vitabunda* Pflugfelder, 1933, and *Paraleonnates tenuipalpa* (Pflugfelder, 1933).

The first of these species belongs to one of the most successful groups of polychaetes in fresh and brackish waters, the Namanereidinae Hartman, 1959 (Wesenberg-Lund, 1958). This group of 34 mainly tropical species is interesting for its ability to inhabit low salinity and/or semi-terrestrial environments, not normally tolerated by other polychaetes, which has resulted in a number of specialized physiological, morphological, and reproductive adaptations (Storch and Welsh, 1972; Glasby, 1999). In 4 of these species, hermaphroditism (or parthenogenesis) has been reported: *Namalycastis indica* (Southern, 1921), *N. hawaiiensis* (Johnson, 1903), *Namanereis catarractarum* (Feuerborn, 1931), and *N. quadraticeps* (Blanchard, 1849) (Johnson, 1908; Feuerborn, 1931; Aiyar, 1935; Runganadhan, 1943; Glasby et al., 1990). The first 3 are Pacific species, but *N. quadraticeps* (apparently a group of species) also occurs in the Black Sea, Mediterranean, and temperate subantarctic regions, including Chile and Argentina. *N. indica* furthermore has direct development and larvae in cocoons (Runganadhan, 1943; Glasby, 1999). Direct development, either externally in cocoons or in the adult tube or internally (viviparity), has been reported in several species of Nereididae (Wilson, 1991). Many of these reproductive adaptations appear to represent remarkable convergences with the clitellates.

Finally, there are 12 further namanereidines known from South America: *Namalycastis abiuma* (Grube, 1872) (Brazil: Santa Catarina), *N. abiuma* sp. gr. (Brazil: Paraná) (Glasby, 1999), *N. arista* Glasby, 1999 (Guyana), *N. brevicornis* (Audouin and Milne Edwards, 1833) (French Guiana; Brazil: Pará) (Glasby, 1999), *N. geayi* (Gravier, 1901) (French Guiana), *N. kartaboensis* (Treadwell, 1926) (Guyana) (Treadwell, 1926) (French Guiana, Surinam) (Glasby, 1999), *N. macroplatis* Glasby, 1999 (Surinam, Brazil: Pará) (Glasby, 1999), *N. senegalensis* (Saint-Joseph, 1900) (French Guiana) (Gravier, 1901) (Surinam; Brazil: Pará) (Glasby, 1999), *N. siolii* (Corrêa, 1948) (Brazil: Amazonas) (Corrêa, 1948), *Namanereis amboinensis* (Pflugfelder, 1933) (Brazil: Paraná) (Lana, 1987), *N. littoralis* (Grube, 1872) (Brazil: Santa Catarina) (Grube, 1872), and *N. littoralis* sp. gr. (Grube, 1872) (Chile; Uruguay) (Glasby, 1999).

I provided this extensive listing of semi-terrestrial polychaetes to illustrate that the evolution of the

clitellates, although representing the most important conquest of land by annelids, was neither the first nor the only event of an at least partial continental invasion within the metameric worms.

Methodological discussion

We have inherited a millenary, essentialistic, taxonomic tradition of classifying organisms by linear and logical divisions into arbitrary typological groups. This outlook has culminated in the Linnaean taxonomy.

The original Hennigian revolution (Hennig, 1950, 1966) promised at long last to introduce system thinking into systematics (Von Bertalanffy, 1968), but empirical taxonomists of a phenetic, atheoretical, and statistical outlook have reverted cladistics to a typological framework.

Computer total-evidence approaches are proving incapable of fully reconstructing the genealogical history of life because modern cladistic taxonomy perpetuates the typological biases of defining groups by character similarities, rather than by shared ancestry, as envisioned by Hennig (1950, 1966).

Once character states such as epidermal glandular pads of questids and annular clitella of euclitellates are coded as independent, unrelated characters, present software computer programs are unable to reunite these states into non-independent, successive, evolutionary-linked transformation series. For this reason, non-polarized characters, particularly molecular data, more often than not, group taxa (such as Polychaeta, *Questa* + Orbiniidae, Parergodrilidae + *Hrabeiella*, Aphanoneura + Parergodrilidae) by plesiomorphic similarities, rather than uncovering exclusively monophyletic groups (such as Clitellata, Apodadrilida, Oligochaeta, Dorsopharyngea, and Euclitellata).

The failure of both molecular (Hall et al., 2004; McHugh, 2005) and total evidence approaches (Colgan et al., 2006) to produce a robust phylogenetic reconstruction of the Polychaeta, and in particular to position the Clitellata, could be a consequence of the failure of quantitative methods to distinguish plesiomorphic from apomorphic similarities. When unexpected results are obtained with molecular data, such as a sistergroup relationships between Clitellata

and Dinophilidae (Hall et al., 2004), the problem may lie with method, rather than warranting the conclusion that morphology will require re-evaluation, or that more 18S r DNA sequence data are needed (Hall et al., 2004). Thus the failure of molecular analysis in positioning the Clitellata within the Annelida and the supposedly few morphological clues in this matter (Rousset et al., 2008) may result from methodological biases in the present cladistic methods.

Cladistic methods presently remain typological, because groups are defined by character similarities, rather than by shared ancestry. Only process-oriented hypotheses under Hennigian principles of character transformations in an evolutionary context can avoid the typological thinking of methodological, quantitative, pattern cladistics, whether based on morphological or molecular data.

Previous approaches to unravel the phylogenetic origin and the subsequent history of the Clitellata, in my opinion, have been only partly successful. Evolutionary morphology overestimates convergences. Numerical cladistic approaches, whether based on morphology, molecules, or total evidence, minimize process assumptions and thus methodologically may fail to distinguish plesiomorphic from apomorphic similarities.

It appears to me unreasonable to leave to the computer program the task of polarizing character states solely on the basis of parsimony considerations starting from unordered characters. Hennigian approaches make it necessary that hypothetical transformations of characters be established a priori to a phylogenetic analysis, and then tested for congruence with other such hypothesis of evolutionary transformations. Erséus (2005) also realizes that a careful a priori assessment of primary homologies is of fundamental importance for the quality of any cladistic study.

Although the qualitative Hennigian approach is often criticized for its a priori establishment of evolutionary hypothesis, the final evolutionary history only emerges a posteriori, by overall congruence of the most consistent data evaluated by reciprocal illumination. The alleged subjectivity of the Hennigian approach is amply compensated for

by the avoidance of typological thinking, a bias that continues to pervade most previous approaches.

Three typological biases may be identified in current quantitative cladistic analyses: (1) present/absent character coding is typological because it breaks a continuum of evolutionary change at arbitrary points into 2 absolute (typological), and falsely independent, character states; (2) divisions of phylogenetic trees into 2 groups (e.g., Polychaeta/Clitellata) is also typological, because it establishes arbitrary limits into 2 typological entities along a continuous lineage of evolving clades; finally, (3) accepting only present characters as apomorphic is typological because evolution involves character change, independently of whether such changes are acquisitions or reductions.

Plesiomorphic character states tend to be more numerous than apomorphic character states in a total phylogenetic analysis for the simple reason that plesiomorphic similarities accumulate from all evolutionary levels, while apomorphies are restricted to the single nodes under consideration and then become hidden from typological perception when further evolving into new apomorphic character states. Thus parsimony programs, by maximizing similarities among “independent” character states, will tend to group by plesiomorphic similarities more often than by apomorphic similarities. For this reason, the responsibility for ordering character states into transformations remains with the phylogenetic researcher.

Finally, an essentialistic cladistic approach is unable to correctly establish homologies among different character states in old groups subject to long morphological histories of character differentiation, because the new character states that become transformed by evolution tend to be coded as different characters.

Conclusions

Despite its subjectivity, only the Hennigian method avoids the typological biases contained in the more widely used quantitative methods for phylogenetic inference, and also in qualitative methods in which plesiomorphic and apomorphic

similarities are not consistently differentiated. I show that morphology is most adequate for uncovering the emergence and the subsequent evolutionary history of the clitellates from marine polychaetes, when interpreted into transformation series, according to Hennigian principles. The Hennigian approach also provides a workable framework for interpreting some of the more recent results suggested by numerical approaches. Many of the conflicting previous results on clitellate phylogeny can be reinterpreted as resulting from artifactual plesiomorphic groupings obtained from quantitative parsimony programs.

Once characters have been hypothesized to form extended evolutionary transformations, they may be treated quantitatively in cladistic packages for the analyses of morphological and molecular characters, separately or in total evidence approaches.

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