

## On the ground pattern of Annelida\*\*

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### Abstract

Annelida, traditionally divided into Polychaeta and Clitellata, are characterized by serial division of their body into numerous similar structures, the segments. In addition, there is a non-segmental part at the front end, the prostomium, and one at the back, the pygidium. New segments develop in a prepygidial proliferation zone. Each segment contains four groups of chaetae made up of  $\beta$ -chitin, a pair of coelomic cavities separated by mesenteries, and septa. The nervous system is a rope-ladder-like ventral nerve cord with a dorsal brain in the prostomium. For the last stem species a trochophore larva and a benthic adult are commonly postulated. There are two conflicting hypotheses describing the systematization of Annelida: the first postulates a sister-group relationship of Polychaeta and Clitellata, the second sees Clitellata as a highly derived taxon forming a subordinate taxon within the polychaetes which, consequently, are regarded as paraphyletic. Depending on the hypothesis, different characters have to be postulated for the stem species of Annelida. Besides segmentation other characters such as nuchal organs, palps and antennae, body wall musculature, cuticle, parapodia as well as structure of the central nervous system and the foregut play an important role in this discussion. Here, the different characters and character states are critically reviewed and analyzed with respect to morphology and function. The consequences for systematization of their phylogenetic interpretation as autapomorphies, synapomorphies or plesiomorphies are outlined. The resulting hypotheses are compared with those relying on molecular data sets.

**Key words:** Annelida, Polychaeta, Clitellata, Arthropoda, Articulata, phylogeny

### Introduction

A discussion of the evolution and phylogeny of the Arthropoda is inevitably connected to the question of their sister group. Until recently, this problem was regarded as having been solved by the naming of the Annelida. Both taxa are traditionally united as Articulata, a view going back to Cuvier (1817) and still widely accepted because of an overall similarity in their segmentation, which has been regarded as a synapomorphy of the two taxa (e.g., Rouse & Fauchald 1997, Scholtz 1997, Ax 1999). This supposed phylogenetic relationship has been seriously challenged on the basis of phylogenetic analyses using 18S rDNA sequences (Anguinaldo et al. 1997), and the Ecdysozoa hypothesis came into discussion (Schmidt-Rhaesa et al. 1998, Wägele et al. 1999, Zrzavý 2001). According to this hypothesis, segmentation has to

be regarded as either convergent or plesiomorphic, at least occurring in the stem lineage of the protostomian taxa. Moreover, in many analyses using molecular or morphological data, Annelida are not monophyletic or at least weakly defined if segmentation is not considered (Schmidt-Rhaesa et al. 1998). Therefore, further discussion of these questions should start with a thorough evaluation of the ground pattern of those taxa typically united as Annelida. Then in a second step an evaluation of the characters observed should be carried out to allow differentiation between plesiomorphies, autapomorphies and, of special interest in this context, synapomorphies of Annelida and their supposed sister group.

The proposed ground plan of the stem species of Annelida and their monophyly are still under discussion. The systematization of the higher taxa in Annelida is one prominent example of different phylogenetic assess-

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ments leading to conflicting hypotheses about phylogenetic relationships and the direction of evolutionary pathways (see Westheide et al. 1999). These conflicting hypotheses based on morphological evidence either postulate a sister-group relationship of Polychaeta and Clitellata (hypothesis 1; Fig. 1A), or see Clitellata as highly derived annelids forming a subordinate taxon within the paraphyletic polychaetes (hypothesis 2; Fig. 1B). As will be reviewed in detail, absence of characters and its phylogenetic evaluation as primary or secondary is the main reason for these contradictory hypotheses within Annelida (Purschke et al. 2000). This is also the case with respect to the Articulata and the Ecdysozoa hypotheses (Schmidt-Rhaesa et al. 1998). Regarding the annelids, the diverging hypotheses concern the monophyly of Polychaeta, the systematization within the latter, and the positions of Clitellata, Pogonophora and Echiura (see Purschke et al. 2000 for references).

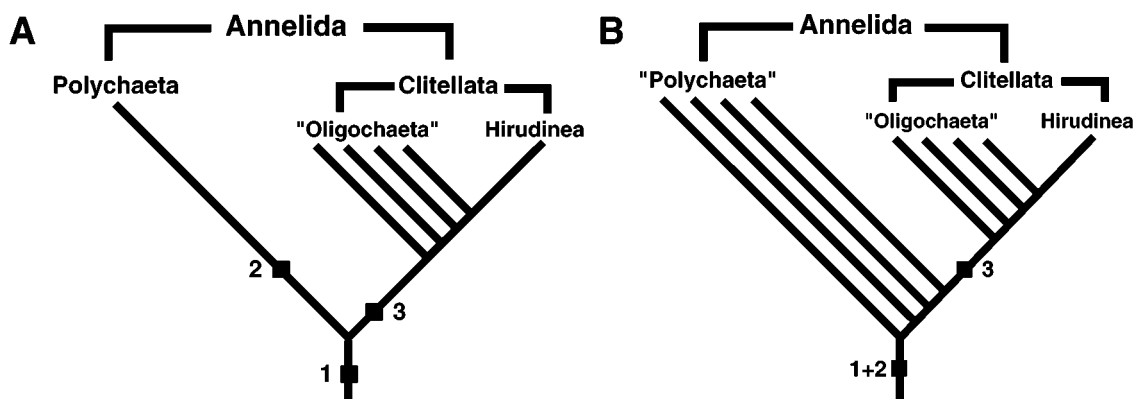
The present paper focusses on the ground pattern of Annelida, their probable monophyly, and the conflicting hypotheses about their phylogenetic relationships. The influence of these relationships on the presumed ground pattern is discussed as well as the apomorphies defining Annelida, Polychaeta and Clitellata. The possible synapomorphies with the taxon Arthropoda are discussed in Scholtz (2002) and Schmidt-Rhaesa (unpubl.).

## Character analysis

### Segmentation in Annelida

The structure of Annelida is based on the serial division of their body into numerous compartments, the segments, each with the same organization and development. In addition, there are two non-segmental regions:

one at the anterior end, the prostomium, and another at the rear, the pygidium (Westheide 1997). The prostomium houses the brain or supraoesophageal ganglion and bears the most important sense organs. The mouth is situated ventrally in the first segment, the anus terminally in the pygidium. Although the first segment is usually called peristomium and regarded to be presegmental due to its development from the trochophore, recent studies on the nervous system indicate that it is nothing but a true segment bearing the mouth (Müller & Westheide 2002, Müller unpubl. observ.). New segments are produced in a prepygidial proliferation zone. The nervous system is considered to be a typical ladder-like ventral nerve cord composed of segmentally arranged paired ganglia connected to each other by means of longitudinal connectives and transverse commissures (Bullock 1965). Moreover, each segment includes a pair of coelomic cavities delimited by a median mesentery and anterior and posterior dissepiments or septa. Blood vessels are formed either in the extracellular matrix (ECM) between adjacent coelomic linings or in the ECM between mesodermal and entodermal or ectodermal tissues (Fransen 1988, Bartolomaeus 1994, Westheide 1997). Myofilaments may be present in the coelomic lining, and parts of the vessels may be contractile (Fransen 1988). If morphologically distinct, such areas are called "hearts". Each segment is supplied with a pair of so-called segmental organs in the form of either metanephridia or protonephridia (Smith & Ruppert 1988, Bartolomaeus & Ax 1992, Bartolomaeus 1997, 1999), which are homologous since they develop from the same anlagen (Bartolomaeus 1999). Epidermal chaetae composed of  $\beta$ -chitin and arranged in four bundles are also characteristic for each segment. Usually, chaetae are absent in the first segment or peristomium.



**Fig. 1.** Cladograms to illustrate the conflicting hypotheses about phylogenetic relationships within Annelida. Paraphyla are indicated by quotation marks and more than one lineage. Numbered solid squares symbolize autapomorphies. **A.** Polychaeta and Clitellata as sister groups within monophyletic Annelida. **B.** Clitellata as sister to only a subordinate taxon of the Polychaeta, which consequently becomes paraphyletic within Annelida; most autapomorphies of Polychaeta in A become autapomorphies of Annelida. Modified from Westheide et al. (1999).

Whether these chaetae are primarily organized in lateral appendages called parapodia – in which case these appendages would belong to the ground pattern of the annelid stem species – has been the subject of vigorous debate (Clark 1977, Fauchald 1977, Rouse & Fauchald 1995, 1997, Westheide 1997). The body wall of Annelida comprises an outer layer of circular and an inner layer of longitudinal muscle fibres, the latter being regarded as arranged in bands (Avel 1959, Stolte 1969, Rouse & Fauchald 1995, Ax 1999). In many marine species, the life cycle consists of a planktonic larval stage, the trochophore, and a benthic adult stage (Westheide 1997, Nielsen 1998, Rouse 1999, Westheide et al. 1999). During embryonic development a specific cleavage pattern of the 2d cell can be observed in clitellates, and in all probability also in polychaetes (see Dohle 1999).

The structure of the body as described above in rough outline exhibits an incredible adaptive potency, which has led to an extraordinary evolutionary differentiation and rapid radiation (McHugh 2000). The result is a high morphological and ecological diversity between the major annelid groups. This is especially the case for those taxa traditionally united as polychaetes, which includes forms ranging from endobenthic tube-dwelling to pelagic, and from the possession of well-developed parapodia to only groups of chaetae to no chaetae at all. Most species live in marine habitats, but others may also occur in freshwater or terrestrial habitats. The same diversity applies to their reproductive biology and feeding (Fauchald & Jumars 1979, Fauchald & Rouse 1997, McHugh 2000, Rouse & Pleijel 2001). Currently, about 80 so-called families are recognized within the polychaetes, and in some cases monophyly has yet to be established (Fauchald & Rouse 1997, Rouse & Pleijel 2001). Finally, evolutionary changes may result in taxa in which segmentation is almost unrecognizable or seemingly absent, as exemplified by Echiura and Siboglinidae (formerly Pogonophora). The systematic position of these two taxa was uncertain for a long time, and they were placed in various positions, but recent morphological and molecular studies provide strong evidence that both are derived annelid taxa and have to be included in the polychaetes (e.g., Bartolomaeus 1995, McHugh 1997, 2000, Rouse & Fauchald 1997, Hessling 2002, Hessling & Westheide 2002).

### Cuticle

In Annelida the epidermis is covered by a cuticle secreted by the epidermal cells and penetrated by microvilli (Fig. 2) (Richards 1984, Storch 1988, Gardiner 1992, Jamieson 1992). The basal collagenous matrix usually comprises orthogonally arranged layers of parallel collagen fibres of various thickness (Fig. 2E–H). Apically the matrix is more electron-dense and forms a more or less

distinct epicuticle without collagen fibres. Often this layer is covered by membrane-bounded epicuticular projections which are thought to be derived from microvillar tips (Richards 1984). The structure of the cuticle is not uniform among Annelida, and numerous modifications of this pattern have been described. Mostly these concern the development of collagen fibres, which may be more or less reduced and even absent. The latter is especially the case in interstitial and other small species (Fig. 2A–D). In these forms the cuticle resembles the egg envelope (Fig. 2A) from which it is derived (Eckelbarger 1978). A typical collagenous cuticle is also present in Echiura, Siboglinidae (Gardiner & Jones 1993, Southward 1993, Storch 1984), and Sipuncula (Rice 1993). Since such a cuticle is absent in all other taxa of the metazoan clade (see Rouse & Fauchald 1995), two phylogenetic implications are conceivable: (1) The collagenous cuticle represents a synapomorphy of Sipuncula and Annelida – or Articulata, depending on whether the Articulata or the Ecdysozoa hypothesis is adopted (Rouse & Fauchald 1995, Ax 1999); (2) If Sipuncula turn out to be derived from a segmented ancestor and thus form an ingroup of Annelida, the collagenous cuticle is an autapomorphy of the latter. To date there is little evidence for the second alternative (Purschke et al. 1997, McHugh 2000), but see figure 1 of Martin (2001) where *Phascolosoma granulatum* falls into the annelid clade!

### Chaetae

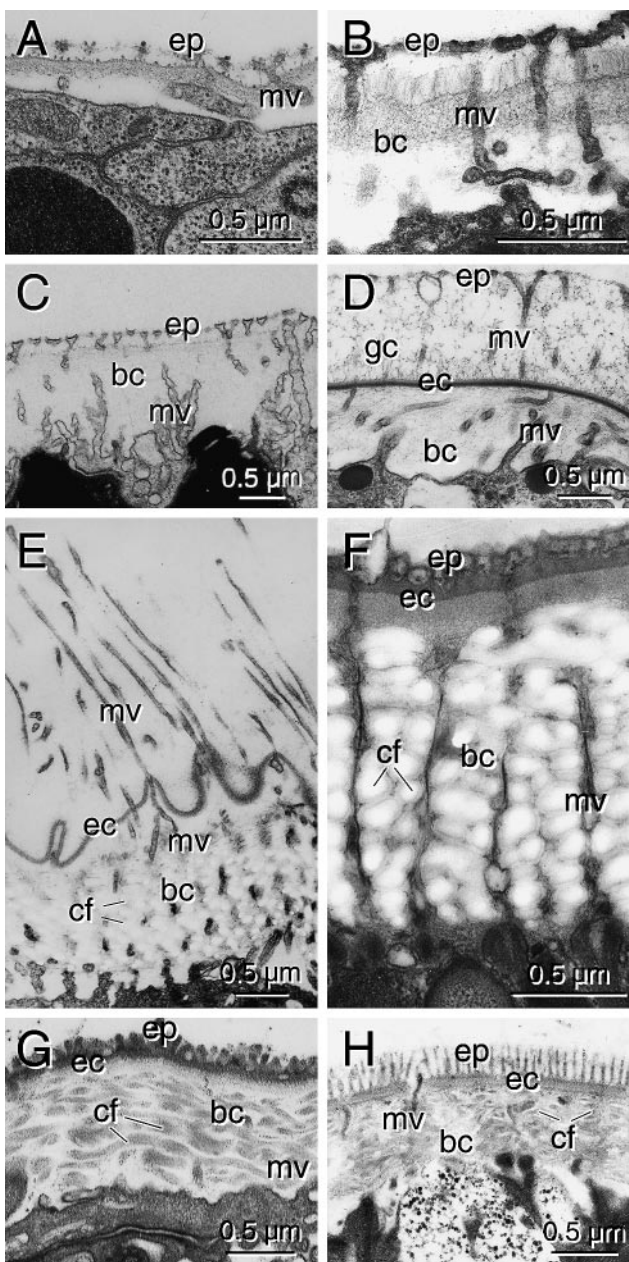
Chaetae are generally regarded as the most characteristic feature of Annelida (Rouse & Fauchald 1995, Westheide 1997). Although morphologically highly diverse, they exhibit the same ultrastructure without exception: they consist of bundles of chitinous tubes held together by sclerotized protein. Each chaeta is produced around the microvillar brush border of a single cell, the chaetoblast, situated in an epidermal follicle (Specht 1988, Bartolomaeus 1995). The chitin – in the form of  $\beta$ -chitin – is secreted by the chaetoblast, and the tubes are formed around the microvilli of the chaetoblast. Number, shape, size and dynamics of these microvilli are the structural basis for the various forms of chaetae observed in annelids (O'Clair & Cloney 1974, Specht 1988, Westheide & Watson Russell 1992, Bartolomaeus 1995). Such chaetae are also present in Echiura and Siboglinidae (Pilger 1993, Southward 1993), but may be absent in certain Annelida, for instance in Dinophilidae, Protodrilidae, Polygordiidae, and Hirudinea. In view of their systematic positions (Westheide 1985, Purschke et al. 1993), it is most likely that all these conditions represent the loss of chaetae rather than primary absence. The epidermal bristles found in some Sipuncula, and the setae of Euarthropoda, are different and considered not ho-

mologous with chaetae found in Annelida (Rouse & Fauchald 1995).

An even more difficult issue concerns the chaetae-like structures present in Brachiopoda and Cephalopoda (Orrhage 1973, Lüter & Bartolomaeus 1997). Although structurally very similar to those of Annelida they are regarded as convergently evolved in these three taxa and thus represent an autapomorphy of Annelida (Lüter & Bartolomaeus 1997, Ax 1999). An alternative view is that these chaetae are homologous, have been lost repeatedly, and represent a plesiomorphy for Annelida. In

this case they would be of no value for phylogenetic assessments of this group. Interestingly, in the analyses of Winnepenninckx et al. (1998) using 18S rDNA sequences Brachiopoda and Phoronida fall into a clade comprising several Annelida as well.

Within Annelida specific types of chaetae have been proposed to represent apomorphies for certain subtaxa, e.g. the uncini, aciculae and the camerate type of chaeta (Glasby 1993, Bartolomaeus 1995, Rouse & Fauchald 1997, Pleijel & Dahlgren 1998). However, this discussion is beyond the scope of the present paper.



**Fig. 2.** Different types of cuticle ultrastructure in Annelida. **A–F.** Polychaeta, **G–H.** Clitellata. **A–B.** Larval type without collagen fibres, the common type in small and interstitial species. **A.** *Nerillidium troglochaetoides* (Nerillidae). **B.** *Dinophilus gyrociliatus*; cuticle traversed by microvilli forming dense cover of epicuticular projections. **C.** *Microphthalmus similis* (Hesionidae); cuticle without collagen fibres, indistinct epicuticle, microvilli project slightly above cuticular surface and form epicuticular projections. **D.** *Kefersteinia cirrata* (Hesionidae); cuticle with long microvilli and prominent glycolyx. **E–H.** Cuticles with collagen fibres (negatively stained in E, F). **E.** *Polygordius appendiculatus* (Polygordiidae); microvilli extending far beyond cuticular surface, epicuticular projections absent. **F.** *Pisione remota* (Pisionidae), pharynx; cuticle with distinct epicuticle and typical epicuticular projections. **G.** *Stylaria lacustris* (Naididae); typical cuticle penetrated by a few microvilli only. **H.** *Lumbricillus buelowi* (Enchytraeidae); showing structural pattern similar to that of the limnetic *S. lacustris*. bc = basal cuticle, cf = collagen fibre, ec = epicuticle, ep = epicuticular projections, gc = glycolyx, mv = microvilli.

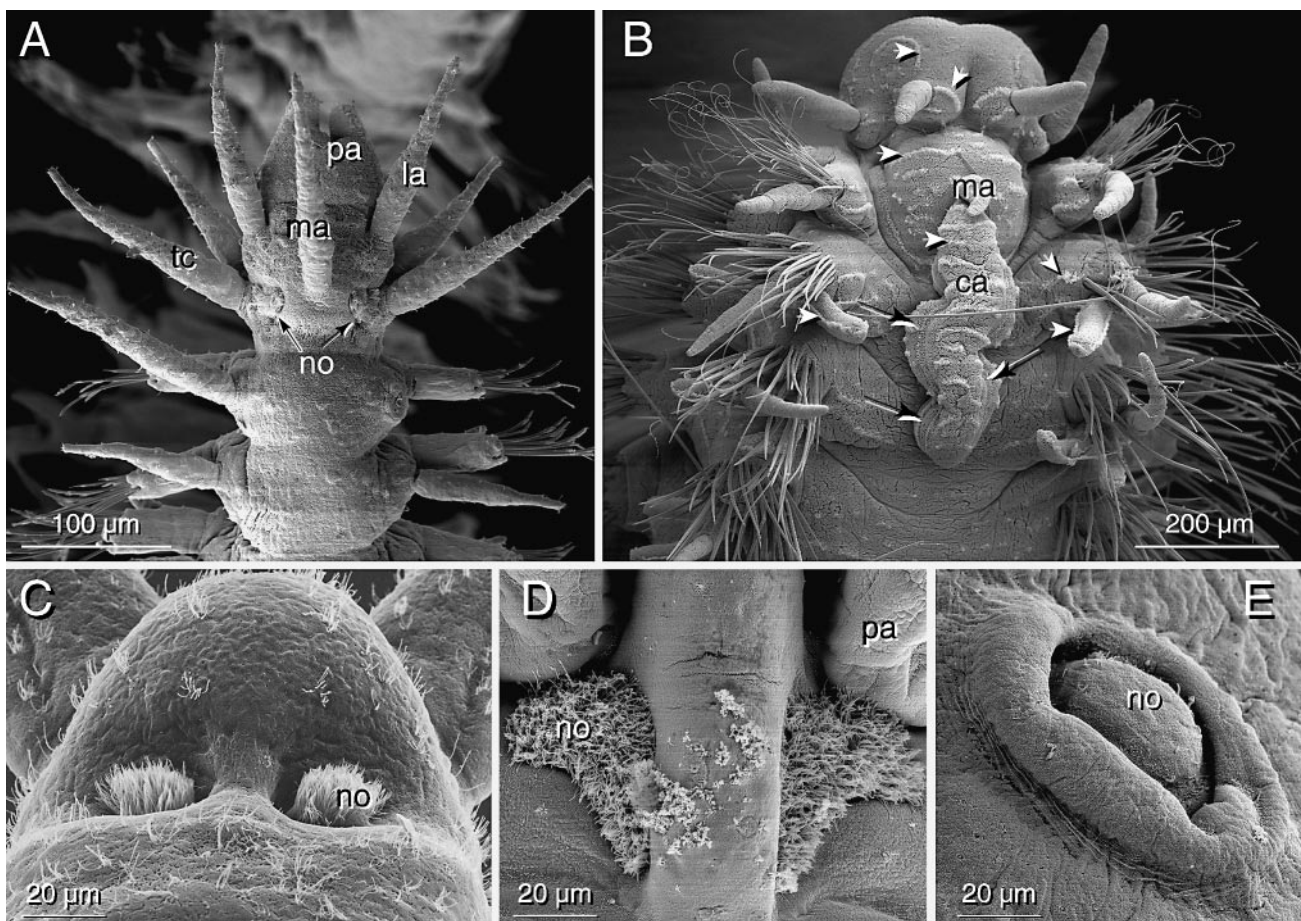
### Epidermal ciliation

In many species of Annelida certain areas on the body surface are equipped with locomotory cilia (Fig. 3A–B). Such cilia generate water currents for feeding, respiration or locomotion. Especially meiofaunal species may move by ciliary gliding rather than muscular activity (Martin 1978, Purschke & Jouin 1988). Such cilia are lacking in Clitellata without exception, although some clitellate species occur in aquatic habitats and have meiofaunal body size (Purschke 1999). Cilia are also absent in the few true terrestrial polychaetes known to date, as well as in species occurring in habitats with low water content: *Hrabeiella periglandulata* Pizl & Chalupsky, *Parergodrilus heideri* Reisinger, and *Stygocapitella subterranea* Knöllner. Moreover, absence of kinocilia is often observed in species with a thick, collagenous cuticle, such as the Polygordiidae. In Sipuncula such cilia are restricted to the tentacles, which bear a

comparatively thin cuticle (Rice 1993). Locomotory cilia are widespread in Metazoa, and thus their absence most likely represents a loss that occurred repeatedly in various taxa within and outside Annelida.

### Sense organs

**Nuchal organs.** Kinocilia are present in sense organs occurring in almost all taxa of Annelida: the nuchal organs (Fig. 3). Situated at the posterior end of the prostomium, they are presumed to have a chemosensory function (Purschke 1997). Although varying considerably in external configuration, they show an overall fine-structural similarity, and there is no doubt about their homology within Annelida (Rouse & Fauchald 1995, 1997, Purschke 1997). In Spionidae similar sense organs are present on the segments in the form of paired longitudinal ciliary bands oriented parallel to the longitudinal axis of the trunk (Jelsing 2002a, b).



**Fig. 3.** Nuchal organs. **A.** *Brania subterranea*. **B.** *Eurythoe complanata*; caruncle with ciliary bands representing nuchal organ (complete arrows); additional arrowheads point to bands of locomotory cilia. **C.** *Saccocirrus krusadensis*. **D.** *Polydora cornuta*. **E.** *Glycera tridactyla*; cone-shaped nuchal organs completely retractile. ca = caruncle, la = lateral antenna, ma = median antenna, no = nuchal organ, pa = palp, tc = tentacular cirrus. Micrographs A, B, D, E: S. Raabe, C from Purschke (1997).

The locomotory cilia are located on the supportive cells and are responsible for a rapid exchange of sensory stimuli. The sensory cells are bipolar primary sensory cells, their perikarya form the nuchal ganglia and their processes the nuchal nerves. The nuchal nerves emanate directly from the brain, as is the case for the separate efferent innervation. The sensory processes are cilia, ciliary branches and microvilli traversing a subcuticular space called the olfactory chamber, which is protected by specialized cuticular or microvillar layers. Many burrowing forms possess completely retractile nuchal organs (Fig. 3E), and in terrestrial polychaetes they are either situated in deep grooves and externally invisible or are altogether absent (Porschke 1986, 1999, 2000).

Nuchal organs are lacking in Clitellata without exception (Porschke 1997, 1999). Whether this lack of nuchal organs is primary or secondary is still controversial and crucial for the systematization of Annelida (McHugh 1997, Porschke 1997, Rouse & Fauchald 1997, Westheide 1997, Porschke et al. 2000). Evidence for a loss of nuchal organs in Clitellata, so that absence represents a derived character state, comes from the reduction and absence of nuchal organs in terrestrial polychaetes, the lack of epidermal cilia in Clitellata, and the backward displacement of the brain (Porschke 1999, 2000, Porschke et al. 2000). In certain polychaetes a similar arrangement can be observed: *Pisione* spp. are characterized by an extremely modified anterior end including reduction of the prostomium and displacement of the brain. The large, bilobed brain is situated in the first three segments, the nuchal organs are absent and obviously have been lost (Siewing 1953, Porschke 1997, Rouse & Fauchald 1997).

Outside of the Annelida, structures named nuchal organs are present in Sipuncula, where they are situated on the introvert, either between or below the tentacles (Rice 1993). Ultrastructural studies in *Onchnesoma squamatum* (Koren & Danielssen) revealed distinct differences from the homonymous structures in polychaetes, which makes homology unlikely (Porschke et al. 1997). This is in contrast to the conclusions reached by Åkesson (1958). Although analogy is now generally assumed (Rouse & Fauchald 1995, 1997), further studies on other sipunculan species are required to obtain a definite answer. In conclusion, according to present knowledge the nuchal organ of Annelida either represents an autapomorphy of Annelida or, in case of a sister-group relationship between Polychaeta and Clitellata, an autapomorphy of Polychaeta (see Porschke 1997, Rouse & Fauchald 1997, Porschke et al. 2000).

**Ocelli.** In Clitellata, ocelli are only present in Hirudinea and certain species of Naididae (Sawyer 1986, Jamieson 1992). These eyes are characterized by the presence of phaesomous photoreceptor cells and supportive cells with shading pigment. Such sensory

cells are known from other species of Clitellata as well, and occur without associated pigment cells in the epidermis or nervous system. Phaesomes are the only type of light-sensitive cell occurring in Clitellata (Stolte 1969, Jamieson 1992, Porschke 1993). An outgroup comparison with polychaetes, Sipuncula and Mollusca shows that these photoreceptor cells are extremely rare, usually rhabdomeric or ciliary photoreceptor cells are present. These photoreceptor cells form an extracellular cavity with a supporting cell which may contain pigment (Eakin & Hermans 1988, Verger-Bocquet 1992, Porschke 2003). This structure also applies to multicellular eyes. Therefore, phaesomes have to be regarded as apomorphic structures in Clitellata in spite of their simple structure (Porschke 2003).

**Palps and antennae.** The second most important sensory structures for a phylogenetic systematization of Annelida are a pair of prostomial appendages, the palps (Fig. 3A–B). Palps are present in many but not all polychaete taxa (Orhage 1995, 1999, Fauchald & Rouse 1997, Rouse & Fauchald 1997, Rouse & Pleijel 2001). In addition, up to three antennae may occur on the prostomium (Fig. 3A–B); these appendages are homonymous but not homologous with the respective limbs of Arthropoda. The comprehensive investigations of Orhage (2001 and references therein) have demonstrated that palps can be homologized on the basis of their innervation in spite of their extraordinary variation in morphology and function. Coincidentally, the palps are innervated by nerves originating from the dorsal and ventral roots of the circumoesophageal connectives (Fig. 4B). Up to 12 different nerve roots have been found arising in different positions from these roots. Apparently, the roots numbered 4, 5, 6 and 9 are more important than the others but not present in every taxon investigated so far. As yet no taxon has been found in which all 12 nerve roots are present. Consequently, the problem of the ground pattern of palp innervation in polychaetes is still unresolved and has to be evaluated in connection with all other characters.

The innervation of the antennae is less complex: there are four nerves emanating from the dorsal commissure of the dorsal root of the circumoesophageal connectives (Fig. 4B). The median antenna is supplied with two nerves, each lateral antenna with only one.

Palps and antennae are lacking not only in Clitellata, but also in certain taxa of polychaetes (Rouse & Fauchald 1997, Rouse & Pleijel 2001). Depending on which of the two conflicting hypotheses is followed, the absence of antennae and palps is interpreted either as primary or as a loss. In the first case palps and antennae are regarded as having evolved within the Polychaeta, in the second as structures already present in the stem lineage of Annelida. The taxa lacking palps and antennae are united as Scolecida by Rouse & Fauchald (1997),

based on parapodia with similar rami and two or more pairs of pygidial cirri as their autapomorphy. They are placed as a sister group of the palp-bearing taxa at the base of Polychaeta, whereas these taxa are regarded as being highly derived in the opposite hypothesis (Westheide 1997). According to the cladistic analysis of Rouse & Fauchald (1997), antennae are highly derived structures present in Aciculata. This group is seen as close to the stem species by Westheide & Purschke in Westheide et al. (1999). Interestingly, in certain taxa of the Scolecida, Orrhage (1966, 1993) found nerves innervating certain areas in the prostomium which have to be homologized with the nerve roots innervating the palps in other polychaetes. These observations may be indicative of loss, especially because certain taxa such as Paraonidae exhibit similarities with palp-bearing forms that suggest a common origin and a different placement in the system (Orrhage 1993).

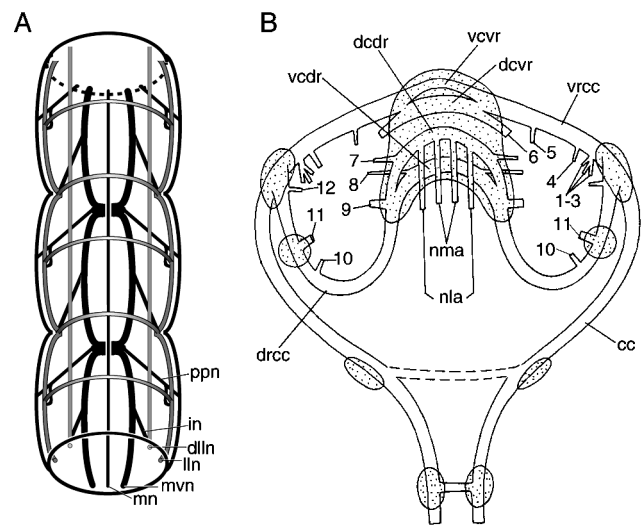
### Central nervous system

The central nervous system – as outlined above – can be reduced to the ventral, rope-ladder-like nerve cord (Fig. 4A), resulting from paired longitudinal cords and metameric ganglia connected by commissures (Bullock 1965). In each segment at least three pairs of lateral nerves arise from the cord. The dorsal brain is connected with the ventral cord by the circumoesophageal connectives, which form an arc around the mouth (Fig. 4B). In polychaetes these connectives are split into dorsal and ventral roots each of which again splits and forms a dorsal and a ventral commissure in the brain (Orrhage 1995). From these nerve tracts the various sense organs and the prostomial epithelium as well as the gut are innervated. The ventral cord usually comprises at least one median nerve in addition to the two lateral trunks of the cord (Bullock 1965, Hessling & Westheide 1999, Müller & Westheide 2002). The trunks of the ventral cord may lie close together or be widely separated from each other (Hessling & Purschke 2000, Purschke et al. 2000). In the latter case, further paramedian nerves may be present. In addition, one or two pairs of longitudinal nerve tracts are commonly found laterally and dorsolaterally (Purschke et al. 2000, Müller & Westheide 2002). Thus, a nervous system with a simple ladder structure appears to be a rare exception, and it actually has an orthogonal appearance (Fig. 4A). The complexity of the nervous system appears not to be related to body size; even meiofaunal species possess highly developed nervous systems (Hessling & Purschke 2000, Müller & Westheide 2002, Purschke & Hessling 2002). Such an orthogonal pattern is not only present in larvae (Hanström 1928, Reisinger 1972) and progenetic forms (Müller & Westheide 2002). It likewise occurs in adults, although the main trunks of the ventral cord become the

most important nerves and certain longitudinal nerves may disappear or fuse with the main trunks (e.g., Purschke et al. 2000, Müller & Westheide 2002). At least an unpaired median nerve is considered to belong to the ground pattern in polychaetes (Bullock 1965, Müller & Westheide 2002).

The nervous system of Clitellata is generally more simple in structure. The most characteristic feature is that the brain is positioned outside the prostomium and lies in one of the following segments (Bullock 1965, Hessling & Westheide 1999). The circumoesophageal connectives are simple and arise anteriorly from the brain. The ventral cord has ill-defined ganglia, the trunks are not separate, and a median nerve cannot be distinguished. Hirudinea, which possess a specific type of ganglia, separate connectives and a median nerve, represent the only exception (Sawyer 1986, Purschke et al. 1993, Hessling & Westheide 1999).

Additional longitudinal nerves are present in Clitellata as well (Hessling & Westheide 1999). They are the only taxon within Annelida in which the central ner-

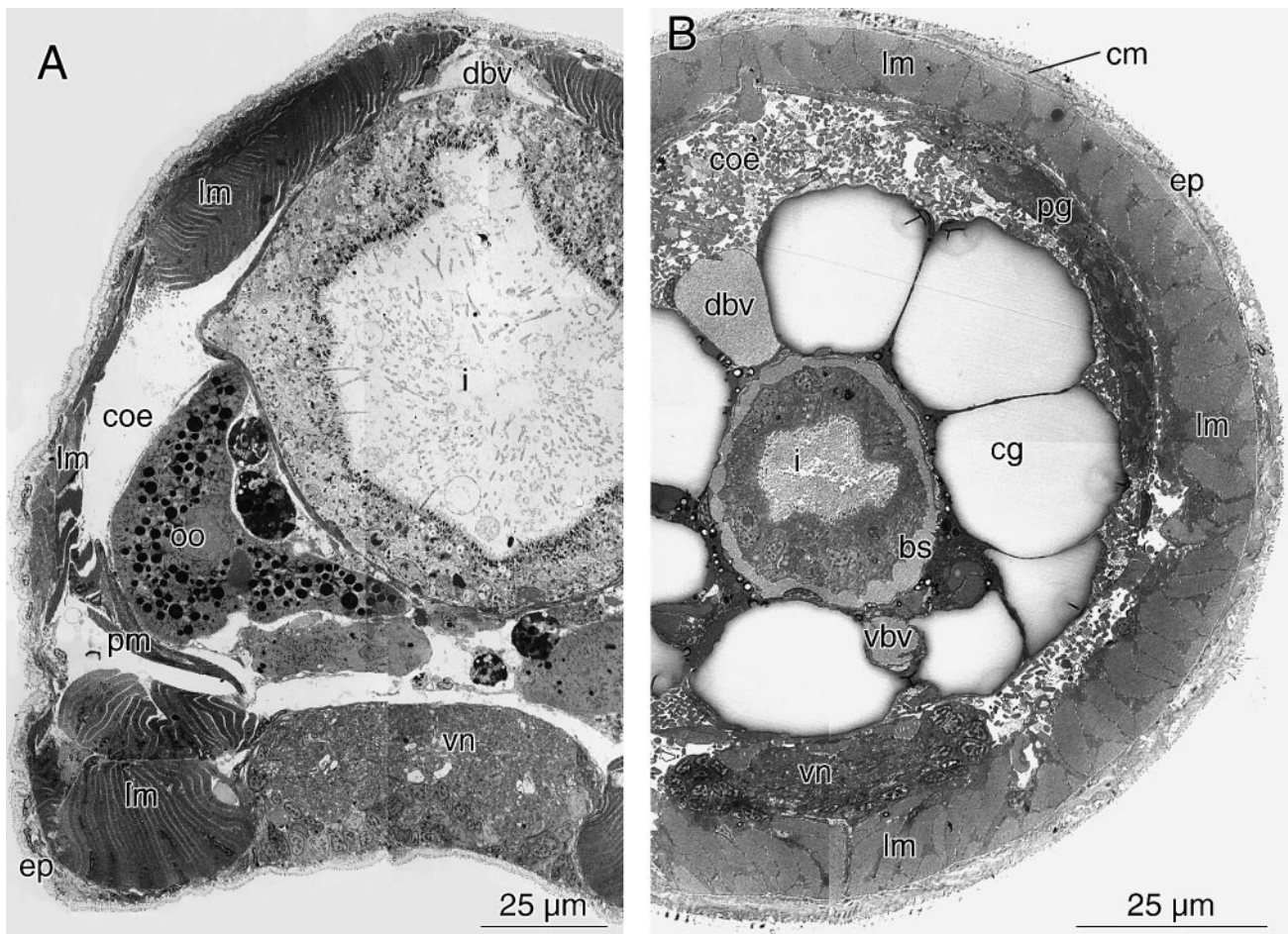


**Fig. 4.** Central nervous system. **A.** Nervous system of the trunk with longitudinal and segmental nerves of a polychaete exemplified by *Parapodrilus psammophilus*. **B.** Tentative general diagram of the cephalic nervous system of Polychaeta, numerals 1–12 refer to palp nerve roots, ganglia stippled. cc = circumoesophageal connective, dodr = dorsal commissure of dorsal root, dcvr = dorsal commissure of ventral root, dlln = dorsolateral longitudinal nerve, drcc = dorsal root of circumoesophageal connective, in = intrasegmental nerve, lln = lateral longitudinal nerve, mn = median nerve of ventral cord, mvn = main nerve of ventral cord, nla = nerve of lateral antenna, nma = nerve of median antenna, ppn = parapodial nerve, vodr = ventral commissure of dorsal root, vcvr = ventral commissure of ventral root, vrcc = ventral root of circumoesophageal connective. A after Müller & Westheide (2002), B after Orrhage (1995).



vous system is entirely subepidermal, even in the smallest oligochaete species (Fig. 5B). That is, brain and ventral nerve cord lie within the coelomic cavity enclosed by an ECM or connective tissue and a coelothelium (Bullock 1965, Stolte 1969, Purschke et al. 2000). This is in contrast to polychaetes, where the nervous system very often has an intraepidermal or basiepithelial position, not only in small but in larger species as well (Bullock 1965, Hessling & Purschke 2000, Tzetlin et al. 2002a). The nerve cord lies between the ventral longitudinal muscle bands (Fig. 5A) and, although situated on a bulge and projecting into the coelomic cavity, is not separated from the epidermis but instead is covered by an ECM continuous with that underneath the epidermis. This basiepithelial position is generally regarded as primitive within Bilateria (Bullock 1965).

With respect to the position of the brain in Clitellata, the backward displacement can be observed during ontogenesis and thus clearly represents a derived character state which is obviously correlated with the small prostomium, terrestrial life style, and burrowing in firm soil (Hessling & Westheide 1999). This is further corroborated by the fact that even in typical limnetic taxa with a large prostomium the brain has a similar position (Hessling et al. 1999). Moreover, in the terrestrial polychaetes *Parergodrilus heideri* and *Hrabeiella periglandulata*, similar features in the nervous system are observed (Purschke 1999, 2000). This interpretation also accounts for the lack of prostomial appendages, external kinocilia, nuchal organs, and parapodia. Moreover, the subepithelial, internal position of the ventral nerve cord may be correlated with the extensive development of the musculature of the body wall in Clitellata (see below).



**Fig. 5.** Cross-sections of trunk segments to show distribution of longitudinal muscle fibres and position of ventral nerve cord. **A.** *Sinohesion genetaliphora* (Hesionidae, Polychaeta); cross-section between parapodia. Note absence of circular fibres in this section. **B.** *Marionina preclitellochaeta* (Enchytraeidae, Clitellata); cross-section between chaetae. Note weakly developed circular musculature represented by single fibres. bs = intestinal blood sinus, cg = chloragocyte, cm = circular muscle, coe = coelomic cavity, dbv = dorsal blood vessel, ep = epidermis, i = intestine, lm = longitudinal muscle, oo = oocyte, pg = pharyngeal gland, pm = parapodial muscle, vbn = ventral blood vessel, vn = ventral nerve cord.



### Body wall musculature

A body wall musculature comprising an outer layer of circular fibres and an inner layer of longitudinal fibres is generally seen as the basic plan in Annelida (Lanzavecchia et al. 1988, Gardiner 1992). The longitudinal muscle fibres are considered not to form a continuous layer but to be arranged in distinctly separate bands (Avel 1959, Stolte 1969, Rouse & Fauchald 1995, 1997). This feature is seen as an autapomorphy for Articulata (Rouse & Fauchald 1997, Ax 1999). However, the muscular system is much more complex, and additional muscles may be present, such as parapodial, chaetal, oblique and dorsoventral muscles. This is especially the case in polychaetes, and the muscular system is sufficiently known only in a few species (Storch 1968, Pilato 1981, Lanzavecchia et al. 1988).

A re-evaluation of the body wall musculature reveals that longitudinal muscles are arranged in bundles only in polychaetes, whereas they form a continuous layer in Clitellata (Fig. 5). In polychaetes there are four to six bands, of which prominent ventral and dorsal pairs are usually present. There may be an additional pair situated dorsolaterally (Storch 1968, Mettam 1971). The dorsal and ventral bands are separated laterally by a wide gap in the regions of the parapodia. The ventral nerve cord lies between the two ventral bands, which are usually far apart (Fig. 5A). In polychaetes with reduced parapodia and peristaltic movements, such as Scalibregmidae, Arenicolidae, and Opheliidae (Storch 1968, Pilato 1981), a more or less continuous layer is formed.

The interpretation of the longitudinal musculature in Clitellata as being arranged in bands is due to the fact that usually chaetal regions in oligochaetes have been figured in textbooks and original papers (e.g., fig. 196 of Avel 1959, but compare fig. 210). In these regions the longitudinal fibres move apart to make room for the chaetal sacs and musculature. Within Hirudinomorpha, only Branchiobdellidae show a continuous layer of longitudinal fibres, whereas in Hirudinea the fibres are aggregated in more or less distinct groups or fascicles, up to 80 in number (Sawyer 1986). It follows that the character state "longitudinal muscle bands" – found as a synapomorphy for Annelida and Articulata in the analyses of Rouse & Fauchald (1995, 1997) and Ax (1999) – is only present in Polychaeta. The situation in Clitellata requires explanation: one possibility is that it represents a derived character state; alternatively, the division of longitudinal muscle fibres into bands could be a convergence in polychaetes. Moreover, against this background, the position of Echiura, coded as not having bands in the cladistic analyses of Rouse & Fauchald (1995, 1997), may have to be reconsidered.

Until recently the absence of circular muscle fibres was regarded as a rare exception in polychaetes, al-

though they are usually less developed than the longitudinal fibres (Lanzavecchia et al. 1988, Gardiner 1992). In species possessing parapodia, the circular muscles are confined to the intraparapodial regions. However, circular muscle fibres are absent in several taxa, among them forms with and without parapodia (see Tzetlin et al. 2002b). Transverse muscle fibres which actually belong to the parapodia may be erroneously interpreted as circular fibres (Tzetlin et al. 2002b), indicating the need for thorough reinvestigations of polychaete muscle systems. In any case, absence of circular muscle fibres has to be taken into account in further discussions of the phylogeny and evolution of Annelida.

### Foregut structure

Polychaetes use a wide spectrum of food sources and show a great diversity of feeding habits (Fauchald & Jumars 1979). Accordingly, structures involved in feeding vary as well, and show numerous specializations (Purschke 1988, Purschke & Tzetlin 1996). However, these structures in the foregut may be classified according to only a few different plans of organization (Fig. 6A–H): (1) axial muscular proboscis (pharynx), (2) non-muscular axial proboscis (pharynx), (3) ventral muscular pharynx, and (4) dorsolateral ciliary folds (Purschke & Tzetlin 1996). In addition, various tentacular structures and ciliation of the anterior end may also be involved in feeding. The muscular pharynges may bear jaws, sclerotized and mineralized regions of the pharyngeal cuticle (Purschke 1988, Saulnier-Michel 1992). In contrast, Clitellata are less diverse (Fig. 6I–K). Especially oligochaetes are rather uniform: usually they feed on decaying plant material or detritus, and a dorsal ciliated pharynx with prominent glands is characteristic for them (Avel 1959, Jamieson 1992). Leeches are either carnivorous or blood-sucking parasites; their pharynges are supplied with axially arranged musculature (Sawyer 1986).

From the widespread occurrence of dorsolateral ciliary folds among polychaetes, Purschke & Tzetlin (1996) drew the conclusion that these simple structures most likely represent a plesiomorphic condition for Annelida (Fig. 6). This is further supported by the fact that these folds are present in juveniles of species which develop other pharyngeal structures, e.g. a non-muscular proboscis, in the adults (Tzetlin 1991). In other species, these folds may persist, and additional structures, especially ventral pharynges, are developed. Moreover, the dorsal pharynx belonging to the ground pattern of Clitellata may have been evolved from such folds (Purschke & Tzetlin 1996). Obviously, such folds are restricted to species with small body size in extant Annelida and are structures adapted for microphagy. It follows that the stem species either was comparatively small and microphagous, or at least a juvenile stage with these charac-

ters was included in the life cycle. Although it appears conceivable that dorsolateral ciliary folds might already have been present in the stem species of Annelida, they most likely are not an autapomorphy but a plesiomorphy present in other spiralian as well (Ax 1999). This is supported by ultrastructural investigations on pelagosphaera larvae of Sipuncula (Tzetlin et al., unpubl. observ.).

## Phylogenetic conclusions

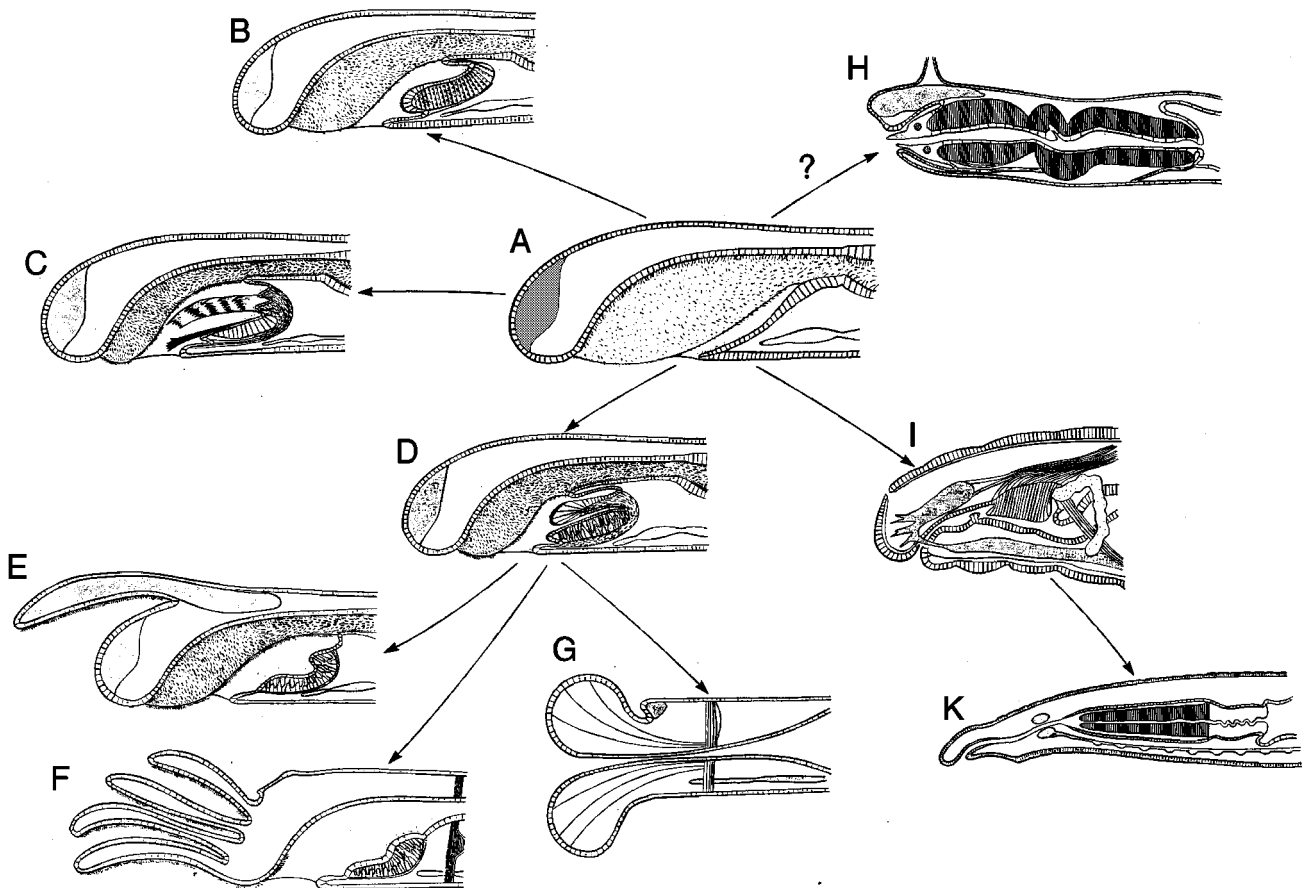
Summarizing the phylogenetic importance of the characters discussed herein, their interpretation as symplesiomorphies, synapomorphies, autapomorphies or con-

vergences may be different in the two hypotheses mentioned (Fig. 1):

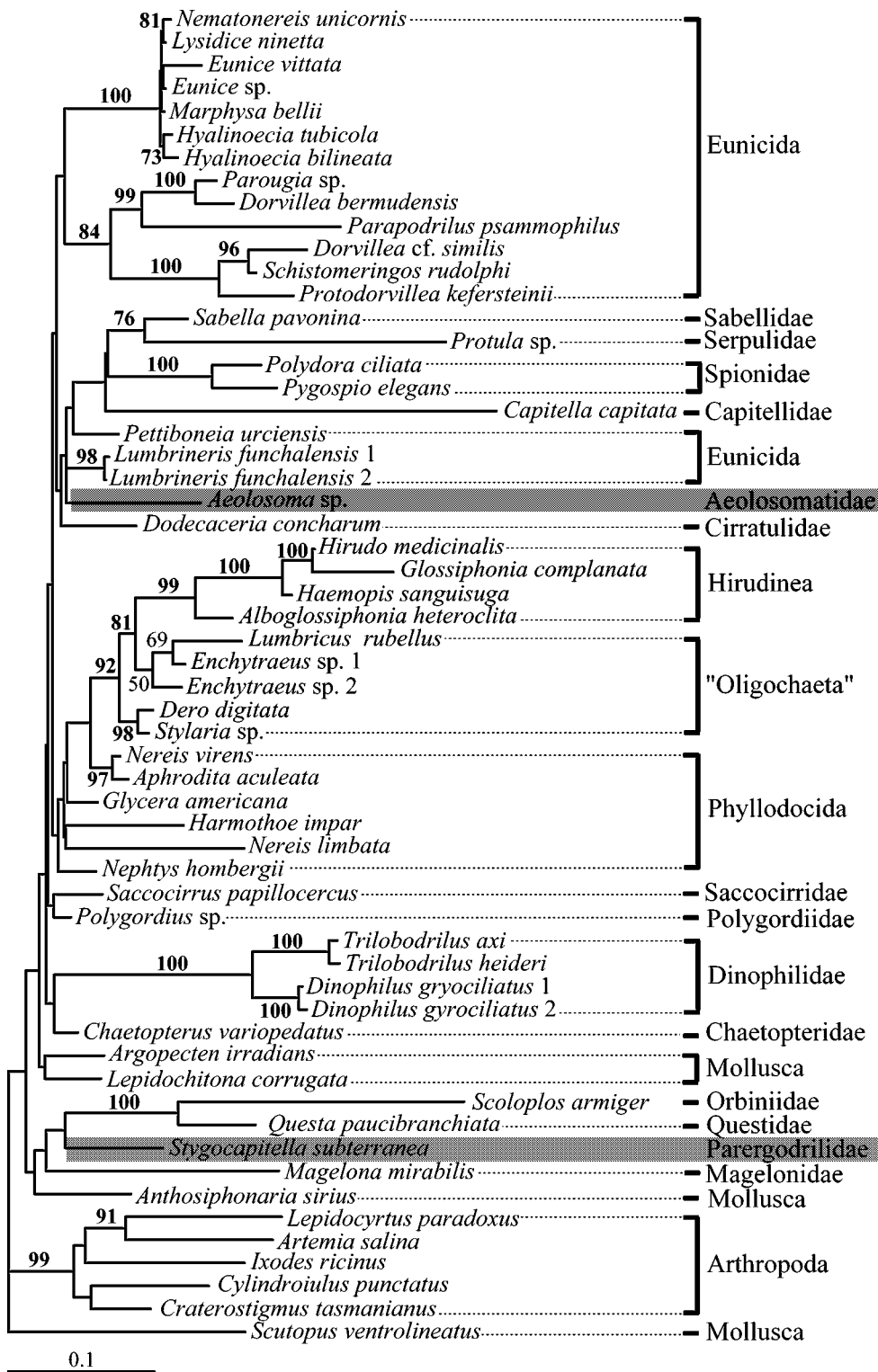
Hypothesis 1: the sister taxa Polychaeta and Clitellata comprise Annelida.

Hypothesis 2: Clitellata is the sister taxon of a certain polychaete taxon, so that "Polychaeta" is paraphyletic.

Methodological differences and philosophies are summarized and discussed in Westheide et al. (1999). One important issue in hypothesis 1 is the problem of rooting the tree obtained from the cladistic analyses (Rouse & Fauchald 1997, Rouse & Pleijel 2001). If the tree is not rooted with Sipuncula, then instead of monophyletic Clitellata the Aciculata comprising Phyllodocida, Amphinomida and Eunicida would represent a para-



**Fig. 6.** Schematic representation of different types of foregut structure related to dorsolateral ciliated folds (DLF). Arrows indicate probable phylogenetic pathways, some of which can be followed during ontogenesis. **A.** DLF as present, e.g., in Polygordiidae. **B–E.** DLF and ventral pharyngeal organs (VPO). **B.** VPO composed of bulbus muscle only (e.g. Dinophilidae). **C.** VPO equipped with jaw apparatus (e.g. Dorvilleidae). **D.** DLF and VPO composed of bulbus muscle, tongue-like organ and investing muscle (e.g. Ctenodrilidae, Protodrilidae, Orbiniidae). **E.** Additional feeding appendages with coelomic cavities (palps) (e.g. Spionidae). **F.** VPO without tongue-like organ, additional feeding appendages (branchial filaments), DLF absent in adults, anterior part of the body separated by muscular septum (e.g. Terebellidae). **G.** DLF and VPO replaced by non-muscular proboscis in adults, a septum separates anterior compartment of the body (e.g. Maldanidae, Capitellidae). **H.** DLF replaced by axial muscular pharynx (Phyllodocida). **I.** Ciliated glandular area (DLF?) restricted to roof of foregut and modified to dorsal pad (oligochaete Clitellata). **K.** Axial muscular proboscis derived from dorsal pharynx (Hirudinea). After Purschke & Tzetlin (1996).



**Fig. 7.** Best tree of the maximum likelihood analysis using 18S rDNA sequences. Conditions used were determined by Modeltest V 3.04: base frequencies = (0.2262; 0.2402; 0.3029; 0.2306); rate matrix = (1.3306; 2.9224; 1.3528; 0.8770; 4.9574; 1.0000); among-site variation with proportion of invariable sites = 0.3343 and gamma distribution shape parameter = 0.6772. Only bootstrap values above 50 are shown. Monophyletic Clitellata (light grey) form a derived group within the annelid clade; the latter being not monophyletic; Arthropoda do not form the sister group of the annelid clade. Aeolosomatidae (dark grey) and Parergodrilidae (medium grey) are distant from Clitellata and appear not closely related to them. Scale bar indicates evolutionary distances in substitutions per site. From Struck et al. (2002).

phyletic stem group for the rest of the annelids, as it is seen in hypothesis 2 (see Rouse & Pleijel 2001). The characters supporting Aciculata in hypothesis 1 again are seen as plesiomorphies taken from the annelid stem species in hypothesis 2 (see Table 1): antennae, prostomial sensory palps, dorsal and ventral parapodial cirri, a pair of pygidial cirri, nephridia in most segments, and aciculae. So far neither Aciculata nor Phyllodocida were recovered in phylogenetic analyses using molecular data (Brown et al. 1999, McHugh 2000, Martin 2001, Rota et al. 2001, Struck et al. 2002).

Certain characters are unanimously considered to be symplesiomorphies of Polychaeta and Clitellata in both hypotheses: a biphasic life cycle with planktonic larval and benthic adult stage, the collagenous cuticle, the orthogonal pattern of the central nervous system, its basiepithelial position, the simple ciliated foregut, and pigment cup ocelli with rhabdomeric photoreceptor cells (Table 1). According to the first hypothesis, which regards Polychaeta and Clitellata as highest ranked sister groups within Annelida, chaetae composed of  $\beta$ -chitin, homonomous segmentation, prostomium, pygidium, a praepygidial proliferation zone, a rope-ladder-like central nervous system, longitudinal musculature arranged in bands, coelomic cavities, blood vessels, and segmental organs are clearly apomorphic. In the second hypothesis, in which Clitellata are sister to only a subordinate taxon within the paraphyletic polychaetes, additional

apomorphies of Annelida are the parapodia, the palps and antennae, the anal cirri, the nuchal organs and the double circumoesophageal connectives. In the first hypothesis these characters are regarded as having arisen later in evolution. Their absence in Clitellata and Echiura is regarded as primary rather than as secondary in hypothesis 1 (see Porschke et al. 2000). If the Articulata hypothesis is followed, Annelida are only weakly defined in hypothesis 1 because most of the apomorphies are related to segmentation and thus become synapomorphies with Arthropoda (Table 1). The parapodia are variously interpreted as evolved in the stem lineage of Articulata, Annelida, Polychaeta, or even within Polychaeta (Rouse & Fauchald 1997, Westheide 1997, Westheide et al. 1999). Only in the case of convergent evolution are Annelida sufficiently supported in both hypotheses. One character typical of Annelida has not been considered in most analyses but should be regarded as an annelid autapomorphy: the specific cleavage pattern of the cell 2d (Dohle 1999). This cell gives rise to one small cell to the right, one small cell to the left, and another small cell towards the animal pole. This pattern has not been observed in any other taxon of Spiralia.

In the further systematization of Annelida, there are two autapomorphies of Polychaeta – nuchal organs and anal cirri – in hypothesis 1, but logically none in hypothesis 2 (Table 2). There is a large number of derived character states in Clitellata in both hypotheses, to which in

**Table 1.** Characters present in the ground pattern of the Annelida. Hypothesis 1: Polychaeta and Clitellata monophyletic; hypothesis 2: Polychaeta paraphyletic, Clitellata sister to subordinate polychaete taxon. Autapomorphies in boldface, plesiomorphies in regular lettering. Characters with asterisks become synapomorphies with Arthropoda if the Articulata hypothesis is followed. Compiled from various sources.

Hypothesis 1	Hypothesis 2
biphasic life cycle with planktonic larva and benthic adult	biphasic life cycle with planktonic larva and benthic adult
collagenous cuticle	collagenous cuticle
?epidermis without kinocilia	epidermis with kinocilia
coelom and blood vessels	coelom and blood vessels
nephridia	nephridia
<b>foregut with dorsolateral ciliated folds</b>	foregut with dorsolateral ciliated folds
microphagous	microphagous
endobenthic	epibenthic
burrowing	crawling
rhabdomeric photoreceptors in pigment cup ocelli	rhabdomeric photoreceptors in pigment cup ocelli
<b>gut a straight tube</b>	gut a straight tube
<b>homonomous segmentation*</b>	<b>homonomous segmentation*</b>
<b>longitudinal muscle bands*</b>	<b>longitudinal muscle bands*</b>
<b>capillary chaetae (<math>\beta</math>-chitin) in four groups</b>	<b>complex chaetae (<math>\beta</math>-chitin) in four groups</b>
no parapodia	<b>biramous parapodia*</b>
<b>small prostomium*</b>	<b>large prostomium*</b>
no prostomial appendages	<b>palps and antennae</b>
<b>pygidium*</b>	<b>pygidium*</b>
no pygidial cirri	<b>pygidial cirri</b>
<b>praepygidial proliferation zone*</b>	<b>praepygidial proliferation zone*</b>
no nuchal organs	<b>nuchal organs</b>
<b>dorsal brain and ventral nerve cord*</b> within orthogonal NS	<b>dorsal brain and ventral nerve cord*</b> within orthogonal NS

the second hypothesis the following have to be added: lack of epidermal kinocilia, simple chaetae, small prostomium, lack of prostomial appendages, lack of nuchal organs, backward displacement of the brain, simple circumoesophageal connectives, phaosomes, and lack of anal cirri (Table 2). All of these are considered to have arisen during invasion of the terrestrial environment (Purschke 1999, Purschke et al. 2000). Some of these characters may have evolved in marine habitats characterized by periodic water deficiency, and thus may have been pre-adaptive for a successful invasion of terrestrial habitats. Unfortunately, the sister group of Clitellata within Annelida cannot be defined at the present time. When this sister group is found, some of the clitellate autapomorphies listed in Table 2 most likely will turn out to be synapomorphies of these two taxa.

Interestingly, the second hypothesis is supported by analyses using molecular data (McHugh 1997, 2000, Kojima 1998, Martin 2001, Rota et al. 2001, Struck et al. 2002). They rely on the sequences of two nuclear genes:

elongation factor-1 $\alpha$  and 18S rDNA. Clitellata are shown to be monophyletic, forming a terminal clade within the paraphyletic polychaetes (Fig. 7). Unfortunately, the phylogenetic signal is still too weak for confident resolution of deeper branches. Similar results were obtained by Brown et al. (1999) using histone H3, U2, snRNA, and 28S rDNA. Thus, the sister group of Clitellata cannot be assigned from these analyses either. Aeolosomatidae and Potamodrilidae, often discussed as a possible sister group of Clitellata, are clearly not related to each other according to molecular and recent morphological data (Hessling & Purschke 2000, Purschke & Hessling 2002, Struck et al. 2002). Whereas Annelida are usually not monophyletic in these analyses, Struck et al. (2002) obtained a monophyletic Annelida in a strict consensus tree of a maximum parsimony analysis, although their interpretation was weakly supported. In addition, the position of Echiura and Siboglinidae (Pogonophora) within Annelida is also supported in these molecular analyses.

**Table 2.** Autapomorphies of Polychaeta and Clitellata with respect to the conflicting hypotheses. Hypothesis 1: Polychaeta and Clitellata monophyletic; hypothesis 2: Polychaeta paraphyletic, Clitellata sister to subordinate polychaete taxon. Apomorphies in boldface, plesiomorphies in regular lettering. Compiled from various sources.

Hypothesis 1	Hypothesis 2
POLYCHAETA	
<b>nuchal organs</b>	nuchal organs
<b>parapodia</b>	parapodia
<b>pygidial cirri</b>	pygidial cirri
CLITELLATA	
epidermis without kinocilia	<b>epidermis without kinocilia</b>
<b>chaetae as simple spines</b>	<b>chaetae as simple spines</b>
no parapodia	<b>no parapodia</b>
small prostomium	<b>small prostomium</b>
no prostomial appendages	<b>no prostomial appendages</b>
no pygidial cirri	<b>no pygidial cirri</b>
no nuchal organs	<b>no nuchal organs</b>
<b>brain situated behind prostomium</b>	<b>brain situated behind prostomium</b>
simple circumoesophageal connectives	simple circumoesophageal connectives
burrowing	burrowing
phaosomes	<b>phaosomes</b>
ciliary cerebral sense organs	ciliary cerebral sense organs
<b>hermaphroditism</b>	<b>hermaphroditism</b>
<b>gonads in specific segments</b>	<b>gonads in specific segments</b>
<b>specific type of spermatozoon</b>	<b>specific type of spermatozoon</b>
<b>spermathecae outside female organs</b>	<b>spermathecae outside female organs</b>
<b>cocoons</b> formed by the <b>clitellum</b> , a girdle of at least two types of gland cells	<b>cocoons</b> formed by the <b>clitellum</b> , a girdle of at least two types of gland cells
<b>external fertilization within the cocoon</b>	<b>external fertilization within the cocoon</b>
<b>ectoteloblasts</b>	<b>ectoteloblasts</b>
<b>no larva</b>	<b>no larva</b>
<b>dorsal pharynx</b>	<b>dorsal pharynx</b>

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