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Polychaete phylogeny based on morphological data – a comparison of current attempts

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Abstract

Annelid phylogeny is one of the largest unresolved problems within the Metazoa. This is due to the enormous age of this taxon and also strongly influenced by the current discussion on the position of the Arthropoda, which traditionally is hypothesized to be the annelid sister taxon. Within the framework of recent discussions on the position of the Annelida, the ground pattern of this taxon is either a clitellate-like, parapodia-less dwelling organism or an organisms that resembles errant polychaetes in having parapodia and gills and probably being a predator. To solve this problem different attempts have been made in the past, cladistic analysis, scenario based plausibility considerations and a successive search for sister taxa base on isolated characters. These attempts are presented and critically discussed. There is at least strong support for the Annelida as wells as for several of its taxa above the level of traditional families; the monophyly of the Polychaeta, however, remains questionable.

Introduction

The phylogenetic relationships among Annelida is still one of the largest unresolved problems in metazoan systematics and is most controversely discussed (Rouse & Fauchald, 1995, 1997; Eibye-Jacobson & Nielsen, 1997; Westheide, 1997; Westheide et al., 1999; Rouse & Pleijel, 2001; Purschke, 2002). Central problems concern the monophyly of Annelida and, presumed they are a monophyletic group, the organization of the annelid stem species as well as the interrelationships between the different annelid taxa. Annelida are multisegmented organisms with a multiple repetition of identically organized segments. The first and the last section differ from this organization. The anteriormost section, called prostomium, contains the cerebral ganglia, and the caudalmost section, called pygidium, contains a terminally or dorsally situated anus. The mouth is situated ventrally behind the prostomium. A growth zone of continuous mitotic activity which gives rise to additional segments lies anteriorly to the anus. Each segment contains a pair of ganglia, a pair of coelomic cavities, a pair of metanephridia and at least paired ventral and dorsal groups of chaetae. Most of these characters vary within the Annelida, and the mentioned generalized description is much more a result of an idealized 'body plan' than of a precise phylogenetic analysis (Nielsen, 2001; Ruppert et al., 2003).

Annelida were recognized as a taxon[1] of segmented soft bodied worms by Lamarck (1801). Cuvier (1812) placed Annelida and Arthropoda

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[1] The term taxon is used here in the sense of group of things that share certain characteristics. Biological taxa are not necessarily monophyletic, although many of them turned out to be. In terms of phylogenetic systematics taxa should be monophyletic.

Table 1. Characters present in the ground pattern of the Annelida. Hypothesis 1: Polychaeta and Clitellata monophyletic; hypothesis 2: Polychaeta paraphyletic, Clitellata related to subordinate polychaete taxon only. Autapomorphies bold, plesiomorphies normal font. Characters marked by asterisks will become synapomorphies with Arthropoda if the Articulata-hypothesis is followed. From Purschke (2002)

Hypothesis 1	Hypothesis 2
Biphasic life cycle with planktonic larva and benthic adult	Biphasic life cycle with planktonic larva and benthic adult
Collageneous cuticle	Collageneous cuticle
epidermis without kinocilia	Epidermis with kinocilia
Coelom and blood vessels	Coelom and blood vessels
Nephridia	Nephridia
Foregut with dorsolateral ciliated folds	Foregut with dorsolateral ciliated folds
Microphageous	Microphageous
Endobenthic	Epibenthic
Burrowing	Crawling
Rhabdomeric photoreceptors in pigment cup ocelli	Rhabdomeric photoreceptors in pigment cup ocelli
Gut straight tube	Gut straight tube
Homonomous segmentation*	**Homonous segmentation***
Longitudinal muscle bands*	**Longitudinal muscle bands***
Capillary chaetae (ß-chitin) in four groups	**Complex chaetae (ß-chitin) in four groups**
No parapodia	**Biramous parapodia***
Small prostomium*	**Large prostomium***
No prostomial appendages	**Palps and antennae**
Pygidium*	**Pygidium***
No pygidial cirri	**Pygidial cirri**
Praepygidial proliferation zone*	**Praepygidial proliferation zone***
No nuchal organs	**Nuchal organs**
Dorsal brain and ventral nerve cord within Orthogonal NS*	**Dorsal brain and ventral nerve cord** within Orthogonal NS*

into a taxon Articulata, a view that is held until today and regarded as the best explanation for the distribution of morphological characters in both taxa (Wägele et al., 1999; Wägele & Misof, 2001; Scholtz, 2002). Since 1997 this view is opposed by the results of molecular analyses that argue for a close relationship of Arthropoda and some taxa of Nemathelminthes (see Aguinaldo et al., 1997; Schmidt-Rhaesa et al., 1998). This taxon has been called Ecdysozoa. If Ecdysozoa should turn out to represent a monophyletic taxon, Annelida were one of the best supported monophyletic taxa (Table 1) within Bilateria belonging to a clade named Lophotrochozoa. The situation is completely different under the perspective of the Articulata-hypothesis: Segmental organisation, generation of additional segments in a caudal preterminal growth zone, paired coelomic cavities in the embryo and metanephridia are synapomorphies of Annelida and Arthropoda then (Bartolomaeus, 1998; Bartolomaeus & Ruhberg, 1999). Whether other characters, like nuchal organs, head appendages and parapodia can be assumed to represent autapomorphies of Annelida depends on the relationships within Annelida (Table 1; for review see Purschke, 2002). The only character that presently supports the hypothesis of monophyletic Annelida is a paired dorsal and ventral group of chaetae in each segment.

Unravelling the relationships among Annelida is the first step to find further evidence that could support Annelida. This paper wants to summarize and discuss the recent attempts to cast light on annelid and especially polychaete evolution. It will concentrate on morphological analyses, which are proposed by Rouse & Fauchald (1995, 1997), Westheide (1997) and our own studies (see Bartolomaeus, 1998; Hausen, 2001; Purschke, 2002). By doing this we also want to substantiate hypotheses on monophyletic taxa within Annelida.

We will show that some of them are supported by a single character only. In these cases, however, this single withstands every outgroup comparison.

Taxa of the Annelida

Traditionally, annelids are subdivided in three systematic entities, i.e. polychaetes, oligochaetes and hirudineans. Only one of them, i.e. the Hirudinea, can clearly regarded as monophyletic. This is sustained by a large number of autapomorphies which include the fixed number of 32 segments plus prostomium and peristomium, a posterior sucker consisting of seven posteriormost segments, spermatophores, a strong development of the oblique musculature, the reduction of the mesenteries and coelomic extensions, as well as separation of the nephrostome from the nephridial duct (s. Purschke et al., 1993).

Certain oligochaetes like Branchiobdellida are discussed to represent the sister taxon of Hirudinea (Purschke et al., 1993), and not a single autapomorphy is found until now, which supports any hypothesis on the monophyletic origin of the oligochaetes (see Erséus, 2005). Despite of this, Hirudinea and all those annelids which traditionally are classified as oligochaetes must have shared a common ancestor. This ancestor is characterized by several autapomorphies, like hermaphroditism, lecithotrophic eggs and the clitellum, a spatially restricted epidermal region where secretory gland cells produce a cocoon, the eggs are shed into, modification of the spiral cleavage and specific development (Purschke et al., 1993) and the special sperm ultrastructure (see Ferraguti, 1984; Ferraguti & Erséus, 1999). The entire taxon has been termed Clitellata and represents a very well supported monophyletic taxon within Annelida.

Initially Echiura and Sipuncula were included into Annelida (see Fauchald & Rouse, 1997; for review), later both taxa were removed. At least for Echiura this assumption has recently been revived. Studies on the development of the echiuran nervous system provided traces of a metamerical organisation (Hessling & Westheide, 2002; Hessling, 2002). These investigations clearly support the view that Echiura are derived from a segmented ancestor and the lack of segmentation is secondary. Moreover, it follows that the echiurid trunk is made up of numerous fused segments. This view receives independent support from molecular analyses (Halanych et al., 2002, Bleidorn et al., 2003a,b). Despite their possible position, Echiura clearly are monophyletic taxon due to their anal sacs (see Bartolomaeus & Quast, 2005). This character is unique among bilaterians and withstands any outgroup comparison.

The most diverse group within Annelida is Polychaeta. Grube (1850) introduced the name Polychaeta to distinguish them from Oligochaeta. While a taxon Sèdentaires (Sedentaria) had already been introduced by Lamarck (1818), the name Annèlides errantes (Errantia) was at first mentioned by Andouin & Milne Edwards (1834). Perrier (1897) resurrected these terms and erected two large taxa, one consisting of mostly vagile and free living polychaetes, the Errantia, and one consisting of hemisessile, sessile and mostly tubicolous polychaetes, the Sedentaria. Fauvel (1923), Uschakov (1955) and others (Hartmann-Schröder, 1971) adopted them for polychaete taxonomy. Parallel to these terms smaller entities were established by Hatschek (1893), especially Archiannelida, Spiomorpha, Serpulimorpha, Terebellomorpha and Drilomorpha as well as Amphinomorpha and Nereimorpha. These taxon names were in part adopted by Benham (1896), Fauvel (1923), Uschakov (1955) and Hartmann-Schröder (1971). In the first half of the twentieth century a taxon Polychaeta consisting of Archiannelida, Errantia and Sedentaria was widely accepted. This system of polychaetes was used until the seventies, although there were doubts, whether errant and sedentary polychaetes were actually reliable entities (Dales, 1962; Day, 1967). Archiannelida was recognized as an artificial assemblage of small annelids that invaded the mesopsammon in different lineages (Jouin, 1971; Westheide, 1985, 1987). However, due to their apparent simple organization, their relationships are largely unresolved till now. The remaining groups, i.e. Errantia and Sedentaria were subsequently eliminated end of the seventies, when Fauchald (1977) presented a system of 17 more or less isolated taxa, which are equally ranked as orders in a more typologically orientated system (Fauchald, 1977; George & Hartmann-Schröder, 1985). All entities above these orders, i.e. taxa like

Terebellomorpha, Spiomorpha or Errantia were eliminated. The old sequence with the errant taxa listed at first, followed by the sedentary ones was changed by Fauchald (1977). By doing this he obviously followed morpho-functional considerations proposed by Clark (1964, 1977), according to which the annelid stem species had an earthworm-like organization without parapodia and head appendages (further discussion see Westheide, 1997). The number of orders was extended by Pettibone (1982) and Hartmann-Schröder (1996).

But, even most of the orders established by Fauchald (1977) were hard to be kept in the view of phylogenetic systematics. In most keys the families became those entities which were easily to characterize (George & Hartmann-Schröder, 1985) and, more recently, by Rouse & Pleijel (2001). The first cladistic analysis of polychaetes by Rouse & Fauchald (1997) was accordingly performed on the family level and a tree consisting of 53 out of about 80 polychaete families was presented. The remaining taxa were excluded from this restricted analysis. This analysis provided the basis of the classification in Rouse & Pleijel (2001). The monophyly of several families, however, was still uncertain (Fauchald & Rouse, 1997).

Prior to any critical evaluation, it seem essential to draw a few conclusions from this extremely short summary of history of polychaete taxonomy (for details see Fauchald & Rouse, 1997; Westheide et al., 1999; Rouse & Pleijel, 2001): Continuous subdividing of the polychaetes, application of such high ranks as orders (Fauchald, 1977) reflects the tremendous structural diversity found within polychaetes. This is certainly a result of the enormous age of this group; their oldest known representatives have been found among middle Kambrian fossils (Conway-Morris, 1979). This fossil record already represents a surprisingly high diversity of body forms. It also reflects the enormous adaptability to different ecological niches, so that polychaetes are found in nearly all marine environments often playing a major role in certain marine systems, as for instance arenicolid species in sandy intertidal or siboglinid (pogonophoran) species in the hydrothermal vent community. However, even a few limnetic, ground water and terrestrial species are known (Purschke, 2002). A second conclusion that can be drawn from the above is that morpho-functional considerations influenced systematization especially if the system also should reflect evolution. This lasts on until the most recent contributions (Westheide et al., 1999; Rouse & Pleijel, 2001; Purschke, 2002).

Cladistic analysis – analysing all characters simultaneously

As there is no doubt that all available characters must be used for any attempt to unravel phylogeny, cladistic methods are clearly those which have to be used (see Westheide et al., 1999; Rouse & Pleijel, 2001). An enormous progress has been made in this respect in the last years; these methods rationalize discussions, they allow to test *a priori* homology hypotheses and trees as results of other analysis and to include further characters. A crucial problem in all cladistic analyses, which often is underestimated in subsequent discussions, is character coding and the resulting data matrices (see below).

Rouse & Fauchald (1997) presented the first cladistic analysis based on data, which were available for a large number of taxa to almost the same extend. Many of these data were extracted from old literature, so that their analysis also made these data available again. With their analysis they provided the first evaluation of morphological data without any *a priori* hypothesis on the evolution of the Annelida. One of the exiting results was that Pogonophora, which thus far were regarded as a separate phylum, have to be included into Annelida. They integrated Pogonophora into Annelida as the taxon Siboglinidae. We want to repeat and comment the most important results of the Rouse & Fauchald (1997) analysis at first, summarize the autapomorphies of the taxa above the family level and relate their names to the older taxonomies (Fig. 1). By doing this we want to focus on such characters that are autapomorphies with respect to any outgroup comparison within annelids. We also will hint at some problems along with analysis.

Siboglinidae (Pogonophora) are a member of Sabellida (sensu Rouse & Fauchald, 1997), which also contains Oweniidae, Serpulidae, Sabellidae and Sabellariidae. The latter three represent the Hatschek's (1893) Serpulimorpha. Rouse & Fauchald's (1997) results indirectly corroborate

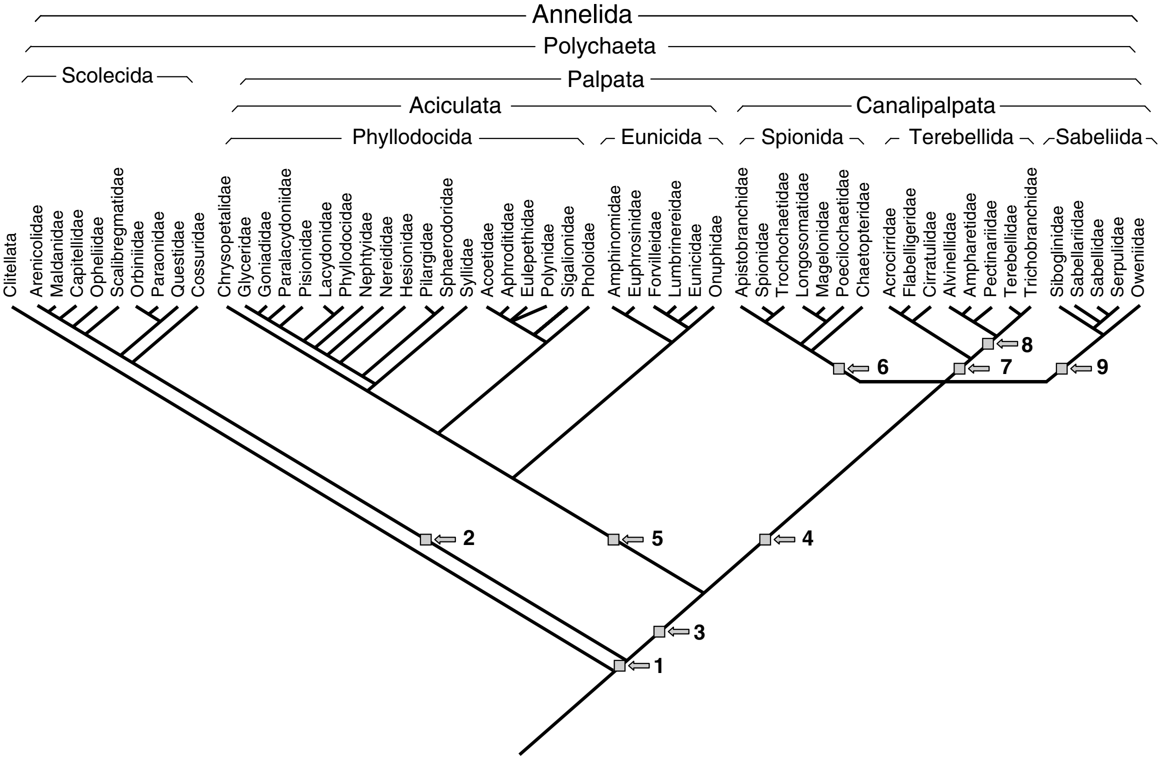

Figure 1. Phylogenetic relationships among the Annelida according to Rouse & Fauchald (1997). The shown tree has been used by the authors to discuss character distribution. It is one of three trees that result from successive weighting of a reduced, a priorily weighted data set. Autapomorphies of selected taxa are: **1** Mixonephridia, nuchal organs as pits or grooves, parapodia. **2** Parapodia with similar rami, two or more pairs of of pygidial cirri. **3** Peristomium limited to lips, palps. **4** Peristomial and grooved palps. **5** Prostomial and (sensory) palps, lateral and medial prostomial antennae, dorsal cirriform cirri, ventral cirri, one pair of pygidial cirri, nephridia and coelomoducts in most segments, acicula. **6** Paired peristomial palps, anterior nephridia and posterior gonoducts, nuchal organs form posterior projections. **7** heart body, absence of chaetae and appendages in the first segment, gular membrane. **8** dorsal branchiae in the first segments, buccal tentacles, coiled gut. **9** limited fusion of prostomium and peristomium, peristomium not limited to lips any longer.

the hypothesis of a sister group relationship between Serpulidae + Sabellidae and Siboglinidae (Bartolomaeus, 1995). The monophyly of Sabellida (sensu Rouse & Fauchald, 1997) is weakly supported by only two characters, i.e. a limited fusion of prostomium and peristomium and a peristomium that is not limited to lips any longer (9 in Fig. 1). However, the first character is homoplasious, the second one is a reduction of an earlier evolved character, an interpretation resulting from the general character distribution. At least the sister group relationship between Sabellidae and Serpulidae is supported by three unique character complexes, (1) their branchial crown is remnant of the prostomium and consists of radioles with paired series of pinnules (Rouse & Fauchald, 1997), (2) the nuchal organ is hidden within a dorsal pit that lies ventral to the nephridiopore or to the distal section of the nephridioduct, respectively (Orrhage, 1980: 119–124; Purschke 1997), and (3) nervous system with inversion of the dorsal and ventral root of the circumoesophageal connectives (Orrhage, 1980). Sabellariidae is regarded as their sister taxon. This hypothesis is substantiated by palp nerve roots 1–3 (Hausen, 2001; Orrhage & Müller, 2005) the chaetal inversion which exchanges the position of the neuro- and notopodial chaetae between thorax and abdomen (Rouse & Fauchald, 1997, but see Bartolomaeus, 2002). Siboglinidae (Pogonophora) share a single pair of excretory organs draining the second segment with the fore-mentioned taxa. The metanephridial duct forms a large caudally extending U; its pori are dorsal. Rouse & Fauchald (1997) also mention uncini and reduction of dorsolateral folds as possible autapomorphies of the Sabellida except Oweniidae. Oweniidae did not group within Sabellida in subsequent analyses (Rouse, 1999, 2000).

Uncini are also found in Terebellidae, Trichobranchidae, Pectinariidae, Ampharetidae and Alvinellidae. Except the hydrothermal vent group Alvinellidae, which were described by Desbruyères & Laubier (1980, 1986) these taxa comprise Terebellida sensu Fauchald (1977), Hatschek's (1893) Terebellomorpha, and Terebelliformia sensu Rouse & Pleijel (2001). The monophyly of this taxon is supported by (1) dorsal branchiae in the first segments, (2) buccal tentacles (Orrhage, 2001) and (3) a coiled gut (Rouse & Fauchald, 1997). At least the latter is unique within polychaetes (8 in Fig. 1). Buccal tentacles are also found in Sabellariidae; their possible homology awaits testing (Orrhage, 1978, 2001). Dorsal branchiae could be autapomorphic if this character were specified to allow discrimination from other branchiae within the polychaetes. Rouse & Fauchald (1997) extended Terebellida by inclusion of Acrocirridae, Cirratulidae and Flabelligeridae. Rouse & Pleijel (2001) classified the latter three plus further taxa like Fauveliopsidae, Ctenodrilidae and *Sternaspis* as Cirriformia within Terebellida. Terebellida (sensu Rouse & Fauchald, 1997) is supported by a heart body, absence of chaetae and appendages in the first segment and a gular membrane (7 in Fig. 1). All characters are homoplasies; their evaluation as autapomorphies depends on the internal relationships within Annelida.

Spionida sensu Rouse & Fauchald (1997) consist of Apistobranchidae, Spionidae, Trochochaetidae, Longosomatidae, Magelonidae, Poecilochaetidae and Chaetopteridae. Their monophyly is supported by paired peristomial palps, anterior nephridia and posterior gonoducts and the fact that nuchal organs form posterior projections (6 in Fig. 1). All species of *Magelona* lack nuchal organs and knowledge on nuchal organs of Chaetopteridae is sparse. In Apistobranchidae the presumed nuchal organs are associated to projections lateral to the palps. This is in contrast to the situation found in Spionidae, Trochochaetidae and Poecilochaetidae. The other characters mentioned in favour for the monophyly of the Spionida sensu Rouse and Fauchald (1997) are homoplasies and their evaluation as autapomorphies depends on the internal relationships as well. A functional separation of the metanephridia into anterior nephridia and posterior gonoducts is also found in terebellidan and sabellidan taxa. Problems along with the evaluation of the palps are discussed below. All taxa except Chaetopteridae form a monophyletic group characterized by spiomorph parapodia. Provided this term could be defined in such a manner that criteria can be given to recognize such parapodia, this would be a clear autapomorphic character. Except the later described Longosomatidae, Spionida sensu Rouse & Fauchald (1997) corresponds to Spioniformia of Benham (1896).

Aciculata consist of mostly vagile polychaetes with parapodia. They were formerly known as Errantia sensu Perrier (1897). The monophyly of this taxon is supported by a number of clear autapomorphies like (1) aciculae inside the parapodia to stabilize them, (2) lateral and medial prostomial antennae and (3) ventral cirri (4 in Fig. 1). The palps are discussed below.

Scolecida are weakly supported by two characters: parapodia with similar rami and two or more pairs of pygidial cirri (2 in Fig. 1). Both characters are parallelisms and not uniform within the group. They depend on the internal relationships among the polychaetes. Being aware of this Rouse & Pleijel (2001) mention that further cladistic analyses might reveal the paraphyly of this taxon. This group is the most basal in their tree.

Three characters support the monophyly hypothesis of Polychaeta, i.e. parapodia, nuchal organs as pits and grooves and mixonephridia (Rouse & Fauchald, 1997) (1 in Fig. 1). The parapodia are unspecified, a problem that results from absence/presence coding of structure and substructures that are logically not independent. It will be outlined below. Using the term mixonephridium Rouse & Fauchald (1997) adopted the terminology of Goodrich (1895). These terms describe two different features of the nephridia, i.e. their specific structure and their function as both, organs to release genital products and to eliminate metabolic wastes from the coelomic cavity. If Rouse & Fauchald (1997) used the term in the latter sense, this must represent a primary feature of metanephridia, because these organs fulfil the same function in Echiura and Sipuncula. As such, mixonephridia can hardly be an autapomorphy of the polychaetes, because at least sipunculids are outgroup to the annelids. Recent results on the structure and formation of nephridia, however, do not allow maintaining the terminology of Goodrich (1895, 1945) as no empirical data support his ideas (see Bartolomaeus & Quast, 2005). During maturity the ciliated funnel of certain metanephridia enlarges. This enlargement has been explained by Goodrich (1945) in the light of the gonocoel theory (Hatschek, 1878; Meyer, 1890; Goodrich, 1895) as witness for a merge between a gonoduct and a metanephridium. In accordance with the gonocoel theory Goodrich (1945) assumed that the gonoduct was a derivative of the coelothelium while the metanephrida had a different origin. Due to the presumed extend of fusion he chose different terms for the presumed fused metanephridia (see Bartolomaeus & Hausam, 2005). In none of the species subsequently studied has such enlargement of the funnel by coelothelially derived cells been observed (see Bartolomaeus, 1999). Thus, Goodrich's terms only inform about enlargement of the metanephridial funnel (metanephromixium) or lack of such an enlargement (mixonephridium). These different terms imply higher information content than they actually have. Some of the polychaetes possess protonephridia during their entire life time (see Table 1 in Bartolomaeus & Quast, 2005). During maturity these organs are used to discharge the genital product from the coelom in some species and acquire a funnel. Proliferation of the proximal duct cells generates this funnel which degenerates at the end of the reproductive period (Stecher, 1968). Again this temporarily restricted phenomenon was interpreted by Goodrich (1945) in the light of the gonocoel theory as remnant of the ancestral gonoduct. He termed the organ protonephromixium, but this term describes merely a modification of the protonephridium during the period of reproduction. In some polychaetes with protonephridia such a modification cannot be observed and the genital products are released by rupture. Goodrich also termed them protonephromixia, because he interpreted some ciliated structure in the coelomic wall as remnant of a funnel. Thus, adopting Goodrich's terms as characters inevitably results in coding a hypothetical process, but not the organ itself. Moreover, recent studies revealed that protonephridia can be found in a variety of different taxa, and not all of them are changed during maturity (Bartolomaeus & Quast, 2005). There is some evidence that all of them are not necessarily homologous among the polychaeta, while certain types, like those with solenocytes seem to be.

Adopting terms when coding data from the older literature causes conflicts with new data, mostly because ancient assumptions on the evolution of organs are also adopted with these terms. This can easily be seen in Rouse & Fauchald (1997) when they code "nephridia and coelomoducts in most segments" for most phyllodocidans. Like shown for the nephridia, new data on the structure of the chaetae can also not be integrated into the Rouse & Fauchald (1997) tree without larger conflicts. Recent studies into the formation and structure of chaetae provided strong evidence that uncini and certain hooded hooks are homologous (Hausen, 2005). While these data in part corroborated the cladistic analysis of Rouse & Fauchald (1997) some of the results indicate a complete different position of different groups of Scolecida, namely Arenicolidae, Maldanidae and Capitellidae. We will outline this in more detail later (Fig. 4).

Beside the central problem of some recycling of literature (Jenner, 2001), character coding itself is a wide field and different character concepts have been developed. Meanwhile it became quite clear that absence/presence coding in parsimony analysis is very problematic (see Jenner & Schramm, 1999). Handling of complex characters with a large number of substructures needs extreme care, because these substructures might be logically not independent from each other. Logical correlation has already been discussed by Sokal & Sneath (1963: 66). Presence of haemoglobin and redness of blood, they mention as an example are logically not independent characters, if blood's redness is strictly a consequence of the presence of haemoglobin (see Fristrup, 2001: 20). If logical independence of the coded substructures is not guaranteed absence/presence coding can cause the reconstruction of non-sense ground patterns (in contrast to Pleijel, 1995 and in accordance with Meier, 1994). Because of their shorter tree length the corresponding non-sense trees can be preferred

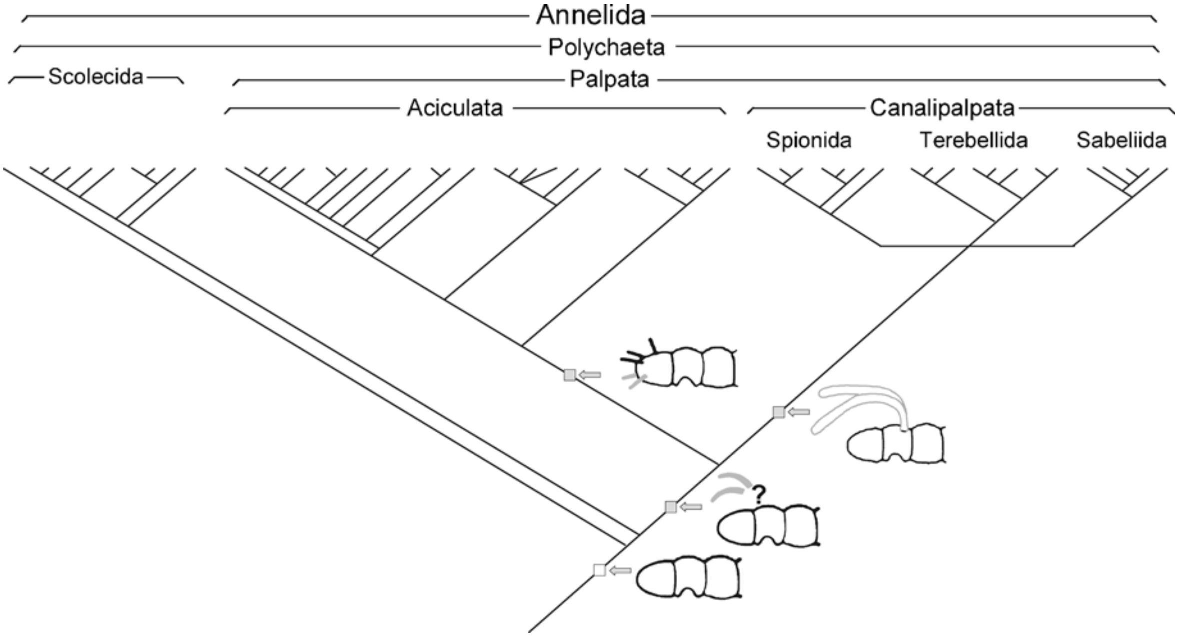

Figure 2. The palp problem. Ignoring logical dependence of palps and their substructures during coding causes non-sense character complexes. Insertion and function of the palps in the ground pattern of Palpata are not specified. Both ways of insertion and both functions are used as autapomorphies above the first node. This clearly results from coding palp substructures (insertion, structure, function) as logically independent characters.

instead of trees that show ground patterns which are at least logically plausible. We want to exemplify this for the basal radiations for the Polychaeta in Rouse & Fauchald (1997) tree (Fig. 2). Palpata are supported by two characters, i.e. (1) a peristomium that is limited to lips and (2) palps (3 in Fig. 1). The highest ranking taxa within the Palpata, Canalipalpata and Aciculata are characterized by peristomial, grooved palps (Canalipalpata) (5 in Fig. 1) or, among other characters by prostomial, sensory palps (Aciculata) (4 in Fig. 1). Considering the stem species of the Palpata one inevitably asks for the quality of the palps. Which position and which structure had the palps that evolved in the Palpata stem lineage? At least one of the two conditions assumed to have evolved in either of the subsequent lineages must be plesiomorphic. Thus, the character composition of the Palpata stem species is incomplete and structural integrity of the stem species is not given. This happened because the palp substructures were handled as logicially independent structures (Fig. 2). A comparable problem occurs when coding parapodia as a character being logically independent of their different morphologies (Rouse & Fauchald, 1997).

We chose this example to show the necessity to remember that as far as this is possible the morpho-functional integrity of the stem species must be guaranteed within a tree. The essential role of such considerations has been outlined by Westheide (1997) and Westheide et al. (1999), but in contrast to these contributions, we are convinced that such considerations cannot result in *a posteriori* assumptions. They can merely be used to estimate whether the character composition generated for a stem species is possible at all – at least from the fact that the functional integrity of a stem species must be maintained.

Evolutionary scenarios – trying to establish the annelid ground pattern

All statements on phylogeny are hypothetical. Some of the hypotheses are less corroborated than others and unravelling phylogeny is a process of continuous corroboration and rejection of hypotheses. While phylogenetic analyses usually

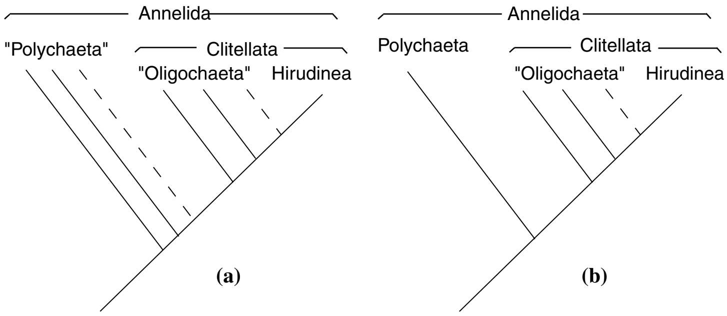

Figure 3. Annelid relationships according to Westheide (1987). The annelid stem species was either an infaunal, clitellate-like organism or a vagile, predatory organism with parapodia used for locomotion. In the latter case, the Polychaeta are not monophyletic. For details in character distribution (see Tables 1 and 2).

start with comparing characters on a lower level (primary homology) there is a long tradition in approaches to unravel phylogenies by starting the reconstruction of the ground pattern or basic character composition of a larger entity (see Ax, 1987, 1996, 2000, 2003; Westheide, 1997). This procedure generally focuses on preselected characters and on the structural and morpho-functional integrity of the assumed stem species. This is not an arbitrary procedure, but character selection is generally made intuitively, often based on an enormous background knowledge concerning the quality and information content of characters. In most cases criteria for character election are hard to test intersubjectively. This does not necessarily result in wrong trees, but tends to overemphasize considerations on character evolution compared to character comparison – and can only be done with a restricted number of characters. While the Rouse & Fauchald analyses (see Rouse & Fauchald, 1997; Westheide et al., 1999, Rouse & Pleijel, 2001) tried to include all available information on polychaete structure that has been gathered for a number of polychaete taxa large enough to allow comparison, Westheide (1997), Westheide et al. (1999) start with morpho-functional consideration to analyse the basal split in Annelida and, thus, start at a rather high taxonomic level and step down to lower levels (Fig. 3).

The general problem is to find a decision between two alternative hypotheses on the organisation of the annelid stem species. Assuming that annelids are monophyletic the stem species was either an epibenthic organism with a prostomium and prostomial appendages, and several segments with parapodia and a strong and diverse chaetation (Fig. 3A), or an endobenthic organism with a small prostomium without appendages and several segments without parapodia and with a weak chaetation (Fig. 3B). The organization of the latter largely corresponds modern clitellate annelids, while that of the assumed epibenthic organism resembles an errant polychaete. A comparison with Arthropoda does not help to decide between both hypotheses, but there is some evidence from the molecular data that Clitellata are embedded within the polychaetes (e.g., Struck et al. 2002). The state of these considerations has recently been summarized by Purschke (2002).

Westheide (1997) proposed the idea that septa evolved to connect the blood lacunae surrounding the gut to the peripheral blood vessels. This is a very interesting functional explanation that gives rise to some assumptions on possible evolutionary pathways. If this were true, enlargement of the surface would allow a better gas exchange. As the volume/surface ratio decreases if an animal increases body size, in aquatic environments one would expect that annelids that have a large body size also possess gills as long as they live in an aquatic environment. Higher oxygen content of the air allows sufficient oxygen supply without special structure that enlarges the body surface. Actually, the large terrestrial clitellates lack such parapodia despite of their large body size. Westheide's (1997) assumption does not inevitably imply that blood vessels were necessarily associated with external gills, as long as the animals did not exceed a certain diameter. It does not necessarily mean that the annelid ancestor had parapodia with gills. How-

Table 2. Autapomorphies of Polychaeta and Clitellata with respect to the conflicting hypotheses. Hypotheses 1: Polychaeta and Clitellata monophyletic; hypothesis 2. Polychaeta paraphyletic and Clitellata related to subordinate taxon of the former. Apomorphies bold, plesiomorphies normal font. From Purschke (2002)

Hypothesis 1	Hypothesis 2
Polychaeta	
Nuchal organs	Nuchal organs
Parapodia	Parapodia
Pygidial cirri	Pygidial cirri
Clitellata	
Epidermis without kinocilia	**Epidermis without kinocilia**
Chaetae simple spines	**Chaetae simple spines**
No parapodia	**No parapodia**
Small prostomium	**Small prostomium**
No prostomial appendages	**No prostomial appendages**
No pygidial cirri	**No pygidial cirri**
No nuchal organs	**No nuchal organs**
Brain situated behind prostomium	**Brain situated behind prostomium**
Simple circumoesophageal connectives	**Simple circumoesophageal connectives**
Burrowing	Burrowing
Phaosomes	**Phaosomes**
Ciliary cerebral sense organs	Ciliary cerebral sense organs
Hermaphroditism	**Hermaphroditism**
Gonads in specific segments	**Gonads in specific segments**
Specific type of spermatozoon	**Specific type of spermatozoon**
Spermathecae outside female organs	**Spermathecae outside female organs**
Cocoons formed by the **clitellum**, a girdle of at least Two types of gland cells	**Cocoons** formed by the **clitellum**, a girdle of at least Two types of gland cells
External fertilization within the cocoon	**External fertilization within the cocoon**
Ectoteloblasts	**Ectoteloblasts**
No larva	**No larva**
Dorsal pharynx	**Dorsal pharynx**

ever, as the annelids are primarily marine and not terrestrial, the stem species must have had a general organisation that resembles errant polychaetes rather then terrestrial clitellates – provided the stem species was large. Thus, those characters all those characters that could support the monophyly of the Polychaeta are plesiomorphies of all polychaetous annelids – and the polychaetes are not monophyletc (Fig. 3A, Tables 1 and 2).

Nuchal organs are characteristic for marine polychaetes; in terrestrial polychaete species they are either modified or lacking (Purschke, 1997, 1999, 2000). In Clitellata they are lacking. From the data available the lack of nuchal organs is functionally related to a terrestrial habitat and to the posterior displacement of the brain (Westheide et al., 1999). The problem now is, to estimate the direction of the evolution that caused this condition. No such organs are found in any outgroup (Purschke et al., 1997), so that the question concentrates on whether the lack in clitellates is primary or secondary. Plausibility considerations seem to allow a decision, but plausibility is a necessary, but extremely weak criterion. The general problem along with the lack of characters is that the hypothesis of a complete reduction cannot be tested by the character in question. There is no chance to find out whether a structure was initially there and has subsequently been reduced, as no testable observation could directly falsify the hypothesis of a complete reduction. Any hypothesis of reduction of a structure instead can be justified indirectly by congruence with other character transformations within a cladistic

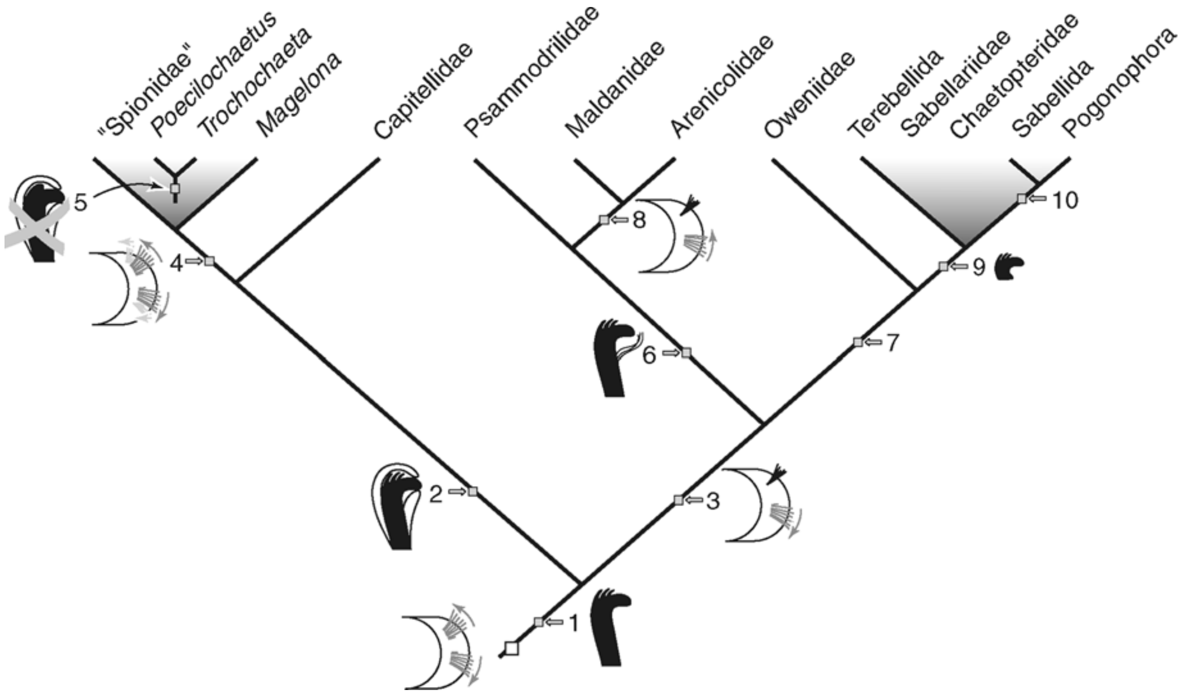

Figure 4. Phylogenetic relationships inferred from comparative analysis of chaeta and sense structures according to Bartolomaeus (1998) and Hausen (2001) – present state of knowledge. The key innovations are indicated by small sketches. **1** Hooked chaeta with a special mode of formation evolved in the stem lineage a taxon consisting of the spionidans (sensu Rouse & Fauchald, 1997) "Spionidae", Magelonidae, Poecilochaetidae, Trochochaetidae and Chaetopteridae, the scolecidans (sensu Rouse & Fauchald, 1997) Capitellidae, Maldanidae and Arenicolidae, the Psammodrilidae, the Terebellida except the Cirratuliformia (sensu Rouse & Pleijel, 2001) and the Sabellida (sensu Rouse & Fauchald, 1997). **2** Hood surrounding the apex of uncinus. Hood consists of two separately formed sheaths. **3** Rows of notopodial chaetae modified into bundles. **4** Additional transversal row of chaetae in neuro- and notopodia (see Hausen, this volume), nuchal organs shifted posteriorly, pave stone microvilli in nuchal organs, special photoreceptors (see Hausen 2001). **5** Reduction of hooded hooks. **6** Uncini with beard, lecithrotrophic development. **7** reduction of neuropodial hooks in chaetiger 1, **8** inverted formative side, sediment feeding. **9** reduction of the manubrial length, replacement of actin filaments at the end of chaetogenesis to attach chaetae; tube by secretions of the anterior ventral epidermis. **10** Nephridia in segment 2, dorsal nephridiopores.

analysis. However, in cladistic analyses loss of a given structure can only be detected if the group under consideration is supported by a sufficient number of autapomorphies (e.g. loss of nuchal organs in Pisionidae rather than primary absence). If the group considered is characterized by a large number of possible secondary absences, the systematic position may be incorrectly inferred (Rouse in Westheide et al., 1999; Purschke et al., 2000). This may account for the exclusion of Clitellata and Echiura from the polychaete clade in the Rouse & Fauchald (1997) tree (see McHugh, 2005).

Compared to the situation found in terrestrial polychaetes, the assumed reduction of nuchal organs implicates a terrestrial stem lineage of the Clitellata (Purschke, 2003). Accordingly freshwater habitats must have been invaded secondarily by Clitellata. If, as implied by molecular studies (see Erséus, 2005) freshwater habitats should be the primary environment of Clitellata, the loss of nuchal organs must have other reasons than terrestrialisation. Interestingly, freshwater polychaetes belonging to Nerillidae and Aeolosomatidae clearly possess these organs (Purschke, 1997; Hessling & Purschke, 2000). However, no final conclusion can be drawn yet, without taking a look at lower taxonomic levels.

Homology hypothesis of isolated structures – starting sister taxon search within the Polychaeta

Different to aiming at a complete cladistic analysis of polychaetes we started to fill the gaps in our knowledge of certain polychaete groups and erected trees using a few isolated structures (Bartolomaeus, 1995, 1998). Starting point had to be a taxon within the polychaetes that was considered to be monophyletic with respect to any outgroup comparison. We chose Sabellida sensu Fitzhugh (1989) and focussed at first on the ultrastructure and development of their neuropodial chaetae, the uncini. Although we are aware of the possible risk of this procedure (excluding possibly informative characters, studying localized maxima only) it allows to evaluate characters within the framework of selected other characters (Fig. 4).

Annelid chaetae are formed within an ectodermal invagination, the chaetal sac. Spatially and temporarily modulation of the apical microvilli pattern of its basalmost cell, i.e. the chaetoblast, determinates the structure of the chaeta (O'Clair & Cloney, 1974). Realizing this as well as the fact that structure and arrangement of chaetae are highly specific for polychaete species and higher taxonomic entities, we assume that the underlying information which guarantees formation of a certain kind of chaetae is rather conservative (see Hausen, 2005). Under this assumption, any hypothesis of the homology of chaetae could, thus, be tested, as an identical formation process was expected for presumed homologous chaetae. Studies of chaetogenesis of the uncini and hooded hooks of certain "sedentary" Polychaeta, revealed that the structure of these chaetae results from a uniform chaetogenesis (Arenicolidae and Maldanidae: Bartolomaeus & Meyer, 1997; Bobin, 1949; unpubl. data; Psammodrilidae and Oweniidae: Meyer & Bartolomaeus, 1996, 1997; Pectinariidae; Amphitritinae, Serpulidae, Sabellidae, Pogonophora (Siboglinidae): Bartolomaeus, 1995, 1998, 2002; Schulze, 2001; further unpubl. data; for summary see Hausen, 2005). One of the major conclusions inferred from theses studies says that several substructures and the course of development support the hypothesis of a homology of the hooked chaetae and uncini. This homology hypothesis has been extended for Capitellidae (Schweigkofler et al., 1998) and Spionidae (Hausen & Bartolomaeus, 1997). The studies allowed inclusion of Pogonophora into Polychaeta in a similar position as recovered in the cladistic analyses (Rouse & Fauchald, 1997, Rouse, 1999, 2000). Pogonophora[2] (Siboglinidae) are sister taxon to Sabellida consisting of Serpulidae and Sabellidae. This sister group relationship is supported by a reduction of the nephridia to a single pair in the second segment and the dorsal position of the nephridiopore. This sister group relationship implies a homology of the sabellid branchial crown and the dorsal tentacle of pogonophorans, which could explain their comparable organization comprising one blood vessel, one nerve and one coelomic cavity per tentacle (B in Fig. 4); other character concerning the reproduction and spermiogenesis are questionable (Bartolomaeus, 1998). Due to the aberrant structure of the central nervous system in Pogonophora, no conclusion can be drawn from their innervation pattern whether these tentacles actually represent palps in *Sclerolinum brattstromi* and *Siboglinum fjordicum* (Purschke, unpubl. obs.). Terebellida (sensu Rouse & Fauchald, 1997, excluding Acrocirridae, Flabelligeridae and Cirratulidae) are the sister group to that taxon, because a reduction of the length of the uncini shaft and replacement of the actin filaments by intermediate filaments to adhere the chaeta to the chaetoblast at the end of chaetogenesis represents the autapmorphy of this taxon. Formation of a tube by secretions of anterior-ventral glands in the anterior body region possibly is a further synapomorphy. Chaetopteridae and Sabellariidae also possess uncini and should belong to this group, although their position is uncertain yet (Fig. 4). The taxon consisting of the latter two and of Sabellida, Pogonophora and Terebellida has been termed Uncinifera (Bartolomaeus, 1998). Oweniidae are regarded as their sister taxon, substantatiated by the lack of hooked chaetae in the first setiger, by reduction of the beard and probably a completely incrusted tube (A in Fig. 4). Sister taxon to Uncinifera plus Oweniidae are Maldanomorpha and Psammodrilidae. Chaetation of the common ancestor of these taxa consists of dorsal capillary chaetae and ventral rows of uncini. Thus, some taxa of Scolecida (sensu Rouse & Fauchald, 1997) are included into the lineage of

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[2] In terms of phylogenetic systematics there is no empirical justification to apply caterories to the taxa. Consequently, certain endings of taxa names introduced to indicate a hierachical level should also be neglected. There is accordingly no need to replace the taxon name Pogonophora by Siboglinidae. Figure 4, thus, uses taxa names irrespective of their endings.

those polychaetes with uncini. These studies were expanded for a possible inclusion of Spionida (sensu Rouse & Fauchald, 1997) and studies into the arrangement of chaetae (see Hausen, 2005) as well as the ultrastructure of unpigmented photoreceptor-like sense organs were included (Hausen, 2001). These studies supported the hypothesis that the spionid taxa except Apistobranchidae and Chaetopteridae are monophyletic and represent the sister taxon of Capitellidae. Presently, we assume that their sister taxon is a group which includes all species with uncini. We want to emphasize that these hypotheses have been concluded from isolated but intensely studied characters and we know that inclusion of further characters may either support this view or may lead to contradicting phylogenies. Provided that chaetal structure is as informative as we believe, palps must have been reduced several times within the Polychaeta (Fig. 4). Besides this, the proposed relationships change the composition of the superfamiliar taxa of Rouse & Pleijel (2001), but also recover a part of them.

Conclusions

Like most other comparative morphological studies we also end up claiming for further morphological investigations as prerequisite to unravel polychaete phylogeny. Out of the different attempts presented here to resolve polychaete phylogeny, cladistic analyses are the most decisive ones. They require a complete matrix containing substantiated homology hypotheses. Presently, however, cladistic analyses of polychaetes suffer from incomplete data sets, ambiguous character coding and provide conflicting trees. Such conflicting trees always indicate that at least one of the homology hypotheses coded in the matrix is not valid – and that these homology hypotheses need a re-evaluation. As long as there are large gaps in our knowledge of polychaete morphology, polychaete evolution can hardly be unravelled. Because any attempt to resolve higher level taxonomy (see Ecdysozoa vs. Articulata discussion: Giribet, 2003; Schmidt-Rhaesa, 2003) needs information on the annelid ground pattern, different attempts tried to infer the ground pattern from the known data and from evolutionary scenarios. This, however, does not succeed in any decisive result (see Purschke 2002), but provides some characters that must belong to annelid ground pattern (see Tables 1 and 2). On the other hand, some progress has been made by comparative studies of selected characters within the polychaetes. During this attempt stepwise search for sister group relationships produced trees while establishing homology hypothesis. They allow to present preliminary results of comparative studies and find questions for tightly focussed studies.

Much progress has been made during the last two decades by resolving the relationships within families using species or genera as lowest category (e.g. Fitzhugh, 1989, 1991; Rouse & Fitzhugh, 1994 for Sabellidae; Bellan et al., 1990 for Opheliidae; Pleijel, 1991; Orrhage & Eibye-Jacobson, 1998 for Phyllodocidae, 1998 for Hesionidae; Licher & Westheide, 1994 for Pilargidae; Pleijel & Dahlgren, 1998 for Chrysopetalidae and Hesionidae; Bartolomaeus & Meyer, 1999 for Arenicolidae; Blake & Arnofsky, 1999 for Spionida; Nygren, 1999 for Syllidae; Blake, 2000 for Orbiniidae; Rouse, 2001 for Siboglinidae/Pogonophora). These attempts allow describing the ground pattern of the families used in cladistic analyses on this level and are extremely reliable, because the taxa they use are clearly monophyletic and possess a uniform character distribution. We are sure that both ways, i.e. stepwise resolving the phylogeny on a low taxonomic level (species or genera level) and gathering further data to complete the morphological data base, will finally provide a sound picture of polychaete evolution.

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References

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff & J. A. Lake, 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. Nature 387: 489–493.

Andouin, J. V. & H. Milne Edwards, 1834. Recherches pour servir a l'histoire naturelle du littoral de la France, ou Recueil de mémoires sur l'anatomie, la physiologie, la classification et les mœurs des animaux de nos côtes; ouvrage accompagné de planches faites d'après nature, 2, Annélides Pt. 1. Crochard, Paris.

Ax, P., 1987. The Phylogenetic System. Wiley, Chichester: 340 pp.

Ax, P., 1996. Multicellular animals. A New Approach to the Phylogenetic Order in Nature, I. Springer, Berlin: 225 pp.

Ax, P., 2000. Multicelluar animals. A New Approach to the Phylogenetic Order in Nature, II. Springer, Berlin: 396 pp.

Ax, P., 2003. Multicellular animals. A New Approach to the Phylogenetic Order in Nature, III. Springer, Berlin: 317 pp.

Bartolomaeus, T., 1999. Ultrastructure, development and function of segmental organs in Annelida. Hydrobiologia 402: 21–37

Bartolomaeus, T., 1995. Structure and formation of the uncini in *Pectinaria koreni*, *Pectinaria auricoma* (Terebellida) and *Spirorbis spirorbis* (Sabellida): implications for annelid phylogeny and the position of the Pogonophora. Zoomorphology 115: 161–177.

Bartolomaeus, T., 1998. Chaetogenesis in polychaetous Annelida – Significance for annelid systematics and the position of the Pogonophora. Zoology (ZACS) 100: 348–364.

Bartolomaeus, T., 2002. Structure and formation of the uncini in *Fabricia stellaris* (Ehrenberg, 1836) – Implication for the evolution of Sabellida (Annelida). Zoologischer Anzeiger 241: 1–17.

Bartolomaeus, T. & B. Quast (2005). Structure and development of nephridia in Annelida and related taxa. Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 139–164.

Bartolomaeus, T. & H. Ruhberg, 1999. Ultrastructure of the body cavity lining in embryos of *Epiperipatus biolleyi* (Peripatidae, Onychophora). Invertebrate Biology 118: 165–174.

Bartolomaeus, T. & K. Meyer, 1997. Development and phylogenetic significance of hooked setae in Arenicolidae (Polychaeta, Annelida). Invertebrate Biology 116: 227–242.

Bartolomaeus, T. & K. Meyer, 1999. Zur Phylogenie der Arenicolidae. Senckenberg Courier 215: 23–29.

Bellan, G., D. Bellan-Santini & J. C. Dauvin (1991) Phénetique et phylogénie des Opheliidae (Annélides, Polychètes). Comptes rendus de l'Academic Science, Paris, Series III 310: 175–181.

Benham, W. B., 1896. The Archiannelida, Polychaeta, Myzostomaria. In Harmer, S. F. & A. E. Shipley (eds), The Cambridge Natural History, 2. MacMillan, London: 241–344.

Blake, J. A. & P. L. Arnofsky 1999. Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. Hydrobiologia 402: 57–106.

Blake, J. A., 2000. A new genus and species of polychaete worm (familiy Orbiniidae) from methane seeps in the Gulf of Mexico, with a review of the systematics and phylogeentic interrelationships of the genera of Orbiniidae. Cahiers de Biologie Marine 41: 435–449.

Bleidorn, C., L. Vogt & T. Bartolomaeus, 2003a. New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. Molecular phylogenetics and evolution 29: 279–288

Bleidorn, C., L. Vogt & T. Bartolomaeus, 2003b. A contribution to sedentary polychaete phylogeny using 18S rRNA sequence data. Journal of Zoological Systematics and Evolutionary Research 41: 186–195.

Bobin, G., 1944. Morphogénèse des soies chez les annélides polychètes. Annales des Institute Oceanographique, Monaco 22: 1–106.

Clark, R. B., 1964. Dynamics in Metazoan Evolution. The Origin of the Coelom and Segments. Clarendon Press, Oxford.

Clark, R. B., 1977. Phylogenetic reconstruction. Verhandlungen der deutschen Zoologischen Gesellschaft 70 175–183.

Conway-Morris, S., 1979. Middle Cambrian polychaetes from the Burgess shale of British Columbia. Philosophical Transactions of the Royal Society B 285: 227–274.

Cuvier, G. 1812. Sur un nouveau rapprochement à établir entre les classes qui composant le Règne Animal. Annales de Muséum Histoire 19: 73–84.

Dales, R. P., 1962. The polychaete stomatodeum and the inter–relationships of the families of Polychaeta. Proceedings of the Zoological Society, London 139: 389–428.

Day, J. H., 1967. A monograph of the Polychaeta of Southern Africa. British Museum (Natural history). Publication 656. British Museum (Natural History), London: 878 pp.

Desbruyéres, D. & L. Laubier, 1980. *Alvinella pompejana* gen.-sp.nov., Ampharetidae aberrant des sources hydrothermales de la ride Est-Pacifique. Oceanologica Acta 3: 267–274.

Desbruyéres, D. & L. Laubier, 1986. Les Alvinellidae, une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines: systématique, biologie et écologie. Canadian Journal of Zoology 64: 2227–2245.

Eibye-Jacobson, D. & C. Nielsen, 1997. The rearticulation of annelids. Zoologica Scripta 25: 275–282.

Erséus, C., 2005. Phylogeny of oligochaetous Clitellata. Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 355–370.

Fauchald, K. & G. W. Rouse, 1997. Polychaete systematics: Past and present. Zoologica Scripta 26: 71–138.

Fauchald, K., 1977. The polychaete worms: definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Sciences Series 28: 190 pp.

Fauvel, P., 1923. Polychétes errantes, 5 (Faune de France). Paul Lechevalier, Paris: 488 pp.

Ferraguti, M. & C. Erseus (1999). Sperm types and their use for a phylogenetic analysis of aquatic clitellates. Hydrobiologia 402: 225–237.

Ferraguti, M., 1984. The comparative ultrastructure of sperm flagella central sheath in Clitellata reveals a new autapomorphy of the group. Zoologica Scripta 13: 201–207.

Fitzhugh, K., 1989. A systematic revision of the Sabellidae–Caobangiidae–Sabellongidae complex (Annelida: Polychaeta). Bulletin of the American Museum of National History 192: 1–104

Fitzhugh, K., 1991. Further revisions of the Sabellidae subfamilies and cladistic relationships among the Fabricinae (Annelida: Polychaeta). Zoological Journal of the Linnean Society 102: 305–332.

Fristrup, K. M., 2001. A history of character concepts in evolutionary biology. In Wagner, G. P. (ed.), The Character Concept in Evolutionary Biology. Academic Press, San Diego: 13–35.

George, J. D. & G. Hartmann-Schröder, 1985. Polychaetes: British Amphinomida, Sphinterida and Eunicida. In Kermack, D. M. & R. S. K. Barnes (eds), Synopses of the British Fauna. Brill Backhuys, Leiden.

Giribeth, G., 2003. Molecules, development and fossils in the study of metazoan evolution; Articulata versus Ecdysozoa revisited. Zoology 106: 303–326.

Goodrich, E. S., 1895. On the coelom, genital ducts, and nephridia. Quarterly Journal of microscopical Science 37: 477–510.

Goodrich, E. S., 1945. The study of nephridia and genital ducts since 1895. Quarterly Journal of microscopical Science 86: 113–392.

Grube, A. E., 1850. Die Familien der Anneliden. Archiv für Naturgeschichte 16: 249–364.

Halanych, K., T. Dahlgren & D. McHugh 2002. Unsegmented annelids? Possible origin of four lophotrochozoan worm taxa. Integrative Comparative Biology 42: 678–684.

Hartmann-Schroeder, G., 1971. Annelida, Borstenwürmer, Polychaeta. In Dahl, M. & F. Peus (eds), Die Tierwelt Deutschlands, 58. G. Fischer, Jena.

Hartmann-Schröder, G., 1996. Annelida, Borstenwürmer, Polychaeta. Zweite Auflage. In In Dahl, M. & F. Peus (eds), Die Tierwelt Deutschlands, 58. G. Fischer, Jena

Hatschek, B., 1878. Studien über die Entwicklungsgeschichte der Anneliden. Ein Beitrag zur Morphologie der Bilaterien. Arbeiten aus dem Zoologischen Institut der Universität Wien und der Zoologischen Station Triest 1: 277–404.

Hatschek, B., 1893. System der Anneliden, ein vorläufiger Bericht. Lotos 13: 123–126.

Hausen, H. & T. Bartolomaeus, 1997. Setal structure and chaetogenesis in *Scolelepis squamata* and *Malacoceros fuliginosus* (Spionidae, Annelida). Acta Zoologica (Stockholm) 79: 179–141.

Hausen, H., 2005. Chaetae and chaetogenesis in polychaetes (Annelida). Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 37–52.

Hausen, H., 2001. Untersuchungen zur Phylogenie "spiomorpher" Polychaeten (Annelida). Logos, Berlin: 145 pp.

Hessling, R. & G. Purschke, 2000. Immunohistochemical (cLSM) and ultrastructural analysis of the central nervous system and sense organs in *Aeolosoma hemprichi* (Annelida, Aeolosomatidae). Zoomorphology 120: 65–78.

Hessling, R. & W. Westheide, 2002. Are Echiura derived from a segmented ancestor? Immunhistochemical analysis of the nervous system in developmental stages of *Bonellia viridis*. Journal of Morphology 252: 100–113.

Hessling, R., 2002. Metameric organisation of the nervous system in developmental stages of *Urechis caupo* (Echiura) and its phylogenetic implications. Zoomorphology 121: 221–234.

Jenner, R. A. & F. R. Schram, 1999. The grand game of metazoan phylogeny – rules and strategies. Biology Reviews 74: 121–142.

Jenner, R. A., 2001. Bilaterian phylogeny and uncritical recycling of morphological data sets. Systematic Biology 50: 730–742.

Jouin, C., 1971. Status of the knowledge of the systematics and ecology of Archiannelida. In Hulings, N. C. (ed.), Proceedings of the First Interantional Conference on Meiofauna. Smithsonian Contribution Zoology 67: 47–56.

Lamarck, J.-B. de, 1801. Système des Animaux sans Vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux; Présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs apports naturelles et da leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées ; Précédé du discours d'ouverture du Cours de Zoologie, donné dans la Muséum National d'Histoire Naturelle l'an 8 de la Républiques. Chez l'auteur Déterville, Paris.

Lamarck, J.-B. de, 1818. Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leur classes, leur familles, leur genres, et la citation des principales espèces, qui s'y rapportent ; précédée d'une Introduction offrant la Détermination des caractères essentiels de l'Animal, sa distinction du Végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie, 5. Déterville and Verdière, Paris.

Licher, F. & W. Westheide, 1994. The phylogenetic position of the Pilargidae with a cladistic analysis of the taxon – facts and ideas. Mémoirs du Muséum national d'Histoire Naturelle, Paris 162: 223–235.

McHugh, D., 2005. Molecular systematics of polychaetes. Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 307–316.

Meier, R., 1994. On the inappropriateness of presence/absence recoding for non-additive multistate characters in computerized cladistic analyses. Zoologischer Anzeiger 232: 201–212.

Meyer, E., 1890. Die Abstammung der Anneliden. Der Ursprung der Metamerie und die Bedeutung des Mesoderms. Biologisches Centralblatt 10: 296–308.

Meyer, K. & T. Bartolomaeus, 1996. Ultrastructure and formation of the hooked setae in *Owenia fusiformis* delle Chiaje, 1842: Implications for annelid phylogeny. Canadian Journal of Zoology 74: 2143–2153.

Meyer, R. & T. Bartolomaeus, 1997. Ultrastruktur und Morphogenese der Hakenborsten bei *Psammodrilus balanoglossoides* – Bedeutung für die Stellung der Psammodrilida (Annelida). Microfauna marina 11: 87–113

Nielsen, C., 2001. Animal Evolution. Interrelationships of the Living Phyla. Oxford University Press, Oxford: 563 pp.

Nygren, A., 1999. Phylogeny and reproduction in Syllidae (Polychaeta). Zoological Journal of the Linnean Society 126: 365–386.

O'Clair, R. M. & R. A. Cloney, 1974. Patterns of morphogenesis mediated by dynamic microvilli: Chaetogenesis in *Nereis vexillosa*. Cell Tissue Research 151: 141–157.

Orrhage, L., 1978. On the structure and evolution of the anterior end of the Sabellariidae (Polychaeta, Sedentaria. With some remarks on the general organisation of the polychaete brain. Zoologische Jahrbücher für Anatomie und Ontogenie der Tiere 100: 343–374.

Orrhage, L., 1980. On the structure and homologues of the anterior end of the polychaete families Sabellidae and Serpulidae. Zoomorphology 96: 113–168.

Orrhage, L., 2001. On the anatomy of the central nervous system and the morphological value of the anteriorend appendages pf Ampharetidae, Pectinariidae and Terebellidae (Polychaeta). Acta Zoologica (Stockholm) 82: 57–71.

Orrhage, L. & D. Eibye-Jabobsen, 1998. On the anatomy of the central nervous system of Phyllodocida (Polychaeta) and the phylogeny of phyllodocid genera: a new alternative. Acta Zoologica (Stockholm) 79: 215–234.

Orrhage, L. & M. C. M. Müller, 2005. Morphology of the Nervous system of Polychaeta (Annelida). Hydrobiologia 535/536 (Dev. Hydrobiol. 179): 79–111.

Perrier, E., 1897. Traité de Zoologie, Fascicule IV. Vers, Mollusques, Tuniciers. Masson et Cie, Paris.

Pettibone, M. H., 1982. Annelida. In Parker, S. P. (ed.), Synopsis and Classification of Living Organisms, 2. McGraw Hill, New York: 1–43.

Pleijel, F., 1991. Phylogeny and classification of the Phyllodocidae (Polychaeta). Zoological Screening. 20: 225–261.

Pleijel, F., 1995. On character coding for phylogeny reconstruction. Cladistics 11: 309–315

Pleijel, F. & T. Dahlgren (1998). Position and delineation of Chrysopetalidae and Hesionidae (Annelida, Polychaeta, Phyllodocida). Cladistics 14: 129–150.

Purschke, G., 1997. Ultrastructure of the nuchal organs in polychaets (Annelida) – new results and review. Acta Zoologica (Stockholm) 78: 123–143.

Purschke, G., 1999. Terrestrial polychaetes – models for the evolution of the Clitellata (Annelida)? Hydrobiologia 406: 87–99.

Purschke, G., 2000. Sense organs and central nervous system in an enigmatic terrestrial polychaete, *Hrabeiella periglandulata* (Annelida). Invertebrate Biology 119: 329–341.

Purschke, G., 2002. On the ground pattern of Annelida. Organisms Diversity and Evolution 2: 181–196.

Purschke, G., 2003. Is *Hrabeiella periglandulata* (Annelida, "Polychaeta") the sitser group of Clitellata? Evidence from an ultrastructural analysis of the dorsal pharynx in *H. periglandulata* and *Enchytraeus minutus* (Annelida, Clitellata). Zoomorphology 122: 55–66.

Purschke, G., F. Wolfrath & W. Westheide, 1997. Ultrastructure of the nuchal organ and cerebral organ in *Onchnesomum squamatum* (Sipuncula, Phascolionidae). Zoomorphology 117: 23–31.

Purschke, G., R. Hessling, W. Westheide, 2000. The phylogenetic position of the Clitellata and the Echiura – on the problematic assessment of absent characters. Journal of Zoological Systematics and Evolutionary Research 38: 165–173.

Purschke, G., W. Westheide, D. Rhode & R.O. Brinkhurst, 1993. Morphological reinvestigation and phylogenetic relationship of *Acanthobdella peledina* (Annelida, Clitellata). Zoomorphology 113: 91–101.

Rouse, G. W., 1999. Trochophore conepts: ciliary bands and the evolution of larvae in spiralian Metazoa. Biological Journal of the Linnean Society 66: 411–464.

Rouse, G. W., 2000. Bias? What bias? Gain and loss of downstream larval-feeding in animals. Zoologica Scripta 29: 213–236.

Rouse, G. W., 2001. A cladistic analysis of Siboglinidae Caullery, 1914 (Polychaeta, Annelida): formerly the phyla Pogonophora and Vestimentifera. Zoological Journal of the Linnean Society 132: 55–80

Rouse, G. W. & K. Fauchald, 1995. The articulation of annelids. Zoologica Scripta 24: 269–301.

Rouse, G. W. & K. Fauchald, 1997. Cladistics and polychaetes. Zoologica Scripta 26: 139–204.

Rouse, G. W. & K. Fitzhugh, 1994. Broadcasting fables: is external fertilization really primitive? Sex, size and larvae in sabellid polychaetes. Zoologica Scripta 23: 271–312.

Rouse, G. W. & F. Pleijel, 2001. Polychaetes. Oxford University Press, New York: 354 pp.

Ruppert, E. E., R. S. Fox & R. D. Barnes, 2003. Invertebrate Zoology. A functional evolutionary approach. Brooks/Cole-Thomson learning, Belmont, CA.

Schmidt-Rhaesa, A., 2003. Old trees, new trees – is there any progress? Zoology 106: 291–301.

Schmidt-Rhaesa, A., T. Bartolomaeus, C. Lemburg, U. Ehlers & J. R. Garey, 1998. The position of the Arthropoda in the phylogenetic system. Journal of Morphology 238: 263–285.

Scholtz, G., 2002. The Articulata hypothesis – or what is a segment? Organisms Diversity and Evolution 2: 197–215.

Schulze, A. 2001. Ultrastructure of opisthosomal chaetae in Vestimentifera (Pogonophora, Obturata) and implications for phylogeny. Acta Zoologica (Stockholm) 82: 127–135.

Schweigkofler, M., T. Bartolomaeus & L. von Salvini-Plawen, 1998. Ultrastructure and formation of hooded hooks in *Capitella capitata* (Annelida, Capitelida). Zoomorphology 118: 117–128.

Sokal, R. R. & P. H. A. Sneath, 1963. Principles of Numerical Taxonomy. WH Freeman, San Francisco.

Stecher, H.-J., 1968. Zur Organisation und Fortpflanzung von *Pisione remota* (Southern) (Polychaeta Pisionidae). Zeitschrift für Morphologie der Tiere 61: 347–410.

Struck, T. H., R. Hessling & G. Purschke, 2002a. The phylogenetic position of the Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of the "Polychaeta", based on molecular data from 18S rDNA sequences. Journal of Zoological Systematics and Evolutionary Research 40: 155–163.

Uschakov, P. V. 1955. Polychaeta of the far eastern seas of the U.S.S.R. Keys to the fauna of the USS 56: 1–445.

Wägele, J.-W. & B. Misof, 2001. On the quality of evidence in phylogeny reconstruction: a reply to Zrzavy's defence of the, ecdysozoa' hypothesis. Journal of Zoological Systematics and Evolutionary Research 39: 165–176.

Wägele, J.-W., T. Erikson, P. Lockhart & B. Misof, 1999. The Ecdysozoa: artifact or monophylum. Journal of Zoological Systematics and Evolutionary Research 37: 211–223.

Westheide, W., 1985. The systematic position of the Dinophilidae and the archiannelid problem. In Conways Morris, S., D. George, R. Gibson & H. M. Platt (eds), The Origins and Relationships of Lower Invertebrates. Oxford Universsity Press, Oxford: 310–326.

Westheide, W., 1987. Progenesis as a principle in meiofaunal evolution. Journal of Natural History 21: 843–854.

Westheide, W., 1997. the direction of the evolution within the Polychaeta. Journal of Natural History 31: 1–15.

Westheide, W., D. McHugh, G. Purschke & G. W. Rouse, 1999. Systematization of the Annelida: different approaches. Hydrobiologia 401: 291–307.