

Recent Views on the Status, Delineation and Classification of the Annelida¹

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SYNOPSIS. In recent years the monophyly of the Annelida and Polychaeta has been questioned, with various authors proposing that groups such as the Arthropoda, Echiura and Pogonophora render the Annelida and/ or Polychaeta paraphyletic. The Clitellata have also been proposed to be a member of the Polychaeta, potentially making this latter taxon synonymous with the Annelida. The relationships within the traditionally formulated Polychaeta have never been investigated using cladistic methodology. Recent classifications of polychaetes show a large number of “orders” with no real attempts to relate the groups in a phylogenetic sense. In this paper a number of recent studies on annelid systematics and classification are reviewed. Special emphasis is placed on the cladistic parsimony analyses of Rouse and Fauchald (1995, 1997) where a comprehensive assessment of the relationships among the various polychaete and annelid groups was attempted. A contrasting result by Westheide (1997) using a different methodology, is also outlined and discussed.

INTRODUCTION

Through most of this century the Annelida has been split into two main groups; the Polychaeta and Clitellata, with myzostomatids being given class status by some workers (Jägersten, 1940; Prenant, 1959), or as members of the Polychaeta (Hartman, 1969; Schroeder and Hermans, 1975; Pettibone, 1982). In addition, several small groups have been regarded as families of uncertain affinities within the Annelida, or “associated” with the Annelida (Fauchald and Rouse, 1997).

While the monophyly of the Clitellata is not currently debated and the classification within the clade is problematic (Omodeo, 1998), the history of the classification within the Polychaeta and the monophyly of the group itself is more contentious. One of the most influential classifications of polychaetes, originally derived from Quatrefages (1866), divided the Polychaeta into two orders (or subclasses); the Errantia and Sdentaria (Fauvel, 1923, 1927; Day, 1967a,

b; Hartman, 1968, 1969). While these authors tended to just list the various polychaete families in either the Errantia or Sdentaria, Hemplemann (1931), Hartmann-Schröder (1971) and Uschakov (1955) were unusual in dividing each of the two subclasses into a number of orders. Their systems resembled some of the classifications of the 19th century (see Fauchald and Rouse, 1997). Day (1967a, p. 19) considered the two major polychaete groups as an “arbitrary grouping” used for “practical purposes” and did not recognize any taxonomic levels between orders and families. Other authors probably had similar attitudes and probably did not regard this system as providing any sort of phylogenetic perspective on polychaetes. Rather, it conveniently divided the group into two relatively even halves.

A system proposed by Dales (1962) rejected the concept of the Errantia and Sdentaria, and used structural relations of the buccal organs and nephridia to furnish criteria for an analysis of the polychaetes at the family level, and resulted in them being classified into 14 orders. Dales (1977) reviewed developments in phylogeny studies since his earlier (Dales, 1962) publication, but left his classification unchanged. Dales

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(1962, 1977) did draw phylogenetic trees of the Polychaeta, albeit somewhat unresolved, but incorporated little of this information into his classification. For instance he did not group the Capitellida and Spionida into a "superorder" or subclass though this is clearly implied in Figure 17 of Dales (1962).

The classification of polychaetes by Fauchald (1977) comprised 17 orders. While delineated differently, the orders contained roughly the same taxa as those listed in Dales (1962) and they were listed without any interrelationships being specified. Fauchald (1977, p. 7) did however state that "the sequence of families indicates an increasing morphological distance from the ancestral polychaete". This implies that the orders he listed last (*e.g.*, Terebellida, Sabellida) were presumably more apomorphic than the first listed taxa (*e.g.*, Orbiniida, Ctenodrilida). Pettibone (1982) recognized 25 orders, including in addition to the orders defined by either Dales (1962) or Fauchald (1977), orders for each of the five "archannelidan" families, and new orders for the Myzostomatidae and Poeobiidae. Pettibone made no mention of the reasons for her classification. Many of the new orders created by Dales, Fauchald and Pettibone were for morphologically unusual families (*e.g.*, Oweniidae, Psammodrilidae, Spinttheridae, Sternaspidae). A recent classification of the Polychaeta by Hartmann-Schröder (1996) includes 22 orders with a few small differences from the system of Pettibone (1982). A detailed history of the classification of polychaetes can be found in Fauchald and Rouse (1997).

All classifications of polychaetes used by authors recently appear to follow the reasoning expressed by Dales (1977, p. 526) whereby "All of the families of the Class Polychaeta are distinct, but some show obvious resemblances while others appear to be isolated. . . . The grouping of families into larger groups presents some difficulties, therefore, and while some groups of families or orders emerge, there remains a series of families with no close affinities with any other group. My own view is that it is better to leave such families in isolated orders until their affinities are understood

than it is to reduce the value and coherence of natural orders by including such families in one or another group on tenuous evidence." This philosophy could equally be applied to the position of the Clitellata, which was treated by all workers on polychaetes as belonging outside the Polychaeta.

In recent years the monophyly of the Annelida and Polychaeta has been questioned with various authors proposing that groups such as the Arthropoda, Echiura and Pogonophora render the Annelida and/ or Polychaeta paraphyletic (Nielsen, 1995; Rouse and Fauchald, 1995, 1997; McHugh, 1997). The Clitellata have also been proposed to be members of the Polychaeta, making this latter taxon synonymous with the Annelida (Nielsen, 1995; McHugh, 1997; Purschke, 1997; Westheide, 1997). In this paper a number of these recent studies on annelid systematics and classification are reviewed, though emphasis is placed on the cladistic analyses of Rouse and Fauchald (1995, 1997).

THE ARTICULATION OF ANNELIDS

The philosophy behind the analyses by Rouse and Fauchald (1995, 1997) was to minimize assumptions about the evolutionary processes in annelids and to make a series of detailed homology assessments across the entire range of taxa concerned. Homology or non-homology (=homoplasy) was then evaluated in terms of overall character congruence (Pinna de, 1991). This meant that no hypotheses about the course of evolution in annelids, any possible hypothetical ancestors, or the evolution of any particular features, were considered *a priori*. The anatomical literature on polychaetes and other taxa was analyzed in detail and homology assessments were coded as characters for a comprehensive array of taxa. The data was subjected to maximum-parsimony analysis and the resulting shortest trees rooted (and characters polarised) by using the outgroup method (Nixon and Carpenter, 1993). All features that were absent from a group (*e.g.*, "nuchal organs") were treated in exactly the same way in the data matrices, *i.e.*, scored simply as absent. The implications of this are that any losses

of features (secondary absences) must be detected during the process of finding the most-parsimonious trees. When a group has a large number of "losses" with respect to other taxa in the analysis, its systematic position may be incorrectly inferred. However, if enough evidence is used in the construction of trees then these losses should be reasonably detected. If morphological evidence is insufficient to do this then molecular sequence data may have to be used as well, though this form of evidence carries its own inherent problems (see below).

Rouse and Fauchald (1995) considered the monophyly of the Annelida and so assessed the relationship of taxa usually associated with annelids; the Pogonophora, Vestimentifera and Arthropoda. Their results suggested that, minimally, the conventionally formulated Annelida, namely the Polychaeta and Clitellata, is paraphyletic. In half of the 18 minimal length trees, the traditionally formulated Annelida, (*i.e.*, "Polychaeta and Clitellata") is paraphyletic if the Pogonophora are excluded. In the remaining minimal length trees a monophyletic Annelida cannot be formulated (consensus tree in Fig. 1). They suggested that the name Annelida cease to be used unless relationships within the Articulata are resolved to show a monophyletic Annelida. The Vestimentifera was the sister group to, or more likely a clade within, the frenulate pogonophores and the name Pogonophora was retained for this group. The name Articulata was applied to the Clitellata, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera. The synapomorphies for the Articulata were the presence of segmentation and longitudinal muscle broken into bands. The definition of the Articulata was formulated as the clade stemming from the first ancestor, and all its descendants, to show repetition of homologous body structures derived by teloblastic growth and longitudinal muscles broken into bands. The Articulata was considered to consist of four clades; the Arthropoda, Clitellata, Polychaeta, and Pogonophora. The analysis by Rouse and Fauchald (1995) assumed the monophyly of the Polychaeta, a taxon that has never been identified by synapomorphy. They concluded that the

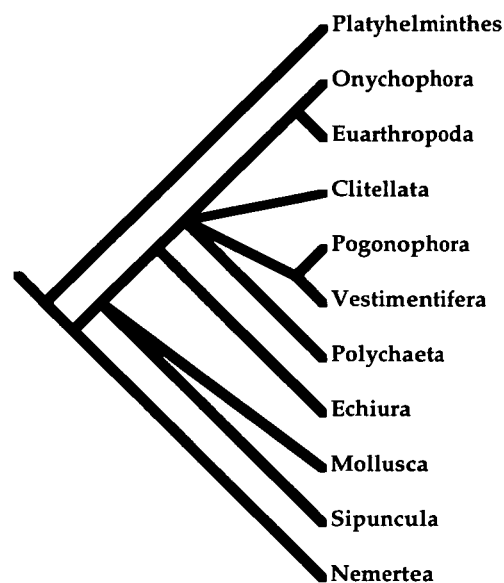


FIG. 1. Strict consensus tree of the 18 minimal length trees found in the analysis by Rouse and Fauchald (1995). They argued that a monophyletic Annelida could not be formulated. Their study assumed the monophyly of the Polychaeta; an assumption assessed in their subsequent study (Rouse and Fauchald, 1997).

Clitellata, "arthropods," and Pogonophora may well prove to fall inside the Polychaeta and that use of these taxa as outgroups for an analysis of polychaete relationships was not justifiable.

The conclusions and methodology in Rouse and Fauchald (1995) were promptly challenged (Eibye-Jacobsen and Nielsen, 1996); this critique was rebutted by Rouse (1997). The discussion focused on cladistic methods, specifically on various possible post-parsimony analysis refinements but there was nothing substantive to the arguments of Eibye-Jacobsen and Nielsen (1996) that was not then addressed in Rouse and Fauchald (1997).

While Rouse and Fauchald (1995, 1997) and nearly all other relevant cladistic papers based on morphology suggest that the annelids and arthropods form a clade (see Eernisse *et al.*, 1992; Nielsen *et al.*, 1996), there have been two studies based on morphological data that have suggested that annelids are closer to molluscs than they are to arthropods (Eernisse *et al.*, 1992; Schram and Ellis 1994). Both of these analyses were

shown to be substantially flawed by Rouse and Fauchald (1995). Eernisse *et al.* (1992) contains numerous scoring errors and problems in character constructions and requires substantial revision. Schram and Ellis (1994) also has problems in character construction and scoring but also had a coding inconsistency between the matrix published by Schram (1991) and that used by Schram and Ellis (1994) to rebut criticism by Backelau *et al.* (1993). Correction of this error (involving nephridia in entoprocts) gives the results obtained by Backelau *et al.* (1993) and provides no support for rejecting the Articulata. Favorable references to Eernisse *et al.* (1992) and Schram and Ellis (1994) by Eernisse (1997) should be viewed with caution.

In contrast to the morphological cladistic analyses there is a growing body of evidence from molecular sequence data that the Articulata is not a valid taxon. Recent analyses using sequence data from 18S rDNA or 18S rRNA, have suggested that the Arthropoda belong to a clade that contains the Nematoda and other taxa that moult their cuticle (Aguinaldo *et al.*, 1997; Eernisse, 1997; Giribet and Ribera, 1998). Aguinaldo *et al.* (1997) erected a new taxon, Ecdysozoa, containing the arthropods, nematodes and some other aschelminth taxa. Halanych *et al.* (1995) suggested that the lophophorate taxa Ectoprocta (=Bryozoa), Phoronida and Brachiopoda were part of a clade whose other members were the Annelida and Mollusca. They called this clade, a common ancestor, and any descendants, the Lophotrochozoa. The Brachiopoda are of some interest since they have chaetae that are identical to those seen in annelids (*e.g.*, Gustus and Cloney, 1972). While other molecular sequence data, such as that from Elongation factor 1-alpha also suggests molluscs are closer to annelids than arthropods (McHugh, 1997), taxon sampling has been limited. More results showing that the Articulata is not monophyletic based on other gene sequences will provide compelling evidence for a re-examination of the morphological basis for the taxon. For example, doubts over the homology of segmentation between arthropods and annelids have been raised previ-

ously (*e.g.*, Minelli and Bortoletto, 1988) and deserve further investigation.

CLADISTICS AND POLYCHAETES

Rouse and Fauchald (1997) assessed the monophyly of the Polychaeta and relationships among the taxa usually included in the group and those traditionally excluded. Polychaete families and the Sipuncula, Echiura, Clitellata, Euarthropoda, Onychophora, Pogonophora, and Vestimentifera were used as terminal taxa largely because this allowed the most heuristic assessment of relationships based on present knowledge, and also permitted many of the current problems in the systematics of polychaetes to be highlighted. Classifications of polychaetes above the level of family were reviewed in Fauchald and Rouse (1997) and found to be unsatisfactory for cladistic analysis. Attempting any analyses below the family level, say at "species" level, was beyond the scope of the study, in terms of computational capabilities, time and available information.

Many characters in the characters used in Rouse and Fauchald (1997) were linked in a variety of ways. For example, the ever-visible pharynx of annelids consists of a number of structures, each of which have been considered systematically important. Each of the pharyngeal features could be scored as individual characters, but the potential general homology among them would be lost. The discussion on how to score linked characters is extensive, but no generally satisfactory agreement has been reached (see Pleijel, 1995). Because of this, and in an attempt to highlight the problem, Rouse and Fauchald (1997) prepared two scoring matrices for their analysis of the Polychaeta. One was based on a 'traditional' multistate character-list (*M*); the other on an absence/presence (*A/P*) character list.

The *A/P* matrix was analyzed using two options. In one (*APe*), equal character weighting was applied; in the other (*APw*) they applied weighting in which the presence of a given feature was weighted as 1; any subsidiary characters were weighted 0.5, and those subsidiary again were weighted as 0.25 and so on. The weighting is of course arbitrary and not a proper so-

lution. However, the use of multistate characters results in loss of information, as outlined by Pleijel (1995), such that a feature at a general level may be absent or present, but also exhibits some informative variation at a less general level. Hence, a multistate character will sacrifice the information at the more general hierarchical level for the more restricted level. Matrices for both scoring patterns outlined above, with all families, about 80 at this time, are presented in Rouse and Fauchald (1997) and is available on the World Wide Web at the following addresses <http://wallace.bio.usyd.edu.au/papers/gregr/>; <http://herbaria.harvard.edu/treebase>

The parsimony program Paup 3.1 (Swofford, 1993) was used and the complete matrices, and ones in which 29 families had been removed, were run using parameters and procedures outlined in Rouse and Fauchald (1997). This meant there were 6 different analyses; three complete analyses (*c*) and three restricted analyses (*r*). The Sipuncula was used to root the resulting trees and polarise the characters. The families removed from the runs are either poorly known, or very small-bodied, or living in unusual environments; after the completion of the analyses all but a three of these families were readily aligned with the major clades based on synapomorphies present.

The taxon Articulata formulated by Rouse and Fauchald (1995) contained a polytomy that was resolved in all analyses by Rouse and Fauchald (1997). In all three coding methods the Arthropoda were sister group to a monophyletic Annelida (formulated below). In the *A/Pwr* analysis the Articulata was supported by the presence of segmentation and longitudinal muscles divided into bands and also the presence of a straight gut. In the *Mr* analysis the Articulata was supported the presence of segmentation and longitudinal muscles divided into bands. These are the same two features that supported the Articulata in Rouse and Fauchald (1995). The Echiura was sister group to the Articulata in all restricted analyses. Nielsen (1995) and Eibye-Jacobsen and Nielsen (1996) included the Echiura in the Annelida on the basis that they have lost segmentation and that chaetae must have

evolved once. The results in Rouse and Fauchald (1997) suggest that chaetae could have evolved twice, once in the Echiura and once in the Annelida, or the presence of such structures is plesiomorphic for the Articulata and they been lost in the Arthropoda. There is no morphological evidence to support the suggestion by Nielsen (1995) and McHugh (1997) that the Echiura have lost segmentation, and the nature of any such possible "loss" has not been fully discussed. Does it mean that the Echiura in fact have many fused "segments" or only a single "segment"? Though teloblastic growth was reported by Hatschek (1980), three subsequent studies (Torrey, 1903; Baltzer, 1925; Newby, 1940) looked for this and found no such thing. Other features such as the presence of multiple epidermal glandular rings, repeated larval ganglia and multiple nephridia (Nielsen 1995; McHugh, 1997) imply that Echiura possess multiple fused segments. However, multiple epidermal glandular rings do not indicate mesodermal segmentation. The formation of larval ganglia in echiurans is by an initial proliferation followed by division of existing ganglia. This is therefore not homologous to the formation of segmental ganglia (Newby, 1940) and cannot be suggested as evidence in favor of the Echiura being "cryptically" multisegmented. The presence of multiple nephridia can be contrasted with the fact that some echiurans have only a single pair of nephridia (Pilger, 1993). Since the relationships within the Echiura are unknown, the plesiomorphic condition for nephridial number cannot as yet be determined. However, since the branch support for the Articulata (and Annelida) is weak, further investigation into the position of the Echiura (and the Sipuncula) should be pursued, using both morphological and molecular sequence data.

In all restricted analyses by Rouse and Fauchald (1997), the traditionally formulated Annelida was monophyletic and comprised two clades, the Clitellata and Polychaeta, though the monophyly of the latter was not well supported. Rouse and Fauchald (1997) found that there is no sister group for the Clitellata within the Polychaeta that can be identified on current mor-

phological evidence. However, the relationships among clitellates are still poorly understood. Further study in this area may identify likely plesiomorphic clitellates that can be targeted for detailed morphological study. The monophyly of the Polychaeta was supported in *Mr* trees by the (homoplastic) presence of palps and the presence of mixonephridia. In *A/Per* and *A/Pwr* trees the Polychaeta was supported by the presence of nuchal organs, nuchal organs as pits or grooves, parapodia and mixonephridia. However, many polychaetes were inferred to have lost some these structures. For instance the Pisionidae and Magelonidae are derived polychaetes but were shown (at least some members) to have lost nuchal organs.

The most interesting result of the analyses presented by Rouse and Fauchald (1997) was that the phylum Pogonophora (including the former phylum Vestimentifera; see Rouse and Fauchald, 1995) clearly appeared within the traditionally formulated Annelida, and in fact represent a derived clade of the Polychaeta. This placement was also recently suggested by Bartolomaeus (1995, 1997), McHugh (1997) and Kojima (1998). Rouse and Fauchald (1995, p. 287) had also suggested "the Pogonophora will be found to fall within the Polychaeta, close to the sabellid/terebellid clade of polychaetes." Bartolomaeus (1995) also advocated a sabellid/terebellid relationship for the Pogonophora, and in fact showed a tree with the Pogonophora as sister group to a Sabellida (comprising the Sabellidae and Serpulidae). Rouse and Fauchald (1997) reclassified the Pogonophora as members of the clade Sabellida (see below). Since the name Pogonophora is misleading at this level the name of the group reverted to that of the first family group name originally formulated for members of the group, that of Siboglinidae Cautley, 1914 (see also McHugh, 1997). The current classification of the Pogonophora is thus made redundant and major revision is required (Rouse, in preparation). All currently named families of Pogonophora become synonyms of the Siboglinidae. The Vestimentifera also fall within the Siboglinidae since it was shown that Jones (1985)

was erroneous in removing this group from the Pogonophora (Southward, 1988; and see review in Rouse and Fauchald, 1995).

Given the variability in results from the different coding methods in Rouse and Fauchald (1997), the choice of which one to use for a new polychaete classification was not straightforward. However, the state of polychaete classification was clearly unsatisfactory (as outlined in the INTRODUCTION) and a new classification was proposed by Rouse and Fauchald (1997). While the placement of many of the taxa in the complete analyses is not surprising and matches current ideas (*e.g.*, Fauveliopsidae, Poeobiidae, pelagic taxa with hypertrophied axial pharynges) others have placements that are certainly incorrect (*e.g.*, Histriobdellidae, Diurodrilidae are most likely members of the clade having a hypertrophied ventral pharynx, not basal polychaetes). Therefore, the new classification was based on a restricted analysis and the taxa that were excluded were placed within the taxon they are most likely to belong. However, the overall topology of the complete analyses also differ significantly from the restricted analyses and this should be kept in mind with reference to the classification presented by Rouse and Fauchald (1997). For example, the position of the clades (Arenicolidae Capitellidae Maldanidae), (Acrocirridae Cirratulidae Flabelligeridae) and Oweniidae differ markedly between the complete and restricted analyses using *A/Pw* coding. Clearly there is much further work to be done.

Given that a restricted analysis was used for the classification, the issue was then which of the coding methods to utilise. *A/Pe* coding was clearly unsatisfactory because of the marked hierarchical linkage of characters. *A/Pw* coding also suffered from this problem but an attempt was made to control the problem. *Multistate* coding suffered from the subjectivity of the original character construction, the lack of testing of the homology assumptions and other problems pointed out by Pleijel (1995). So, while essentially an arbitrary decision, the *A/Pwr* analysis was deemed to be the best solution. The consensus tree derived from

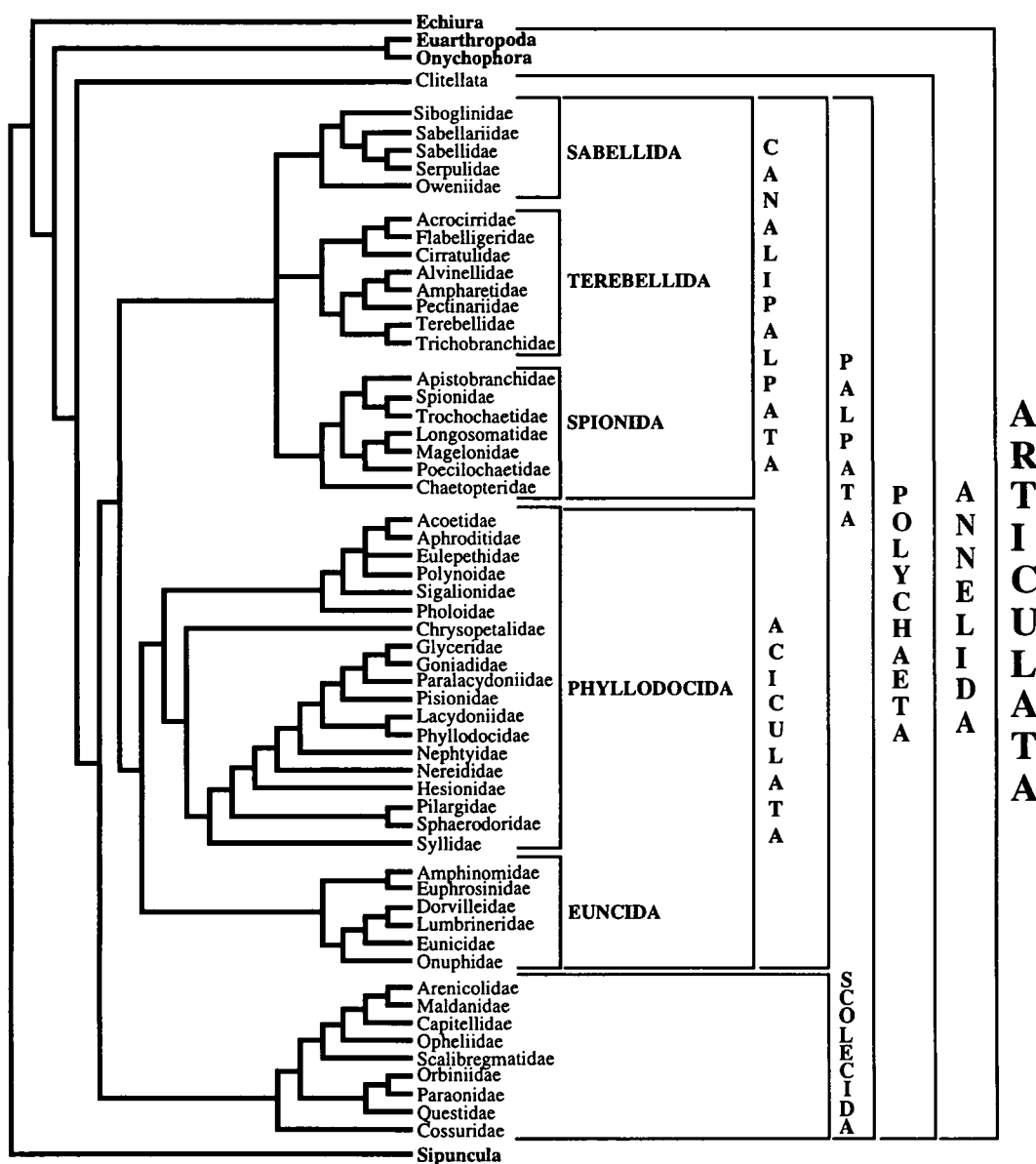


FIG. 2. Basic classification of the taxa used by Rouse and Fauchald (1997). The 29 annelid taxa excluded from this tree were placed within clade names shown here based on a more inclusive analysis and arguments in the text (see Table 1 for the classification of excluded taxa). Note the Pogonophora (and Vestimentifera) are now referred to by the name Siboglinidae and this family is a member of the Sabellida.

this analysis is shown in Figure 2 and shows the major clade names.

The Polychaeta was divided into the clades Palpata and Scolecida. The Palpata was divided into the Aciculata and Canali-palpata. The Aciculata was a strongly supported clade and the name refers to one of

the synapomorphies for the group, the presence of aciculae. The Canali-palpata was not strongly supported but the name refers to one of the group's synapomorphies, the presence of grooved palps. The Aciculata was divided into the clades Phyllococida and Eunicida. These are names that are cur-

TABLE 1. *Classification of polychaete families.**

Polychaeta
Scolecida
Arenicolidae, Capitellidae, Maldanidae, Opheliidae, Orbinidae, Paraonidae, Questidae, Scalibregmatidae
Palpata
Aciculata
Eunicida
Amphinomidae, Dorvilleidae, Eunicidae, Euphrosinidae, Hartmaniellidae, Histriobdellidae, Lumbrineridae, Oeonidae, Onuphidae
Phyllodocida
Acoetidae, Alciopidae, Aphroditidae, Chrysopetalidae, Eulepethidae, Glyceridae, Goniadidae, Hesionidae, Ichthyotomidae, Iospilidae, Lacydoniidae, Lopadorhynchidae, Myzostomatidae, Nautilienellidae, Nephtyidae, Nereididae, Paralacydoniidae, Pholoidae, Phyllodocidae, Pilargidae, Pisionidae, Polynoidae, Pontodoridae, Sigalionidae, Sphaerodoridae, Syllidae, Typhloscolecidae, Tomopteridae
Aciculata, <i>incertae cedis</i>
Aberrantidae, Nerillidae, Spintheridae
Canalipalpata
Sabellida
Oweniidae, Siboglinidae, Sabellidae, Sabellariidae, Serpulidae
Spionida
Aristobranchidae, Chaetopteridae, Longosomatidae, Magelonidae, Poecilochaetidae, Spionidae, Trochochaetidae, Uncispionidae
Terebellida
Acrocirridae, Alvinellidae, Ampharetidae, Cirratulidae, Ctenodrilidae, Fauveliopsidae, Flabelligeridae, Pectinariidae, Poeobiidae, Sternaspidae, Terebellidae, Trichobranchidae
Canalipalpata, <i>incertae cedis</i>
Polygordiidae, Protodrilidae, Protodriloididae, Saccocirridae
Polychaeta <i>incertae cedis</i> :
Aeolosomatidae, Potamodrilidae, Parerogodrilidae, Psammodrilidae

* Note that families are listed in alphabetical order under clade names and further details about relationships within major clades are available in Rouse and Fauchald (1997).

rently in common use (see Fauchald and Rouse, 1997), though the formulation of the Eunicida by Rouse and Fauchald (1997) included the Amphinomidae and Euphrosinidae. The Canalipalpata has three major clades whose relationships were unresolved using the *A/Pwr* analysis. They were given the names Sabellida, Spionida and Terebellida. These are names also currently in use. The formulation of the Spionida is similar to current usage but the other two names have somewhat radical memberships. The Sabellida was formulated to include the Siboglinidae (=Pogonophora) and Oweniidae. The Terebellida included the five families usually associated with the name but additionally the taxa Acrocirridae, Flabelligeridae and Cirratulidae. Most of the 29 families that were excluded from the restricted analyses can be easily placed in the above classification (see Table 1). The families that were proposed to be paraphyletic generally have their excluded members placed in close proximity *e.g.*, Ctenodrilidae

with Cirratulidae; Poeobiidae and Fauveliopsidae with the Flabelligeridae.

THE DIRECTION OF EVOLUTION WITHIN THE POLYCHAETA

Westheide (1997) and Westheide and Purschke (*in* Westheide *et al.*, 1999) have adopted a different approach to Rouse and Fauchald (1997) in their assessment of annelid relationships (see also Giangrande and Gambi, 1998). This involves the use of a procedure in which characters are evaluated on the basis of functional considerations, such as habitat, body size and reproductive biology. The justification is that such consideration allows the construction of scenarios of phylogeny and of ancestral "species." This approach results in a phylogenetic hypothesis (Fig. 3) that considers oligochaetes and leeches as derived polychaetes and that provides an elaborate scenario about the ancestral annelid.

The argument by Westheide (1997) and Westheide and Purschke (*in* Westheide *et*

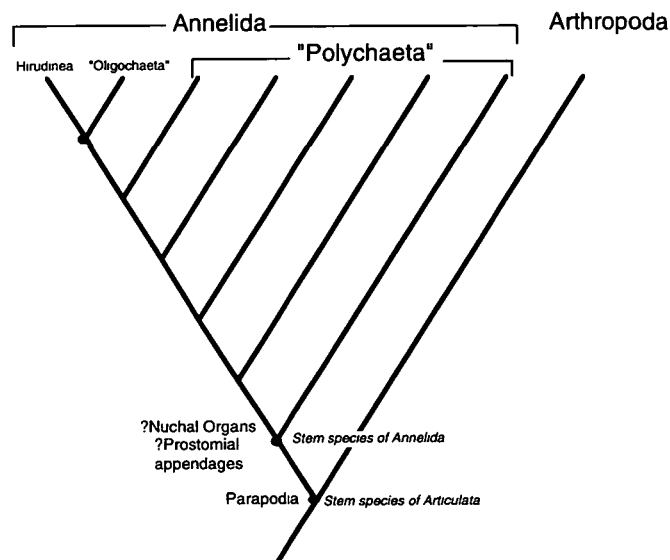


FIG. 3. Phylogenetic relationships within the Articulata according to Westheide (1997). This hypothesis involves an elaborate scenario about annelid evolution which is outlined in the text.

al., 1999) to establish that the plesiomorphic annelid had elaborate parapodia is based on the origin and primary functional significance of septa. They suggest that septa, the fundamental elements in segmentation, are primarily the prerequisite for the existence of blood vessels that run transversely. In order for transversely running vessels to be formed in an elongate organism, the coelom must be subdivided into pairs of spaces in such a way as to produce double layers of epithelia, with the basal matrices facing one another. Westheide (1997) speculated that serially arranged transversely running blood vessels became necessary to supply correspondingly serially arranged external appendages on both sides of the body, which could be the precursors of parapodia. The formation of septa, and hence segmentation, would thus be directly correlated with the development of parapodia, and parapodia with chaetae would be part of the basic body plan of the Annelida (or the Articulata). Their reasoning also places particular emphasis on the demonstration that the clitellate annelids are a highly evolved taxon in the Annelida. They argue that the Clitellata must be inferred, on the basis of functional considerations, to have arisen not in the marine but in the terrestrial habitat.

Westheide (1997) and Westheide and Purschke (*in Westheide et al.*, 1999) do not, however, identify the sister group for the Clitellata within the Polychaeta.

Thus, Westheide and Purschke (*in Westheide et al.*, 1999) postulate the following characters for the "basic annelid body plan": biphasic life cycle with planktonic trochophore larva and benthic adult stage, adult with (1) homonomous segmentation, (2) biramous parapodia with numerous chaetae, (3) dorsal bristles with a protective function, (4) gonads in all segments, (5) metanephridia, (6) prostomium with paired palps and presumably three antennae, (7) nuchal organs, (8) simple ciliated foregut (dorsolateral folds), at least in the juvenile stages, (9) collagen cuticle, (10) epibenthic mode of life. This hypothetical organism would currently fall within the clade Phyllococida.

CONCLUSIONS

The studies by Rouse and Fauchald (1995, 1997) represent the first attempt to analyze the currently available morphological data on annelids in a synthetic manner. Previous attempts at polychaete classification (reviewed in Fauchald and Rouse, 1997) have been based on a relatively small

selection of the available evidence. While the analyses by Rouse and Fauchald (1997) suffer from the flaws of incomplete knowledge about taxa and problems with coding of data they arguably represent a considerable advance in polychaete systematics. Rouse and Fauchald (1997) deliberately avoided all reference to hypothetical ancestors or hypotheses about the evolution of annelids or polychaetes. The reason for this lies in the argument that evolutionary history of a feature can be inferred after all homology hypotheses have been rigorously assessed, in both a primary sense, and then in the context of congruence with other data in a parsimony analysis (Pinna *et al.*, 1991). To introduce any evolutionary scenarios (*e.g.*, Westheide, 1997, as described above) and ordering of character states is to add additional assumptions that cannot be adequately assessed. There is currently no morphological evidence to suggest possible sister groups for the Clitellata or Echiura among the extant Polychaeta, though recent molecular sequence data does suggest placement of each group within the Polychaeta (McHugh, 1997; Kojima, 1998), admittedly with no real accuracy. The methodology for inferring phylogeny seen in Westheide (1997) and Westheide and Purschke (*in* Westheide *et al.*, 1999) involves the development of elaborate scenarios of hypothetical ancestors. While they may state that this is a Hennigian procedure (the reader can decide whether this is in fact the case) it does involve many assumptions and lacks elements of repeatability.

The conflict between the molecular sequence data analyses published to date (*e.g.*, McHugh, 1997; Kojima, 1998) and the morphological analyses by Rouse and Fauchald (1997), in terms of the placement of the Clitellata and Echiura, could be caused by several factors. One possibility is that the Echiura and Clitellata have lost a number of morphological features that would help identify their sister group within the Polychaeta. Further morphological study may uncover these "losses." However, the molecular sequence data sets assembled to date have been marked by both a limited number of taxa and characters (McHugh, 1997; Kojima, 1998). The

use of molecular sequence data is by no means simple and issues such as the deletion of, for instance, third base positions, or transition/transversion weighting are hotly debated. Also, the use of tree building algorithms such as neighbour-joining and maximum likelihood, in addition to maximum parsimony are controversial (Swofford *et al.*, 1996; Kluge, 1997; Siddall and Kluge, 1997). It is interesting to note that Kojima (1998) and McHugh (1997) used the same gene Elongation factor 1-alpha, but different taxon sampling, and came to conflicting conclusions concerning the "ancestral annelid." McHugh (1997) stated that her results supported the view that ancestral condition of annelids was morphologically similar to some extant epifaunal polychaete groups and contradicted the view that the ancestral annelid was a burrowing form (Fauchald, 1974). Kojima (1998) on the other hand appears to support Fauchald's (1974) hypothesis. Clearly molecular sequence data is no panacea, rather comprehensive taxon sampling and extensive data sets (with the use of molecular sequence data as well as detailed morphological studies) should be regarded as essential to resolving questions about annelid relationships. There are serious issues involved in combining morphological and molecular data (De Queiroz *et al.*, 1995; Kluge, 1997) but this is arguably a productive approach and there is much to be done.

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