



The articulation of annelids

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The aim of this paper is to assess the monophyly of the Annelida. Also, recent cladistic analyses of metazoan taxa, using a variety of data, have shown incongruities with regards to annelids and associated taxa that should be resolved. The Platyhelminthes is selected as the taxon to root our minimal length trees and polarise our characters in a parsimony analysis; ingroup taxa being Mollusca, Nemertea, Sipuncula, Echiura, Pogonophora, Vestimentifera, Euarthropoda, Onychophora, and the groups most commonly regarded as true 'annelids', the Clitellata and Polychaeta. We use 13 characters and a total of 33 states. This results in 18 minimal length trees of 23 steps. The consensus tree has the topology (Platyhelminthes (Nemertea (Sipuncula Mollusca (Echiura (Polychaeta (Vestimentifera Pogonophora) Clitellata (Euarthropoda Onychophora)))))). The name Articulata is applied to the Clitellata, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera. The Vestimentifera is the sister group to, or more likely a clade within, the frenalate pogonophores, and the name Pogonophora is retained for this group. 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. The name Annelida should not be used unless relationships within the Articulata are resolved to show it is a monophyletic taxon. The taxon name Articulata, originally formulated to include the Annelida and Arthropoda by Cuvier, is defined as the clade stemming from the first ancestor to show repetition of homologous body structures derived by teloblastic growth with a pygidial growth zone (segmentation) and longitudinal muscles broken into bands. The Articulata is considered, on current evidence, to consist of four monophyletic groups; the Arthropoda, Clitellata, Polychaeta, and Pogonophora, though the latter group may be a clade of polychaetes. If this is shown, the Pogonophora should revert to the original family name Lamellisabellidae Uschakov, 1933. An indented classification reflective of the cladistic pattern is provided. Other recent hypotheses about metazoan systematics are analysed.

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'When I use a word,' Humpty Dumpty said in rather a scornful tone, 'it means just what I choose it to mean — neither more nor less.' 'The question is,' said Alice, 'whether you *can* make words mean so many different things.' (Carroll 1872: 124).

The phylum Annelida to which the Polychaeta and several other groups of worms belong, is difficult to classify into classes and orders (Day 1967: 19).

The evolutionary relationships between the annelid classes are relatively clear in outline, although the detailed phylogeny of these worms presents little more than a series of unsolved, and probably insoluble problems (Clark 1969: 44).

Introduction

The use of cladistic methodology has recently been applied to questions about the phylogenetic relationships among metazoan taxa, using morphology (Brusca & Brusca 1990; Schram 1991; Eernisse *et al.* 1992; Backeljau *et al.* 1993; Scheltema 1993; Schram & Ellis 1994), molecular sequence data (Turbeville *et al.* 1992; Halanych *et al.* 1995; Winnepenninckx *et al.* 1995), or combined data sets (Wheeler *et al.* 1993). While the use of methods with

repeatable results is long overdue in metazoan systematics, these papers have relied on morphological information, phylogenetic hypotheses, and a taxonomic system developed over more than 150 years. This has contributed to distinct problems in these recent papers. Some of the problem areas can be identified as:

1. Unquestioned assumptions of homology (or non-homology) often influenced by varying traditions in usage of morphological names (i.e. terminology influence);
2. Lack of consideration for character independence;
3. Unquestioned assumptions of monophyly by basing analyses on a given Linnean taxonomic level (e.g. class, phylum);
4. Errors in scoring (Schram 1991, see Backeljau *et al.* 1993; Eernisse *et al.* 1992).

Examples of each these types of errors will be discussed in this paper. While the consequences of these problems may have led to dubious conclusions, the data used by the authors cited above are available, allowing the opportunity for further analysis. Interestingly, while trees with differing topologies have been presented (compare Eernisse *et al.* 1992 with Wheeler *et al.* 1993), few, if any, suggestions of changes in classification have been made.

As an example of the current flux in ideas about metazoan relationships, the placement of the Annelida is illustrative. Brusca & Brusca (1990) suggested the following topology; (Arthropoda (Annelida (Pogonophora Vestimentifera))), though they could not identify a synapomorphy for the Annelida. Schram (1991) suggested that the Pogonophora were the sister group to the Arthropoda (= Onychophora and Euarthropoda) and this clade was the sister group to the Annelida, though the methods and conclusions have been criticised (Eernisse *et al.* 1992; Backeljau *et al.* 1993; but see Schram & Ellis 1994). Eernisse *et al.* (1992) proposed that the Annelida was the sister group to the Pogonophora and that this clade was the sister group to the Mollusca. They found that a clade consisting of the Onychophora, Kinorhyncha, Tardigrada, and Euarthropoda was the sister group to the Nematoda, with previously proposed synapomorphies for arthropods and annelids being homoplasies. Wheeler *et al.* (1993) found the Euarthropoda and Onychophora to be the sister group to the Annelida, whilst using the Mollusca to root their trees; a hypothesis that is certainly most commonly favoured among metazoan systematists (see reviews in Eernisse *et al.* 1992; Wheeler *et al.* 1993). Schram & Ellis (1994), in re-analysing and correcting Schram's (1991) data, show the following topology; (Pogonophora (Annelida (Mollusca (Sipuncula Echiura))). The 'arthropods' are then the sister group to this clade. The cladistic hypotheses of Brusca & Brusca (1990), Eernisse *et al.* (1992), Wheeler *et al.* (1993), and Schram & Ellis (1994) will be assessed in the discussion.

Through most of this century, the Annelida has been split into two main groups; polychaetes and clitellates, with myzostomids being given class status by some workers (e.g. Jägersten 1940; Prenant 1959), or that of a family within the Polychaeta (Hartman 1969; Schroeder & Hermans 1975; Pettibone 1982). In addition, several small groups have been regarded as families with uncertain affinities within the Annelida, or 'associated' with the Annelida. Virtually all opinions about the classification of annelids, with the exception of clitellates (e.g. Brinkhurst & Nemecek 1987; Jamieson 1988a), have been based either on pre-evolutionary notions, evolutionary systematics (see Mayr 1969), or merely a philosophy of using classifications as identificatory systems only.

This paper is the first in a two part exercise. In a forthcoming analysis, we examine the relationships amongst the families of the Polychaeta (Fauchald & Rouse in prep.; Rouse & Fauchald in prep.). However, no synapomorphy for the members of the taxon Polychaeta has been demonstrated, and determining ingroup and outgroup taxa for an assessment of relationships within this group is difficult. Thus, we were obliged to consider a possibly paraphyletic Polychaeta in relation to the Clitellata and the Myzostomida. This then led us to the issue of the monophyly of the Annelida itself and to assess the relationship of taxa usually associated with annelids; the Pogonophora, Vestimentifera (Gardiner & Jones 1993; Southward 1993), and Arthropoda (Wheeler *et al.* 1993). This raised the issue of outgroup considerations for the assemblage, and to perform a relatively 'coarse' analysis of the relationships among the major protostome groups. With an appropriate outgroup estab-

lished, we then intend to assess the relationship amongst polychaete taxa (using the 'family' level), the Clitellata, Pogonophora, Vestimentifera, and Arthropoda (Fauchald & Rouse in prep.; Rouse & Fauchald in prep.).

This paper is structured such that we provide a justification for the selection of taxa and characters used. Thirteen morphological characters were used for a cladistic parsimony analysis of the following taxa: Clitellata, Euarthropoda, Nemertea, Mollusca, Sipuncula, Echiura, Platyhelminthes, Pogonophora, Polychaeta, Onychophora, and Vestimentifera. The resulting trees and transformation series are discussed, and the implications for the monophyly of various taxa are assessed. We then present a naming system more reflective of the cladistic pattern. Finally, we assess some recent hypotheses on the systematic position of annelids and associated taxa.

Methods

Taxa included in the analysis

Major taxa considered in this analysis show spiral cleavage, mouth opening from the blastopore, and with mesoderm almost always derived from the 4d micromere, or are considered as having a modification of these features. The ingroup taxa comprise organisms most usually viewed as protostomes: Nemertea, Mollusca, Sipuncula, Echiura, Polychaeta, Pogonophora, Vestimentifera, Clitellata, Onychophora, and Euarthropoda. The outgroup is the Platyhelminthes.

Platyhelminthes. Three groups, the free-living 'turbellarians', the parasitic trematodes, and the cestodes have traditionally been considered platyhelminths. Recent schemes have considerably revised their relationships and taxonomic status. For example, the Turbellaria is no longer regarded as a monophyletic taxon (Ehlers 1985a, b). Trematodes and cestodes, usually considered separate classes, have features presumed to be related to their parasitic existence (Hyman 1940; Noble & Noble 1971; Brusca & Brusca 1990), and are now considered derived platyhelminth taxa (Ehlers 1985a, b). Platyhelminth monophyly has been questioned (Smith *et al.* 1985), and relations within the group as well as with other groups are still under debate (Ax 1985; Ehlers 1985a, b; Rieger 1985; Smith & Tyler 1985). A synapomorphy proposed by Ehlers for the Platyhelminthes is the absence of mitosis in differentiated epidermal and somatic cells. For the purposes of this study, the Platyhelminthes serves as an outgroup on the basis of the lack of a complete digestive system and absence of a coelom. Scoring for the taxon is based on the 'turbellarian' grade (Ehlers 1985a, b).

Onychophora and Euarthropoda (= Arthropoda). One of only two non-vertebrate classes used by Linné (1758), the Insecta was divided into seven classes, six of which contained insects only. The seventh, Insecta Aptera, included wingless insects, crustaceans, arachnids, and myriapods (Linné 1758: 344). Cuvier (1812: 73) recognized the Articulata as a distinct 'embranchement' among animals. The group was diagnosed by the presence of segments, a circumoesophageal nerve ring, and a double ventral nerve chord with ganglia (Cuvier 1817: 509–510). The Articulata included four classes; annelids, crustaceans, arachnids, and insects, with no hierarchical arrangement amongst them. Von Siebold (1848) fused the three non-annelid articulate classes, Crustacea, Arachnida, and Insecta into a single group and gave this assemblage the name Arthropoda. This corresponded to the Insecta of Linné (1758) and Lamarck's (1815: 457) diagram showing the insects, arachnids and crustaceans (including barnacles) as a separate lineage from the annelids. Siebold (1848) did not refer to the Articulata, and in fact resurrected the Linnean concept of Vermes by placing annelids with other worm-like groups. Grube (1850) erected the Onychophora, containing *Peripatus*, as an order of the Annelida. The validity of the taxon Arthropoda has been debated since soon after its diagnosis by Siebold (1848), initially due to arguments about the placement of the Onychophora (see Tiegs & Manton 1958 for a review). More recently, arguments that the Arthropoda is polyphyletic and should be split into the Uniramia, Chelicerata, and Crustacea have been presented (Tiegs & Manton 1958; Manton 1964, 1977; Anderson 1973; Manton & Anderson 1979) and rejected (Weygoldt 1979; Wheeler *et al.* 1993).

We consider here the Onychophora to be the sister group to the

usually accepted 'arthropods' (Euarthropoda), and evidence concerning the monophyly of these taxa can be found in Brusca & Brusca (1990) and Wheeler *et al.* (1993). A suggestion by Ballard *et al.* (1992), based on 12S rRNA sequence data, that the Onychophora are not the sister group to the Euarthropoda but fall within this clade has been criticised (Wägele & Stanjek 1995). While recent studies using both molecular sequence and morphological data have supported the monophyly of the Arthropoda, the number of taxa from within the supposed sister group, the annelids, has been surprisingly small (Ballard *et al.* 1992; Eernisse *et al.* 1992; Wheeler *et al.* 1993). The assumption in these analyses appears to have been that the Annelida is monophyletic and that a single species of polychaete and one or two clitellates is adequate to represent the 'clade'. We perceive that this bias is due, in part, to the recent stable taxonomic status of 'class' for the polychaetes. In reality, polychaetes are a diverse group that has yet to be shown to be monophyletic, and may yet be shown to include such 'high-level taxa' as the clitellates and arthropods. In our opinion, the limited number of annelid taxa studied in molecular studies to date leaves the monophyly of the Annelida open to question.

The status of the Onychophora and euarthropods has important implications for the question 'what is an annelid?' Assuming arthropods are monophyletic, their relationship with annelids can be one of three possibilities: (1) They could be the sister group to the Annelida. This is a common hypothesis, and the name Articulata is often used for the group (see Eernisse *et al.* 1992); (2) Alternatively, arthropods may not be the sister group, or even closely related, to the Annelida (see Eernisse *et al.* 1992; Halanych *et al.* 1995; Winnepenninckx *et al.* 1995); (3) The third possibility is that arthropods have a sister group within the Annelida. Previous explicit formulations in regard to option (3) have been presented by Anderson (1973), Sawyer (1984, 1986) and Jamieson (1986, 1987a). All three authors accepted the possibility of arthropod polyphyly and discussed the annelids mainly with reference to the Uniramia, proposing a (Clitellata+Uniramia) relationship. Sawyer (1984, 1986) was more explicit and proposed that the Uniramia are the sister group to the Hirudinea, though many of his arguments are *ad hoc*. Jamieson (1986) reviewed the evidence and presented arguments, largely based on sperm ultrastructure and embryology, for a ((Clitellata Onychophora) (Myriapoda Hexapoda)) hypothesis (see below, Character 13). Jamieson (1987a) also discussed other hypotheses with regard to the Annelida (= Polychaeta and Clitellata) and Uniramia being monophyletic or paraphyletic. These will be assessed in the light of our results (see Discussion).

We have included both the Onychophora and the Euarthropoda in our analysis. The apomorphies supporting the monophyly of the Onychophora and Euarthropoda, respectively, are extensive (Wheeler *et al.* 1993). The Onychophora are usually considered to be the most plesiomorphic arthropod clade (Wheeler *et al.* 1993) and show many features that are 'annelid'-like (Brusca & Brusca 1990: 668). Including the Onychophora and Euarthropoda does present some problems using our character set. For instance, among arthropods, only a few crustaceans show any elements of spiral cleavage, and no arthropod can be said to derive mesoderm from the 4d micromere (Anderson 1973). Also, their cuticle structure and circulatory system are markedly different from other taxa in the analysis. This has resulted in the Onychophora and Euarthropoda being given unique states for characters 1, 8, and 12 (see below). However, for most characters, we could score the onychophorans and euarthropods on homology assessments that did not require additional 'arthropod' states. As Wheeler *et al.* (1993: 3) state in supporting arguments against the polyphyletic origin of arthropods: 'degree of apomorphy is no argument against homology (Hennig 1966), it may simply be that a great deal has happened since the taxa diverged'.

Clitellata. The Clitellata is considered monophyletic based on the common presence of a clitellum, the organisation of the reproductive system, and sperm ultrastructure (Michaelsen 1928; Jamieson 1981; Ferraguti 1984; Sawyer 1984; Purschke *et al.* 1993). The clitellates are most often divided into two groups; the Oligochaeta and Hirudinea, and are considered as subclasses or classes (Brusca & Brusca 1990: 387). The Hirudinea (leeches) are considered by some to be a monophyletic taxon comprised of true leeches, branchiobdellids, and acanthobdellids (Sawyer 1986; Brusca & Brusca 1990: 388). Others suggest these three groups are not exclusive sister taxa (Brinkhurst & Gelder 1989; Holt 1989). Purschke *et al.* (1993) summarised the evidence for considering all three leech groups as clitellates, but concluded that while the acanthobdellids and true leeches ('Euhirudinea') are sister taxa, the branchiobdellids very likely evolved independently from a different 'oligochaete' ancestor, so that the similarities between these and the true leeches represent convergences. The problem is irrelevant in the current context as all authors agree that the leech-like taxa and the 'oligochaetes' belong to the same monophyletic taxon, the Clitellata.

The Oligochaeta is paraphyletic if the Hirudinea (or the three leech-like groups) are the sister group to one clade or another within the oligochaetes, as seems to be the prevailing opinion (Michaelsen 1928;

Brinkhurst & Nemec 1987; Erséus 1987; Jamieson *et al.* 1987; Jamieson 1988a). When a specific sister group to the Hirudinea is agreed upon, they will lose their high taxonomic rank. The taxon name for the clade including the leeches could reasonably be the Oligochaeta or Clitellata; the former is suggested by Jamieson *et al.* (1987). However, even though Oligochaeta is an older name (Grube 1850) than Clitellata (Michaelsen 1928), the latter was explicitly formulated to include the Hirudinea, and hence follows the priority principle for phylogenetic taxon names of de Queiroz & Gauthier (1990, 1992).

The Clitellata, when first erected by Michaelsen (1928), included acolosomatids, hirudineans, and oligochaetes. The former are no longer considered members of the Clitellata (e.g. Bunke 1988 and references therein, see also below). The name Euclitellata was coined by Jamieson (1983) for the clitellates after studying the anatomy of questid polychaetes. He concluded that there is no homology between the clitellum of questids and that of clitellates, but that the latter should have a new name. We prefer to retain the name Clitellata for this group since it is older and is essentially the same taxon concept. No particular group of polychaetes has been identified as a sister group to the Clitellata. The acolosomatids, and the morphologically similar potamodrilids, are discussed below.

Echiura. The echiurids were originally considered members of the same group as the annelids (Cuvier 1817; Lamarck 1818). They were grouped with the sipunculids and priapulids in the Gephyrea by Quatrefages (1847), a group subsequently eliminated by Sedgewick (1898). Sedgewick considered echiurids as a group of annelids but Newby (1940) proposed a separate phylum, Echiura, based on a detailed embryological study of *Urechis caupo*. His proposal has been generally accepted (Stephen & Edmonds 1972: 343).

Echiurids are triploblastic, coelomate metazoans; the digestive tract is straight; segmentation is regarded as absent (Newby 1940). Two apomorphies identifying the Echiura are the flattened or grooved proboscis, formed from the prostomium, and the presence of anal sacs (see Pilger 1993 for a review).

Mollusca. While Linné (1758) included molluscs in at least three of his subgroups of Vermes, Cuvier (1795a, b) and Lamarck (1801) separated molluscs from worms. Most members of the Mollusca were 'correctly' placed by Cuvier; however, he also included various other groups such as brachiopods, barnacles, serpulid polychaetes, and tunicates that we do not accept today. The recognition of serpulids as polychaetes was fully acknowledged after the middle of the 19th century (Mörch 1863). Molluscs are triploblastic spiralians; their plesiomorphic coelomate condition appears to be established (Reynolds *et al.* 1993; Morse & Reynolds in press). At least one group, the monoplacophorans, has serially repeated organs but other molluscan taxa do not show these features (Brusca & Brusca 1990), and segmentation or serial repetition does not appear to be plesiomorphic for the clade. A mantle and radula are present in most, but not all, molluscs; the radula, for example, is absent in the Bivalvia, but otherwise these structures are synapomorphies for the clade (see Eernisse *et al.* 1992).

Nemertea. Nemertean are coelomate and triploblastic with spiral cleavage. The coelom is limited to the rhynchocoel and circulatory system (Turbeville 1986). Nemertean are regarded as unsegmented, though serial repetition of gonads can occur (Brusca & Brusca 1990). When included at all, recent morphological analyses have placed the Nemertea as the sister group to the clade that includes the Mollusca and Annelida (Brusca & Brusca 1990; Schram 1991; Eernisse *et al.* 1992). Turbeville *et al.* (1992), using 18S rRNA data, found nemerteans to be a member of the clade including molluscs, sipunculids, and annelids, but could not reliably resolve relationships among these groups.

Pogonophora. The Pogonophora (and Vestimentifera) are of some significance in the history of metazoan classification. The various controversies surrounding the systematic placement and taxonomic status of these organisms can be linked to a combination of incomplete observations and differing philosophies, and continues to this date (Southward 1993; Gardiner & Jones 1993; Ivanov 1994).

Caullery (1914a, b, 1948) described *Siboglinum weberi* as a new kind of invertebrate because of its lack of a digestive tract, though he felt that the tube bore some resemblance to that of the hemichordate *Rhabdopleura*. Caullery also compared the anterior region of the body to that of *Balanoglossus*, another hemichordate. Uschakov (1933) described a similar species, *Lamellisabella zachsi*, as an aberrant sabellid polychaete in a new sub-family, Lamellisabellidae (*sic*). Johansson (1937, 1939) placed *Lamellisabella* in a separate class, Pogonophora (first spelled Pogonofora), but not placed in any phylum, based on extensive investigations of Uschakov's material of *L. zachsi*. Uschakov (1940) followed Johansson's (1937) suggestion in accepting the non-polychaete affinities

of the taxon. Note that neither author considered *Siboglinum*. Dawydoff (1948) regarded *Siboglinum* as related to the hemichordates, based on statements made by Caullery (1914a, b, 1948), but did not seem to be aware of the Pogonophora, despite the elevation of this taxon to phylum rank by Beklemishev (1944). Pearce (1949) listed the Pogonophora, apparently with reference to *Lamellisabella* only, as a separate phylum among the deuterostomes, and Ulrich (1950) independently came to a similar conclusion, placing the Pogonophora as one of five Stämme (= phyla) within the taxon Archicoelomata, containing also the lophophorates, chaetognaths, enteropneusts, and echinoderms. Interestingly, Ulrich appeared unaware of *Siboglinum*; he compared *Lamellisabella* to various terebellomorph polychaetes and accepted the similarities in reduction of septa and in the development of anterior nephridia. Despite these similarities, he concluded that *Lamellisabella* could not be a polychaete, since it lacked a ventral nerve cord, a circumoesophageal connective, and had nothing that resembled true metamerism (Ulrich 1950). He recognised that the mouth and anus were unknown (Ulrich 1950: 5 and 7), but assumed that a digestive tract was present (Ulrich 1950: 10).

Ivanov (1951) compared *Siboglinum* and *Lamellisabella* and was the first to recognise that the two genera must belong to the same taxon, the Pogonophora. Ivanov (1954) described several new pogonophores and placed the group 'between' the enteropneusts and pterobranchs. Subsequently, he reiterated that pogonophores were deuterostomes and gave them a new name Brachiata, with the status of phylum (Ivanov 1955). Hartman (1951, 1954) reviewed the taxonomic history of pogonophores and argued against a deuterostome relationship, suggesting that the group might be a polyphyletic assemblage from various polychaete groups such as the Sabellidae, Ampharetidae, and Terebellidae. Ivanov (1956) and Jägersten (1956) rejected her statements, emphasising the similarities among pogonophores and their supposed deuterostome affiliation. Ivanov (1956) denied the homology of the 'platelets' in pogonophores with the uncini of some polychaetes, arguing (erroneously, see George & Southward 1973) that uncini develop differently, and platelets were analogues brought about by a similar, tubicolous lifestyle. Jägersten (1956) accepted platelets as homologous with chaetae, but used the similar structure of brachiopod chaetae to argue for a previous wide distribution of chaetae in the Metazoa, presumably with subsequent losses in other taxa. Interestingly, Jägersten (1956) regarded the pogonophoran nervous system as including a ventral double cord, in contrast to Ivanov (1959) who argued that the entire system was dorsal and single.

Jägersten (1956) alluded to the likelihood that pogonophores studied to that date were incomplete. Webb (1964a, b) demonstrated that this was the case, and described the hitherto missing posterior end of *Siboglinum ekmani* and *S. fiordicum*, the opisthosoma. He described the posterior end as having superficial segmentation with chaetae arranged in longitudinal rows. After this discovery, further debate on the systematic position of the pogonophores ensued. Some authors felt they were deuterostomes and hence embryos had radial cleavage, the nerve cord was dorsal, and the body was tripartite, composed of protosoma, mesosoma, and metasoma (Ivanov 1970, 1975a, b; Johansson 1968). Alternatively, pogonophores were regarded as protostomes showing spiral cleavage, a ventral nerve cord, and metameric segmentation (Liwanow & Porfirjewa 1967; Nørrevang 1970a, b; van der Land & Nørrevang 1975). Webb (1969b) presented a hypothesis suggesting that the Polychaeta was a paraphyletic assemblage. He suggested a clade comprised of pogonophores, polychaetes such as sabellids and terebellids, along with the 'lophophorates' and hemichordates. This clade was then the sister group to remaining polychaetes. Orrhage (1973b) refuted Webb's (1969b) hypothesis but did not discuss the systematic position of the Pogonophora.

Many pogonophores brood larvae, and development has been described for several species. The species that brood larvae have large yolky eggs and the early cleavage patterns have been interpreted both as 'modified' radial cleavage (Ivanov 1975a, b), or 'modified' spiral cleavage (Nørrevang 1970a, b; Bakke 1975, 1976, 1980, 1990). Annelid embryos with a large yolk content often have cleavage patterns that are not obviously spiral (Anderson 1973); the argument that pogonophores have radial cleavage may have been an interpretation based on expectation. The lecithotrophic pogonophoran larva, with its dense endodermal mass (Southward 1980) and two rings of cilia is now usually interpreted as a modified form of 'trochophore' (Southward 1988; Bakke 1990; see also Nielsen 1987 for interpretation of ciliary bands in larvae).

Traditional metazoan dorso-ventral orientation generally follows from the positional relationship between the digestive tract and nervous system. Normally, 'annelids' have a dorsal brain (or cephalic ganglion) connected by a circumoesophageal ring to a double ventral nerve cord (Dales 1963). Deuterostomes have a single nerve cord located dorsal to the digestive tract (Brusca & Brusca 1990). The absence of an obvious gut, the intraepidermal position of the nerve cord, and degree of fusion

along the length of the cord allowed some workers to interpret the nerve cord in pogonophores as being dorsal and single (Beklemishev 1944; Ivanov 1956, 1959, 1963). However, clear drawings by Ivanov (1959), suggesting an anterior ring-like nerve cord configuration and the double nature of the cord in some parts of the body, contradict this observation. In *Siboglinum ekmani*, Jägersten (1956: 225) also noted that the anteriormost part of the nerve cord is double, and fuses in the middle of the mesosoma. Jägersten concluded that the nerve cord is ventral. A strand of tissue running through the brain of pogonophores was first illustrated by Caullery (1914a, b), confirmed by Jägersten (1956: 224), and illustrated by Ivanov (1960, copied as Fig. 11 in Johansson 1968). This strand of tissue running anteriorly through the brain, representing the remnants of a gut (see below), certainly suggested the possible presence of a circumoesophageal ring. Recent studies of larval development also indicate that the nerve cord is in fact ventral (Southward 1988, 1993).

As noted above, pogonophores were often interpreted as being tripartite or oligomeric, i.e. having three distinct body regions or 'segments' (see review by Webb 1969b). The reason for this emphasis lies in a long tradition of interpreting the hemichordate body as consisting of three segments (summarised in Hyman 1959); these segments were found also in echinoderm larvae (Gislén 1930), and were demonstrated to be present in phoronids (Zimmer 1980). After the discovery of the missing posterior end of pogonophores, Webb (1964a, c, d) concluded that, while the segmented opisthosoma made the body appear polymeric, pogonophores were in fact still oligomeric; the opisthosoma was the metasoma with superficial segmentation. He regarded what had previously been called the metasoma as a second region of the mesosoma containing gonads. Ivanov (1964, 1965) found the previously 'missing' posterior end but regarded it as the end of the metasoma with secondary segmentation. Johansson (1968: 8) accepted Webb's new interpretation; yielding a short protosoma, a very long mesosoma, divided into agonadal and gonadal regions, and a short, segmented opisthosoma (= metasoma). He also agreed with Webb that, despite the presence of the 'segmented' opisthosoma, pogonophores must be deuterostomes. Liwanow & Porfirjewa (1967) and van der Land & Nørrevang (1975) maintained that the posterior end was truly segmented, and, along with the presence of chaetae, clearly showed an annelid relationship for the Pogonophora.

The maintenance of a belief in the tripartite nature of the pogonophoran body in the face of the discovery of the segmented, chaeta-bearing, posterior end may be linked, in part, to the theory of heteronomy. In many polychaetes, for example nereidids and serpulids, the three first segments were thought to be formed simultaneously. This finding can be traced to Gravelly (1909), and was accepted and supported by polychaete workers (e.g. Segrove 1941; Schroeder & Hermans 1975) until Grant (1981) and Marsden & Anderson (1981) demonstrated that the first three pairs of chaetal sacs form sequentially in the serpulid *Galeolaria caespitosa*. Similar studies of nereidid development are warranted. Significantly, Gravelly (1909: 620) himself stated that 'the simultaneous appearance of a small number of "primary" segments is almost certainly a secondary type of development derived from a condition such as that found in *Ophryotrocha*', and he noted that in other polychaete clades, segments all form sequentially. Goodrich (1945: 126) Anderson (1959, 1973) maintained a similar view. However, the observation on nereidids and serpulids was taken to be a general condition, and the heteronomy concept developed into a theory identifying two different kinds of segmentation (Ivanov 1928; Schroeder & Hermans 1975: 164 review the history of the concept). The heteronomy theory was used to argue that the coelom originated once. An idealised series of developmental stages, from diploblastic to triploblastic to coelomate, demonstrated progressive evolution (Beklemishev 1952; Ivanov 1960 and others) with subsequent radiation of 'higher' taxa (see Ivanov 1975a: Fig. 18). The major premise of the heteronomy theory, that segmentation in annelids has two different forms, one of them homologous to the deuterostome condition, cannot be supported by more critical examination of the observations on which it was based.

At a conference on the systematic position of the Pogonophora, published in 1975 (several papers have been quoted here), the various conflicting historical viewpoints were presented. The dorso-ventral orientation of pogonophores was still unsettled, and additional confusing terminology was proposed to resolve the issue. In reality, with the discovery that all previous specimens had been incomplete by Webb (1964a, b), much of the argument about the deuterostome position of pogonophores became irrelevant. Liwanow & Porfirjewa (1967) had argued for a relationship of the Pogonophora with sedentary polychaetes. Nørrevang (1970a, b) had already concluded that pogonophores were clearly protostomes, related to annelids, after a study of the embryology of a species of *Siboglinum* and review of the evidence. Nørrevang (1970b) did maintain, however, that the Pogonophora should still be regarded as a phylum. Ivanov (1988, 1989) continued to support an isolated position for the group. Ivanov (1988) accepted that cleavage is spiral and that several other features showed similarities with

polychaetes, but he maintained that the Pogonophora are one of five coelomate 'superphyla', along with the Trochozoa, Tentaculata, Chaetognatha, and Deuterostomia.

Polychaeta. Grube (1850) erected the Appendiculata Polychaeta as an order of the Annelida, and Ashworth (1912) provides a review of the subsequent placement of, and classification within, the Polychaeta. The history of the group will be reviewed in detail elsewhere (Fauchald & Rouse in prep.). In this analysis, we assume that the Polychaeta, comprising those taxa usually regarded as such (e.g. Day 1967; Hartmann-Schröder 1971; Fauchald 1977; Pettibone 1982) is a monophyletic assemblage. Though no synapomorphy has been demonstrated for the group to date, we include in here a proposed synapomorphy; the presence of nuchal organs (Brusca & Brusca 1990; Fauchald & Rouse, pers. obs.). The issues of the monophyly of the Polychaeta, and a systematic analysis at the family level, are considered, in forthcoming papers (Fauchald & Rouse in prep.; Rouse & Fauchald in prep.).

Sipuncula. Originally considered among the Vermes Intestina by Linné (1767), the sipunculids were related to the Holothuria by both Lamarck (1816) and Cuvier (1817). Sedgewick (1898) raised the sipunculids to the level of phylum, and this has been subsequently widely accepted (Hyman 1959; Stephen & Edmonds 1972). Sipunculids are triploblastic coelomates with no segmentation (Stephen & Edmonds 1972); early larvae resemble trochophores, but may develop into elaborate teleplanic forms before settling (Rice 1981, 1988). The anterior end of the adults, the introvert, is retractable, and the digestive tract is U-shaped and attached by a set of muscles to the base of the introvert. Scheltema (1993) regarded the Sipuncula as sister group to the Mollusca. This, however, involves several *ad hoc* assumptions, and only three taxa were considered, molluscs, sipunculids, and annelids.

Vestimentifera. Webb (1969a) described a new pogonophoran species, *Lamellibrachia barhami*, from slope depths off San Diego, California. Webb assigned this new species to a new class, Afrenulata, new order, Vestimentifera, and new family, Lamellibrachiidae. He assigned all previously described pogonophores to the class Frenulata. Later, related taxa were found near geothermal vents in the eastern Pacific Ocean and elsewhere. These very large animals, vestimentiferans as they were called, were described by Jones (1981a, b). Jones (1981a) added to the classification of the Pogonophora by erecting two subphyla. The subphylum Obturata contains the class Afrenulata, and the subphylum Perviatia contains the Frenulata. Subsequently, a separate phylum was erected for the Obturata by Jones (1985b), which he called the Vestimentifera because this was the most familiar name. Jones argued that, in spite of the many similarities between the two groups, the form of the various coelomic cavities in the Vestimentifera was so different from the Pogonophora that the taxonomic status of phylum was warranted.

Most authors (but see Ivanov 1988, 1989, 1994) presently agree that the Vestimentifera and Pogonophora are protostomes related to the Annelida; based on the presence of a ventral nerve cord and circumoesophageal ring, presence of chaetae, and development of the body segments from a pygidial growth zone. Van der Land & Nørrevang (1975: 98) discussed relations among annelids, pogonophores, and vestimentiferans, and concluded that both the Pogonophora and Vestimentifera were classes of the Annelida, most closely related to the Polychaeta. They preferred to maintain these two new annelid classes as separate, even though they recognised similarities between them. Southward (1988) and Ivanov (1994) considered recognition of the phylum Vestimentifera untenable; the vestimentiferans must belong in the Pogonophora. Southward (1988) suggested that pogonophores be reduced to a class of the Annelida or be assigned to the phylum Brachiata erected by Ivanov (1955; considered a synonym of the Pogonophora by Ivanov 1963). Southward (1988) indicated that her uncertainty about placing the pogonophores was because of missing embryological evidence, though Southward (1991) considered the Pogonophora as a class, presumably of the Annelida. Based on sperm ultrastructure, Jamieson (1987b, 1988b) proposed that the Pogonophora (including vestimentiferans) may have a 'special relationship with the proto-clitellates rather than with polychaetes' (Jamieson 1988b: 424).

Recent cladistic morphological studies of members of the Metazoa have accepted the taxonomic status of the Pogonophora as a phylum when placing them as the sister group to the Annelida (Brusca & Brusca 1990: 882; Eernisse *et al.* 1992: Fig. 4), Arthropoda (Schram 1991) or an Annelida, Sipuncula, Echiura, Mollusca clade (Schram & Ellis 1994). The phylum status of vestimentiferans has either been rejected (e.g. Southward 1988, 1991; Southward & Coates 1989; Eernisse *et al.* 1992), or not considered by workers (e.g. Carey *et al.* 1989; Schram 1991). Terwilliger *et al.* (1987), using haemoglobin morphology, suggested that Vestimentifera and Annelida are most closely related to one another,

with the Pogonophora the sister group to this clade, which is consistent with Jones' (1985a) statements based on morphology and anatomy. The consequences of this suggested pattern are discussed below. Phenetic analyses of haemoglobin amino acid sequence data (Suzuki *et al.* 1989) and elongation factor-1 alpha amino acid sequence data (Kojima *et al.* 1993), and phenetic and parsimony methods on 28S rDNA (Williams *et al.* 1993) and 18S rRNA (Winnepenninckx *et al.* 1995), have suggested a close relationship of vestimentiferans and pogonophores to annelids or echiurans. However, among these molecular studies, only Kojima *et al.* (1993) and Winnepenninckx *et al.* (1995) included a range of metazoan taxa. Williams *et al.* (1993: 450) suggested that the frenulate pogonophores and the vestimentiferans 'are not particularly close' but did not comment on the possible sister-group relationships.

In the present analysis, we maintain the Vestimentifera and Pogonophora as separate taxa. The possibility that recognition of the Vestimentifera results in a paraphyletic Pogonophora seems very likely (see Discussion). What needs to be assessed is the relationship of these taxa with the 'annelids' and the implications this has for a taxonomy intended to reflect phylogenetic relationships.

Taxa excluded from the analysis

As well as major groups, certain taxa that have been assigned the status of family (e.g. Lobatocerebridae Rieger, 1980) are considered in this section because of their uncertain affinity.

Aeolosomatidae and Potamodrilidae. The aeolosomatids, long listed among the clitellates (Michaelsen 1928; Stephenson 1930; Reynolds & Cook 1976), have been excluded from that taxon (Brinkhurst 1971; see also Jamieson 1988a). Bunke (1967) removed the genus *Potamodrilus* from the Aeolosomatidae and erected the Potamodrilidae. Timm (1981), recognising the Aeolosomatidae only, created a new subclass, Aphanoncura, and new order Aeolosomatida (see also Timm 1987). This position was supported by Kasprzak (1984) and Brinkhurst & Nemecek (1987). Bunke's (1967, 1988) detailed descriptions clearly demonstrate that nuchal organs are present in both taxa. This suggests that the groups should be considered in relation to polychaetes, and their position will not be considered further in this paper.

Annelida. The status of the Annelida is briefly reviewed here to provide support for our decision to doubt the monophyly of this taxon. Lamarck (1801: 33–35) erected the group 'Animaux sans vertèbres' and separated it into seven classes; 'Mollusques', 'Crustacés', 'Arachnides', 'Insectes', 'Vers' (= Vermes, or worms), 'Radières' (echinoderms and sipunculids), and 'Polypes' (mainly coelenterates), thus separating the arthropods into three distinct groups. 'Vers' was divided into 'Vers extérieurs' and 'Vers intestins' by Lamarck (1801: 315). He used the presence or absence of 'organes extérieurs' to divide the former into two unnamed groups. Lamarck (1802, 1809) applied the name 'Annélides' to the first section of the Vers extérieurs, those with 'organes extérieurs'. The leeches were listed among the Vers extérieurs without distinct external organs. The name Annélides was derived from the Latin *annulus*, meaning a little ring, in reference to the presence of segments. Lamarck later, incorrectly, latinised Annélides to Annelida (Lamarck 1818). The correct form is Annulata and the group was periodically referred to as such (Grube 1850: 281; Malmgren 1867). However, Annelida has been the name most often used for the group, though its membership and taxonomic rank have varied (see Ashworth 1912).

As outlined in the introduction, the Annelida is now usually said to include the taxa Polychaeta and Clitellata, with the latter sometimes formulated as two separate classes, the Oligochaeta and Hirudinea (see Brusca & Brusca 1990). Interestingly, while the monophyly of the Annelida has rarely been questioned, it has also not been demonstrated convincingly. In studies identifying the taxon Articulata in cladistic terms by Ax (1984, 1987) and Weygoldt (1986), the Annelida was not identified by synapomorphy. Brusca & Brusca (1990) also did not show a synapomorphy for the members of the Annelida. As discussed above, other authors (Anderson 1973; Sawyer 1984, 1986; Jamieson 1986, 1987a) have suggested that an arthropod assemblage may have a sister group within the Annelida. With this in mind, we used the two commonly accepted groups of annelids, polychaetes and clitellates, as separate taxa.

Archannelida. Hatschek (1893, see also Hatschek 1878b) created the class Archannelida for a group of small polychaetes. The archannelids were presumed primitive with a simple body-structure, including poorly developed, or missing parapodia, and ventral pharyngeal structures of similar morphology. They also tended to be obviously ciliated as adults, in a variety of patterns (Goodrich 1912; Westheide 1985). The features identifying this taxon are now regarded as convergences, many of which

are related to the small size of specimens (Hermans 1969; Fauchald 1974; Westheide 1985; Purschke 1988). The Archiannelida is now considered polyphyletic and most of the archiannelidan families have been proposed as belonging to clades including larger-bodied taxa (e.g. protodrilids and saccocirrids with spioniforms, Orrhage 1974; Purschke & Jouin 1988). Histriobdellids are currently considered modified eunicemorphs (Fauchald 1977), and dinophilids are also associated with this group (Westheide 1985; Eijbye-Jacobsen & Kristensen 1994). In spite of these developments, the taxon Archiannelida is still used by some authors (Bailey-Brock 1987; Kozloff 1987; Minichev & Bubko 1993), and as a separate systematic heading in Zoological Record as late as volume 125 (issued in December 1989). We do not refer to archiannelids in our present analysis, and the 'archiannelidan' families will be considered elsewhere.

Deuterostomes and lophophorates. The position of 'deuterostome', 'lophophorate' and 'pseudocoelomate' taxa in relation to the 'protostomes' is unclear (see review by Eernisse *et al.* 1992). Some workers place the deuterostomes as the sister group to a (variously formulated) protostome clade (e.g. Brusca & Brusca 1990; Eernisse *et al.* 1992; Nielsen 1994). It may well be that spiralian, as used in this paper, are a paraphyletic group (Winnepenninckx *et al.* 1995). However, there has not been a suggestion that deuterostome or pseudocoelomate taxa are closely related to 'annelid' taxa, and resolving their position is beyond the scope of this study. We also did not include lophophorate taxa in our analysis, largely because of conflicting assessments about their morphology. Brusca & Brusca (1990) summarise the argument as to why brachiopods and other lophophorates are now viewed as deuterostomes. Molecular sequence data, using 18S rDNA sequences, presented by Field *et al.* (1988) and Halanych *et al.* (1995) led them to suggest that lophophorates such as brachiopods, phoronids, and bryozoans fall well within the protostome clade. However, the range of taxa included was not comprehensive. Halanych *et al.* (1995) went so far as to name a clade, Lophotrochozoa, for the lophophorates, molluscs, and annelids. It is curious that, in seeking the systematic placement of lophophorate taxa, Halanych *et al.* (1995) did not include hemichordates such as pterobranchs in their analysis. Halanych (1993) found the tentaculate arms of the pterobranch hemichordate, *Rhabdopleura normani*, to be homologous with lophophores of brachiopods, phoronids and bryozoans.

It is well known that the chaetae of brachiopods show striking similarities with those of the Echiura, Annelida, and Pogonophora (Gupta & Little 1970; Orrhage 1971, 1973a; Gustus & Cloney 1972; Storch & Welsch 1972; George & Southward 1973). Further studies at the morphological and molecular level, including all relevant taxa, are needed to clarify the position of lophophorate taxa, and they are not considered further in this study.

Lobatocerebridae and Jenneria. *Lobatocerebrum* was originally described as an annelid (Rieger 1980), possibly related to the clitellates (but see Brinkhurst 1982: 1044), though they have few macroscopic 'annelid' features. Rieger (1980) reported the nephridia to be metamerically arranged, and used other cytological evidence for placing the family among the annelids. Rieger (1988: 378–379) discussed the relations among the lobatocerebrids and various groups, including annelids and acoelomate phyla, but left the position of the family undetermined. Rieger (1991b) described the sperm of the lobatocerebrids as having an acrosomal tube and mitochondrial derivatives between the centrioles and the nucleus, the former present only in clitellates (Ferraguti 1983; Jamieson *et al.* 1987). The structures of the sperm represent potential synapomorphies for lobatocerebrids and clitellates. This implies that the absence of so many other annelid features in *Lobatocerebrum* are losses, or, alternatively, that they are the most plesiomorphic members of the clitellate clade. The Lobatocerebridae require further investigation.

Another small worm described by Rieger (1991a), *Jenneria pulchra*, is also of interest. The body consists of a pre-oral rostrum, the main body, and a posterior tail with an anus. The body regions are separated by septa. Parapodia and chaetae are absent. The digestive tract is complete, and protonephridia are present. *J. pulchra* has not been considered in this study, though it deserves further study.

Myzostomida. In the latter part of this century, myzostomids have been explicitly treated as a family or order of polychaetes (Hartman 1969; Schroeder & Hermans 1975; Pettibone 1982), or ignored altogether in polychaete texts (Day 1967; Hartmann-Schröder 1971; Fauchald 1977) or as a class of annelids (e.g. Dales 1963; Clark 1969: 41–44; Brusca & Brusca 1990). Clark (1978) even suggested that there was little evidence to retain them within the Annelida. The group was also the subject of some debate during the last century. The first scientist to describe a

myzostome, Leuckart (1827, 1836), regarded them as trematodes; Lovén (1840, also 1842) as tardigrades. Siebold (1848) placed them within the Chaetopoda (i.e. Polychaeta) but also looked on them as a 'link' to the Trematoda. Van der Hoeven (1856) placed them in the Crustacea, and Diesing (1858) considered them leeches. Von Graff (1877, 1884) grouped the Tardigrada, Lingulitidae, and myzostomes into the Stechelopoda. Stummer-Traunfels (1903) compared the myzostome nervous system to that of the crustaceans, and the eversible pharynx to that in platyhelminths. Beard (1884) described successive addition of parapodia and chaetae in myzostomid larvae, similar to that seen in polychaetes and, as did Wheeler (1898, 1899, 1905), argued for their position within the Chaetopoda (= Polychaeta). Prenant (1959) gave an overview of myzostomid structure and biology and reviewed most of the history of the group. Recently, Mattei & Marchand (1987) put forward the suggestion that the Myzostomida and Acanthocephala are sister taxa, and should form the phylum Procoelomata. This opinion was based largely on similarities in sperm structure. While admitting that the position of the Acanthocephala is uncertain and deserves closer investigation (see Conway Morris & Crompton (1982) for a comprehensive review of ideas on acanthocephalan phylogeny), Mattei & Marchand's paper appears to be an instance of emphasising one suite of characters to the exclusion of all other evidence.

Other evidence has clearly indicated that myzostomes are a group of annelids, and probably polychaetes. Descriptions of development in myzostomids show that they have spiral cleavage and teloblastic growth with segments added sequentially at the posterior end (Beard 1884; Jägersten 1940; Kato 1952). Jägersten (1936) showed that myzostomid chaetae are similar to those seen in polychaetes, and also considered the myzostomids to have a coelom, though it is limited to the ducts and branches of the male and female reproductive systems (Jägersten 1940). Pietsch & Westheide (1987) demonstrated that myzostomids have serially repeated pairs of protonephridia, and it appears that structures previously called nephridia by Jägersten (1940) are in fact coelomoducts. Eeckhaut & Jangoux (1993) described the serially repeated lateral sensory organs of myzostomes and compared them with polychaete nuchal organs, though a more useful comparison would have been with polychaete lateral organs (Fage 1906). Parapodia, here defined as lobes that are supported by musculature, derived mostly from circular muscles, which usually support chaetae, are clearly present in most polychaetes and myzostomids (Beard 1884; Fauchald 1977; Eeckhaut & Jangoux 1993). The features of the parapodia of myzostomids that resemble those of certain polychaetes include the presence of aciculae (Jägersten 1936). Aciculae, or internalised chaetae that support parapodial structures, are found in eunicemorph, amphinomid, and phyllocimorph taxa (Fauchald 1977). The parapodia of myzostomids can also be interpreted as representing the neuropodial rami, a feature of many polychaetes with a muscular axial pharynx. This eversible axial pharynx is also seen in myzostomids (Jägersten 1940; Eeckhaut *et al.* 1994). All of these features support the view that myzostomids fall well within the polychaetes, and that a sister group relationship amongst polychaetes with a muscularised axial pharynx should be assessed. This issue will be studied in another publication, and they are not included in this analysis.

Characters

The nature of current computer programs for cladistic analysis restricts the use of characters that are nested hierarchically. Hence, the use of the character 'chaetae' with two states, *absent* or *present*, does not logically allow for further characters to identify clades based on the nature of the chaetae in the same analysis. If a further character based on types of chaetae is added, then a '?' is usually added to the matrix for taxa for which the character is inappropriate. However, the taxa so scored will be assigned a state for the type of chaetae that may be meaningless (Platnick *et al.* 1991; Maddison 1993). In a review of how to deal with missing data and inappropriate characters, Maddison (1993: 580) states 'Perhaps the eventual solution will be to write new algorithms for computer programs that will allow the characters to be coded independently but that will consider interactions between characters.' In the meantime, this problem, when (or if) it is recognised by workers, can be addressed by using a FIG/FOG approach with a series of analyses at different hierarchical levels (Watrous & Wheeler 1981). Alternatively, absence/presence coding is advocated by Pleijel (in press), though this does present linkage problems in terms of weighting features which can be broken into many discrete characters. The use of multistate characters has been advocated by Maddison (1993), with a resulting loss of information. This loss of information, as outlined by Pleijel (1995), is that a feature at a more general level may be absent or present, but exhibits some informative variation at a less general level. Hence, a multistate character will sacrifice the information for the more general hierarchical level. Here we use characters that are, for the most part, arguably independent and binary, but have carefully considered several

multistate characters where binary coding would have been misleading or erroneous.

A total of 13 characters were used, with a total of 33 character states. The characters are those normally invoked in discussions of relationships among 'protostomes' (Brusca & Brusca 1990; Eernisse *et al.* 1992). The characters under study are discussed in detail to determine whether they can be multistate or should be binary. Nine of the characters are binary characters. Four characters are multistate. Characters and states are shown in Appendix 1. Sources for character data for each taxon are shown in Appendix III.

1. Embryonic cross formation. During spiral cleavage, certain cells derived from the first and second quartet can form transitory cross-shaped patterns centred at the apical end of the embryo (Salvini-Plawen 1988; Scheltema 1993). The cross patterns are formed by different blastomeres. Polychaetes (Salvini-Plawen 1988), clitellates (Needham 1990), and echiurids (Newby 1940) show one form, with the cross formed by the blastomere cells $1a^{112}$ – $1d^{112}$, and molluscs and sipunculids show a cross formed by blastomere cells $1a^{12}$ – $1d^{12}$ (Meglitsch 1972; Scheltema 1993). Salvini-Plawen (1985, 1988) rejected the use of this feature for phylogenetic inference because of its absence in any form in such taxa as the 'Turbellaria', Nemertea, and certain molluscan clades. We do not accept such a view, and it should be noted that Scheltema (1993) has indicated the existence of a cross in each of the major molluscan clades. While studies on cleavage of pogonophores now indicate that cleavage is spiral and complete (Ivanov 1988; Bakke 1990), it is not yet possible to determine what form of 'cross' is present. No studies of early cleavage in the Vestimentifera have been performed. Onychophorans (and many euarthropods) have cleavage that is meroblastic, leading to a uniform blastoderm around a yolk mass. Where cleavage is total, it appears that this is associated with viviparity, and the eggs are small and secondarily yolkless (Anderson 1973). Members of the Euarthropoda that do not show meroblastic cleavage are limited to a few groups such as the Xiphosura, some other chelicerates, and various crustaceans (Anderson 1973). In any case, the holoblastic spiral cleavage seen in crustacean embryos such as barnacles is not regarded as homologous to that seen in other taxa (Anderson 1973). It is difficult to directly compare onychophoran and euarthropod early embryos with those of taxa showing spiral cleavage, and we have coded them with a unique state for this character. We treat this character as multistate with four states; 0, Spiral cleavage with cross absent; 1, Spiral cleavage with interradiate or 'annelid' cross; 2, Spiral cleavage with radiate or 'molluscan' cross; 3, Meroblastic or other non-spiral cleavage. Since pogonophore are known to have holoblastic spiral cleavage, they were allowed to have either state 0, 1, or 2. Since there are no data on cleavage in the Vestimentifera, they were scored with a '?'.

2. Coelom. A schizocoelic coelom is formed when solid mesodermal clusters, derived from a mesentoblast, hollow out and develop coelomic spaces within (Brusca & Brusca 1990). There are different final forms that the schizocoelic coelom can take. However, homology assessments amongst these forms are difficult to make. The result of a multistate character on the schizocoelic coelom could reasonably be a series of autapomorphies, with the information content of the presence of the coelom being lost. We recognise the nemertean rhynchocoel and lateral vessels, and the pericardial cavity of molluscs, as coelomic in nature (Turbeville & Ruppert 1985; Turbeville 1986, 1991; Brusca & Brusca 1990; Reynolds *et al.* 1993; Morse & Reynolds in press). The absence of a coelom in platyhelminths may or may not be secondary (Smith & Tyler 1985), but this does not influence our scoring. Small polychaetes often lack a complete coelomic lining (Fransen 1980), but despite this, we consider the plesiomorphic polychaete condition to be coelomate. Echiurids and sipunculids have open coelomic spaces (Stephen & Edmonds 1972), as do most clitellates (Cook 1971; Jamieson 1981). The occlusion of the coelom in some members of the Hirudinea and replacement with a haemocoel is regarded as a secondary phenomenon (Fernández *et al.* 1992). The nature of the coelom in the Pogonophora and Vestimentifera is the subject of some debate (see Southward 1988), but these taxa can be regarded as schizocoelous coelomates (Southward 1988, 1993; Gardiner & Jones 1993, 1994). A schizocoelic metameric coelom forms in the onychophoran and euarthropod embryo but is restricted in the adults to the gonads and parts of the excretory system (Anderson 1973; Brusca & Brusca 1990; Storch & Ruhberg 1993; Wheeler *et al.* 1993). We have used a binary character with the states: 0, Coelom absent; 1, Coelom present.

3. Segmentation. Taxa in the analysis have mesoderm derived from the 4d blastomere, or its positional equivalent in the case of the Onychophora (Anderson 1973), though this has yet to be demonstrated for the Pogonophora and Vestimentifera. In euarthropods with meroblastic cleavage, there is no way of tracing cell lineages compared with those

showing spiral cleavage. Where holoblastic 'spiral' cleavage occurs, as in some crustaceans, Anderson (1973) has shown that the mesoderm does not arise from 4d. However, the segmented condition found in polychaetes (Anderson 1973), clitellates (Anderson 1973), pogonophores (Southward 1993), vestimentiferans (Jones & Gardiner 1989; Gardiner & Jones 1993) and arthropods (Anderson 1973) is regarded as homologous by most authors (Brusca & Brusca 1990; Wheeler *et al.* 1993; but see Eernisse *et al.* 1992), and we accept this hypothesis here. Brusca & Brusca (1990: 885–886) define segmentation as the 'repetition of homologous body structures derived by teloblastic growth'. This also involves a posterior growth zone from which the body segments arise (Anderson 1973). We do not regard the serial repetition of nephridia and/or gonads that can occur in some nemerteans and molluscs (Brusca & Brusca 1990) as homologous with segmentation. We have used a binary character with the states: 0, Segmentation absent; 1, Segmentation present.

4. Circumoesophageal nerve ring. The nerve ring connects the dorsal cephalic ganglion (or brain) at or near the anterior end to the rest of the nervous system, which is developed as a few (one to four) longitudinal nerve trunks. This is found in all taxa in the analysis except the Platyhelminthes and Nemertea (see Brusca & Brusca 1990). In the latter group, a nerve ring is present, but it surrounds the rhynchocoel (Turbeville 1991). The history of the interpretation of the nerve ring in pogonophores was discussed above, and it has been shown that a transitory gut passes through the brain in vestimentiferans (Gardiner & Jones 1993). We used a binary character with the states: 0, Circumoesophageal nerve ring absent; 1, Circumoesophageal nerve ring present.

5. Digestive tract. A digestive tract with mouth and anus, an ontogenetic derivative of the endoderm (Schroeder & Hermans 1975), is present in all spiralian, except in a few, mostly parasitic, groups (e.g. cestodes and Acanthocephala) and the Platyhelminthes. We have used a binary character to describe the digestive tract, with the platyhelminths having the state 0, mouth and digestive tract present, anus absent. While in some platyhelminths, an anal pore (or pores) is present (Hyman 1951a), we do not regard this condition as homologous with the condition found in other taxa (see Ax 1984, 1987). A complete gut with an anus (state 1) is present in all members of the ingroup, even if it may be lost in the adults (e.g. Vestimentifera and Pogonophora).

6. Gut lumen. Given the absence in the adult of a distinct gut lumen, the nutrition of pogonophores had been the subject of some debate (Ivanov 1955; Jägersten 1956; Southward & Southward 1966). It was determined that the trophosome of the vestimentiferan *Riftia* contains masses of chemoautotrophic bacteria (Cavanaugh *et al.* 1981; Cavanaugh 1985), and a symbiotic association was evident. The nutrition of pogonophores was found to be the same as in the vestimentiferans (Southward *et al.* 1981; Southward 1982). The occurrence of apparently symbiotic bacteria beneath the cuticle in the tubificid clitellates of the genera *Inanidrilus* and *Olavius* (see Erséus 1984), is not regarded as homologous to the condition seen in the Pogonophora and Vestimentifera. A gut in *I. leukodermatus* and *O. albidus* is said to be absent (Giere 1981; Richards *et al.* 1982) though this may have been in reference to the absence of a gut lumen, since an endodermal strand does appear to be present in both species (Giere 1981; Jamieson 1992). In pogonophores and vestimentiferans, the endoderm is voluminous and filled with bacteria to form the trophosome, a very different situation to *Inanidrilus* and *Olavius* spp. Dubilier *et al.* (1995) have also shown that the sub-cuticular bacteria of *I. leukodermatus* are more closely related to those occurring on a nematode than to those of the vestimentiferan *Riftia pachypila*. The eggs of pogonophores and vestimentiferans do not contain bacteria, so how they entered the juveniles became an issue of considerable interest. In studies of juveniles of the vestimentiferans *Ridgeia* and *Riftia*, Southward (1988) and Jones & Gardiner (1988, 1989) demonstrated the presence of a temporary mouth and anus, as well as a lumen in the area of the future trophosome. They suggested that bacteria probably enter through this transient digestive tract, and that the trophosome is a thickened gut wall, collapsing the lumen. So far, a complete digestive tract has not been recognised during development of any pogonophore, but Flügel & Calsen-Cenic (1992) demonstrated the transitory presence of an anus and a short posterior gut lumen in the larvae of a species of *Siboglinum*. Southward (1993: 349, 351) has noted a small lumen in the trophosome of pogonophores. We have therefore used a binary character based on the nature of the gut. Pogonophores and vestimentiferans have a gut lumen that is largely occluded by an expanded gut wall filled with bacteria (state 1). All other taxa in the analysis have a permanent gut lumen (state 0).

7. Excretion. Nephridia are primarily excretory in function and ectodermal in origin (Goodrich 1945; Smith & Ruppert 1988). Protonephridia

are closed by a terminal cell, and metanephridia open into a coelomic cavity (Bartolomaeus & Ax 1992). The structure and distribution of nephridia were discussed by Goodrich (1895, 1945); the ultrastructure of these organs has been studied by Smith & Ruppert (1988). Platyhelminths (Rieger *et al.* 1991) and nemertean (Turbeville 1991) have protonephridia only. Adult sipunculids (Stephen & Edmonds 1972; Rice 1993), echiurids (Stephen & Edmonds 1972; Pilger 1993), clitellates (Cook 1971; Fernández *et al.* 1992; Jamieson 1992), onychophorans (Storch & Ruhberg 1993) and euarthropods (Meglitsch 1972; Weygoldt 1986; Brusca & Brusca 1990; Wheeler *et al.* 1993) have metanephridial derivatives only.

The description by Smith & Ruppert (1988) of molluscan excretory organs as being metanephridial is based on a functional interpretation rather than structural aspects. Salvini-Plawen (1988) argued that the excretory organs of molluscs showed no homology with metanephridia, and that they had a mesodermal origin (*contra* Brusca & Brusca 1990). Reynolds *et al.* (1993) suggested that coelomic ultrafiltration is the plesiomorphic state for the Mollusca and described podocytes in aplousophorans which are always found in metanephridial systems (Smith & Ruppert 1988). However, since there is at present little evidence for a metanephridial homologue in the molluscan excretory system, we gave them a separate state for this character.

Pogonophores have an anterior pair of protonephridia according to Southward (1980), although a detailed description has yet to appear. Southward's (1993) discussion of the fine structure of the excretory system in several pogonophores is difficult to interpret in terms of assigning the states metanephridia or protonephridia. The nephridia of *Siphonobranchia laevis* could be interpreted as metanephridia (Southward 1993: 353) whilst those of *Oligobranchia gracilis* and *Siboglinum* spp. appear to be protonephridial (Southward 1993: 354–5). For the purposes of this study, we will accept Southward's (1980) designation of protonephridia as present in pogonophores, since the word 'metanephridia' has not been mentioned for these taxa. In the vestimentiferans *Lamellibranchia barhami* and *L. luyesi*, van der Land & Nørrevang (1975) mention a pair of anterior metanephridia with a single median dorsal opening to the exterior. Each nephridium opens to a coelomic space, and thus can be classified as metanephridial, though Gardiner & Jones (1993) questioned whether the spaces into which the ducts open are coelomic. Jones (1985a) and Gardiner & Jones (1993) studied other vestimentiferans, and regarded the excretory ducts with a single exit dorsally as coelomoducts. We view them here as metanephridial derivatives (i.e. mixonephridia) structurally similar to those of sabellid and serpulid polychaetes (Orrhage 1980). Southward (1988), in a study on the development of vestimentiferans, found these structures to have an appearance like flame cells, lending support to a nephridial interpretation.

Polychaetes have been found to have both protonephridia and metanephridia (Goodrich 1945; Smith & Ruppert 1988). We regard metanephridia to be the plesiomorphic polychaete state. Firstly, many taxa with protonephridia are extremely small, and have sister groups with metanephridia; admittedly, the relations among these clades are unresolved, but these small taxa are unlikely to represent the plesiomorphic polychaete condition (Fauchald & Rouse in prep.). Secondly, larger polychaete taxa with protonephridia such as the Glyceridae, Pisionidae, Phyllodoctidae, and Nephtyidae (Goodrich 1945) all belong to a derived clade of the Polychaeta, and protonephridia may be secondarily derived in this instance (Rouse & Fauchald in prep.; see discussion in Glasby 1993).

We acknowledge that the state 'metanephridia' is linked to having a coelom and so cannot occur in acoelomate taxa such as platyhelminths. However, many coelomates have protonephridia as adults (many polychaetes; see Smith & Ruppert 1988), or metanephridial systems and limited coelomic spaces (onychophorans and euarthropods), and we were interested in the transformation of this character and the assumption that protonephridia are homologous. We used a multistate character with the states: 0, Adult protonephridia present; 1, Adult metanephridia or 'derivatives' present; 2, Molluscan excretory system.

8. *Cuticle*. With reference to the taxa discussed here, a cuticle can be defined as an external non-living layer secreted by the epidermis (Brusca & Brusca 1990). Rieger (1984: 389) regards a cuticle as the fibrous and/or granular materials which are associated with the outer surface of the epidermis. The nature of this cuticle can be such that microvilli are present and secrete a network of fibres (in part collagenous where identified to date). This form of cuticle is found in the Clitellata (Richards 1978, 1984; Jamieson 1992), Polychaeta (Richards 1978, 1984; Storch 1988), Pogonophora (Southward 1993), Sipuncula (Storch 1984; Rice 1993) and Vestimentifera (Gaill *et al.* 1991; Gardiner & Jones 1993). In the Echiura, preliminary analysis indicates that a collagenous cuticle is present (Storch 1984; Menon & Arp 1991). Such a cuticle is absent in the Platyhelminthes and Nemertea, where microvilli and a glycocalyx may be present but there is no collagenous matrix (Rieger

1984; Rieger *et al.* 1991; Turbeville 1991). The Mollusca show a fibrous cuticle but the protein component is unique and called conchin (Brusca & Brusca 1990). In the Onychophora and other arthropods, the cuticle does not contain collagen fibres but has two layers with a large chitinous (alpha chitin) component (Weygoldt 1986; Brusca & Brusca 1990; Storch & Ruhberg 1993; Wheeler *et al.* 1993). Molluscs can also produce large quantities of chitin, but this is not associated with the cuticle *per se* (Grégoire 1972). Chaetae also have a large chitin component (beta chitin) and are cuticular (Richards 1978; Specht 1988), but we do not consider them to be homologous with the arthropod cuticle. Based on this data, we used a multistate character, cuticle, with the states: 0, Cuticle with glycocalyx only; 1, Cuticle present (with conchin); 2, Cuticle present (with fibrous, collagenous, matrix); 3, Cuticle present (with a large alpha chitin component).

9. *Chaetae*. Chaetae (setae) are bundles of chitinous, thin-walled cylinders held together by sclerotized protein. They are produced by a microvillar border of invaginated epidermal cells (O'Clair & Cloney 1974; Richards 1978). Specht (1988) additionally regarded them as cuticular structures that develop within epidermal follicles. Chaetal ultrastructure is similar in cases examined to date (Orrhage 1971; Storch & Welsch 1972; Gustus & Cloney 1972; George & Southward 1973; Jamieson 1981). While Orrhage (1973a) found some ultrastructural differences between pogonophoran and annelid chaetae, these were not seen in a similar study by George & Southward (1973), and the differences were rejected as trivial by Southward (1993). The ventral hooks of echiurids are chaetae (Orrhage 1971; Pilger 1993); the epidermal bristles found in some sipunculids are structurally completely different and are not chaetae (Rice 1973). The claws of onychophorans and setae of euarthropods (Brusca & Brusca 1990) are not considered homologous with chaetae. We regard chaetae as being independent of the type of cuticle present, though as it turns out they are only present in some of the taxa scored with a collagenous cuticle.

The presence of dorsal and ventral bundles of chaetae has been considered a synapomorphy for the Annelida (Wheeler *et al.* 1993). In the Echiura, paired ventral chaetae are present anteriorly and one or more rings of chaetae may be present posteriorly (Pilger 1993). In polychaetes, many groups have single, usually ventrally located, segmental chaetal bundles (Fauchald 1977). While many authors have assumed that paired dorsal and ventral bundles of chaetae represent the plesiomorphic polychaete condition (e.g. Fauchald 1974, 1977; Westheide 1985), this assertion has yet to be properly assessed. Within the clitellates, there are typically four equatorial bundles of chaetae, though they may be absent, or even form complete rings (Jamieson 1992). Chaetae are thought to have been lost in leeches (Purschke *et al.* 1993). In pogonophores, two girdles of chaetae may completely encircle the trunk region, and in the opisthosoma, there are a dorsal and a ventral pair of chaetae in each segment (Southward 1993). In the Vestimentifera, chaetae are only present in the opisthosoma and form a row on each side of most segments (Gardiner & Jones 1993). Owing to the uncertainty about the homology of chaetal distribution patterns, we left this as a binary character with the states: 0, Chaetae absent; 1, Chaetae present.

10. *Nuchal organs*. Nuchal organs are ciliated, paired, sensory structures, innervated from the posterior part of the brain (Mill 1978; Storch & Schlötter-Schrehardt 1988; Brusca & Brusca 1990). They are present in nearly all polychaetes (Fauchald & Rouse in prep.) and are absent in clitellates (Jamieson 1988b). Sipunculids are here considered as not having nuchal organs. The structure termed a nuchal organ in this group is a single external lobe (sometimes subdivided), or cephalic organ (Stephen & Edmonds 1972; Rice 1993) innervated from the front of the brain (Rice 1993). The cephalic organ is also single, but in some sipunculids, a pair of cephalic tubes leads to the exterior (Hyman 1959: 615, 647). Turbeville (1991) regards the nemertean cerebral organs to be unique to the group. The heteronemertean cephalic grooves resemble nuchal organs positionally and possibly structurally (see overview in Hyman 1951a), but have yet to be investigated in detail. These, and similar sensory structures, may be homologous to nuchal organs; however, cephalic grooves are here regarded as being more similar to the sensory structures of some flatworms than to those of polychaetes. No structures homologous with nuchal organs are present in either molluscs or echiurids (Brusca & Brusca 1990; Pilger 1993). Onychophorans and euarthropods have no epidermal cilia (Weygoldt 1986; Wheeler *et al.* 1993) and hence cannot have nuchal organs. Nuchal organs have not been reported for the pogonophores, or vestimentiferans. For this study, we coded them as unknown (?) since their absence has yet to be demonstrated. We used a binary character for nuchal organs with the states: 0, Nuchal organs absent; 1, Nuchal organs present.

11. *Longitudinal muscle bands*. All taxa included in this analysis show the presence of outer circular muscle layers and inner longitudinal

muscle layers (Brusca & Brusca 1990) with a few exceptions in some of the groups. In taxa such as the Platyhelminthes (Rieger *et al.* 1991), Nemertea (Turbeville 1991), Sipuncula (Rice 1993), Echiura (Pilger 1993), and Mollusca (Brusca & Brusca 1990), the longitudinal muscles form sheets. In the Clitellata (Avel 1959), Polychaeta (Storch 1968), Pogonophora (Southward, 1993), Onychophora (Manton 1967; Storch & Ruhberg 1993) and Euarthropoda (Brusca & Brusca 1990; Wheeler *et al.* 1993) the longitudinal muscles form a number of discrete bands, usually either 4 or 5. The organization of vestimentiferan musculature has not been fully reported, but Figs 19 and 20 in Jones (1985a) suggest that bands are present ventrally at least. In a few members of the Sipuncula and Echiura, the longitudinal muscles are divided into many distinct bands (Brusca & Brusca 1990; Pilger 1993; Rice 1993) but we do not regard this as homologous to the large discrete bundles seen in other taxa. We used a binary character with the states: 0, Longitudinal muscle sheets present; 1, Longitudinal muscle bands present.

12. Circulatory system. A blood vascular system is usually regarded as a remnant of the blastocoel, or it develops in regions that have replaced the blastocoel. Essentially it is a primary body cavity lined with an extracellular matrix rather than cells (Bartolomaeus 1988; Ruppert & Carle 1983). Blood vascular systems can be either viewed as closed or open, with the former having blood contained in discrete vessels that are separate from the coelom. Most coelomate taxa possess a closed vascular system (Ruppert & Carle 1983). Open circulatory systems have some discrete vessels, but the blood and the body cavity fluid are the same, i.e. a haemocoel is present (Ruppert & Carle 1983). It is usually argued that this condition is associated with a reduced coelom (Hyman 1951a; Brusca & Brusca 1990; Bartolomaeus 1994). There is no evidence for any form of circulatory system in the Platyhelminthes (Rieger *et al.* 1991). In the Sipuncula, there is no circulatory system, and the spacious coelom fulfils the functions of gas exchange and fluid transport (Rice 1993). The Echiura (Pilger 1993), Pogonophora (Southward 1993), Vestimentifera (Gardiner & Jones 1993), and Clitellata (Jamieson 1992) have a closed circulatory system. Within the Clitellata, a number of leeches show a limited circulatory system (Brusca & Brusca 1990), but this is unlikely to be the plesiomorphic condition for the clade. Similarly, a circulatory system is absent in the echiurid *Urechis caupo* (Pilger 1993), but we assume this to be a loss. Most polychaetes have a closed circulatory system (Gardiner 1992), and it is here assumed to be the plesiomorphic state for the taxon. Polychaetes where circulatory system is limited or absent are either very small, or are larger polychaete taxa with protonephridia, such as the Glyceridae, Pisionidae, and Phyllodoctidae (Smith 1992). These taxa belong to a derived clade of the Polychaeta (Rouse & Fauchald in prep.). The Onychophora, and other arthropods, have an open circulatory system comprised of a haemocoel, a muscular ostiate heart and some short vessels (Brusca & Brusca 1990; Storch & Ruhberg 1993; Wheeler *et al.* 1993). In the Mollusca, the principal body cavity is also a haemocoel, and hence there is an open circulatory system (Brusca & Brusca 1990; Reynolds *et al.* 1993). However, it is not considered homologous to the arthropod system. The heart is surrounded by a coelomic remnant, unlike the arthropods, and the heart itself is chambered rather than ostiate (Brusca & Brusca 1990). The nemertean 'circulatory' system is an autapomorphy, as postulated by Bartolomaeus (1988). It is thought to be derived from coelomic components (Turbeville 1986, 1991; Bartolomaeus 1988) and this is not homologous with a closed circulatory system. Thus, although the coelom functions as a circulatory system, we have coded the Nemertea as absent for this character. We used a multistate character for the circulatory system with the states: 0, Circulatory system absent; 1, Circulatory system present, closed; 2, Circulatory system present, open with chambered heart; 3, Circulatory system present, open with ostiate heart.

13. Mitochondria in sperm. Sperm ultrastructure has been used to provide systematic characters in a variety of taxa (e.g. Jamieson 1987a). Our aim in this paper has been to use characters that are as arguably independent as possible, and we used one here based on sperm ultrastructure. The position of mitochondria in spermatozoa of metazoans is usually around the centrioles anchoring the axoneme (e.g. in polychaetes Jamieson & Rouse 1989). This anchoring apparatus then abuts the sperm nucleus. Jamieson (1986) noted that Onychophora and clitellates, virtually alone amongst the Metazoa, show the interpolation of a group of mitochondria between the anchoring apparatus and the sperm nucleus. Jamieson (1986, 1987a) used this as evidence to support the hypothesis that the Clitellata are the sister group to the Onychophora. We have incorporated this character in a large data set as a test of Jamieson's (1986, 1987a) hypothesis. We have used a binary character with the states: 0, Sperm mitochondrial interpolation absent; 1, Sperm mitochondrial interpolation present.

Cladogram construction

Cladistic analyses were performed using PAUP 3.1.1 (Swofford 1993). Multistate characters were treated as unordered (non-additive), with equal weights, and unknown character states were coded as a '?'. For character 1, 'Embryonic cross formation', the Pogonophora were scored with 0, 1, or 2 using the OR separator '/' since they do not have the arthropod state 3 (meroblastic cleavage). Tree searches were performed using the exhaustive search command. Zero-length branches were collapsed, and MULPARS was activated. We have chosen the Platyhelminthes to root the most parsimonious trees and polarise the characters used (Maddison *et al.* 1984; Nixon & Carpenter 1993). Ingroup taxa are the Clitellata, Echiura, Euarthropoda, Mollusca, Nemertea, Onychophora, Pogonophora, Polychaeta, Sipuncula, and Vestimentifera. There are 13 characters, and the data matrix is presented in Appendix II. Analysis of character state distributions and optimisations were performed using PAUP and MacClade 3.01 (Maddison & Maddison 1992). MacClade assesses all possible transformations (i.e. both 'Delayed' transformations and 'Accelerated' transformations).

Results

The exhaustive search option found 18 minimum length trees (Figs 1A–1F, 2A–2F). They had a length of 23 steps, a consistency index (CI) of 0.87 (with uninformative characters removed CI = 0.85) and a rescaled CI of 0.765. Characters 2, 'Coelom' and 5, 'Digestive tract', were uninformative, with all ingroup taxa having the state 'present'. The strict consensus tree is shown in Fig. 3. There were three areas of instability among the 18 trees: 1. In six minimal length trees (Figs 1A, 1D, 1G, 2A, 2D, 2G), the Sipuncula were the sister group to the clade, using the consensus tree topology, (Echiura (Polychaeta (Vestimentifera Pogonophora) Clitellata (Onychophora Euarthropoda))); in six other minimal length trees, the Mollusca were the sister group to this clade, rather than the sipunculids (Figs 1B, 1E, 1H, 2B, 2E, 2H); in the remaining six minimal length trees (Figs 1C, 1F, 1I, 2C, 2F, 2I), the molluscs and sipunculids were the sister taxa, and this clade was the sister group to (Echiura (Polychaeta (Vestimentifera Pogonophora) Clitellata (Onychophora Euarthropoda))). Thus, there are three basic tree topologies before considering the taxa that are the main object of study.

2. The clade (Pogonophora Vestimentifera) was either the sister group to the Polychaeta (Figs 1A, 1B, 1C, 2A, 2B, 2C, 2G, 2H, 2I); formed a polytomy with the Polychaeta and (Clitellata (Euarthropoda Onychophora)) (Figs 1D, 1E, 1F); formed a polytomy with Clitellata and Polychaeta, and this clade was then the sister group to the (Euarthropoda Onychophora) (Figs 1G, 1H, 1I); or formed a polytomy with the (Euarthropoda Onychophora), Clitellata, and Polychaeta (Figs 2D, 2E, 2F), this clade then being sister group to the Echiura.

3. The Clitellata were either the sister group to the (Onychophora Euarthropoda) (Figs 1A, 1B, 1C, 1D, 1E, 1F); were sister group to the (Polychaeta (Pogonophora Vestimentifera)) (Figs 2G, 2H, 2I); or were part of the three types of polytomies as stated in (2).

Based on the topology represented on Fig. 1A, transformations for all characters in the analysis are shown in Figs 4–6. Alternative transformations that appear in the other tree topologies are discussed in the text and shown in Fig. 7.

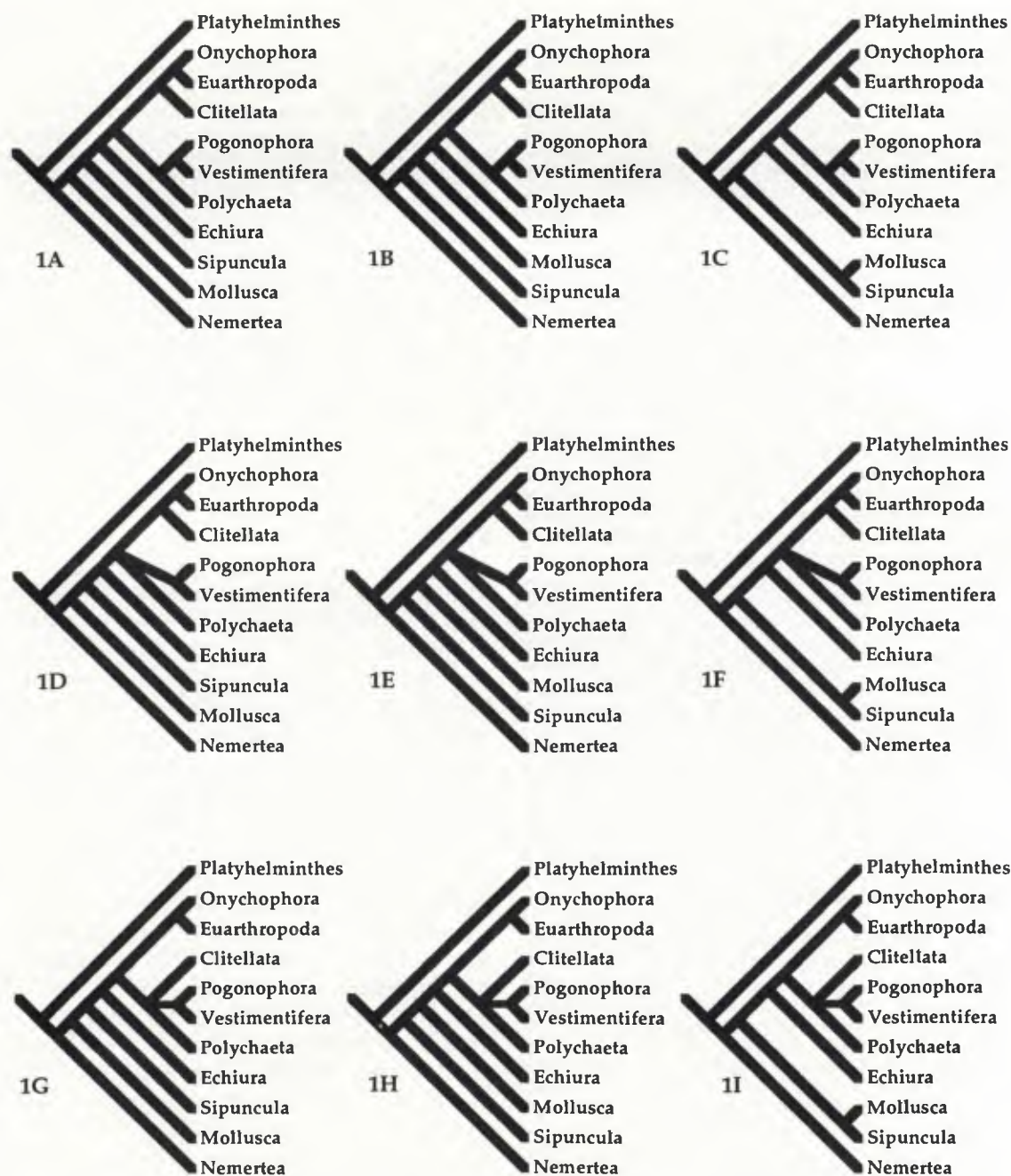


Fig. 1. Nine of the minimal length trees (18) resulting from our search, with lengths of 23 steps and CI of 0.87 rooted using the Platyhelminthes. The Articulata is comprised of the following taxa: Arthropoda (= Euarthropoda and Onychophora), Pogonophora (including vestimentiferans), Clitellata, and Polychaeta.

Character state transformations

Cleavage patterns. Figure 4A is representative of the transformation (with a length of three steps) for cleavage patterns found in 12 of the 18 topologies. The transformation series in Fig. 4A shows the grade Platyhelminthes and Nemertea with the cross absent (state 1), changing to the molluscan cross (state 1) for the mollusc and sipuncu- lid grade. An annelid cross is present in the Echiura, Polychaeta, and Clitellata and, in the context of the available evidence from other characters, is assigned to the Pogonophora and Vestimentifera in all optimizations. In the six minimal length trees where the Sipuncula are sister group to the Mollusca (Figs 1C, 1F, 1I, 2C, 2F, 2I), the presence of the molluscan cross (state 1) is the only synapomorphy supporting this topology. For these trees, there are two possible alternative transformation series

for this character, as suggested by the equivocal region on the branch between the Nemertea and (Mollusca Sipuncula) in transformation series shown in Fig. 7A (which is the tree shown in Fig. 1C). Either the plesiomorphic condition for all ingroup taxa, except the Nemertea, is the absence of a cross (state 0), or the plesiomorphic condition is the 'annelid' cross (state 2). The presence of the molluscan cross then allows for the Mollusca and Sipuncula to be sister taxa. The meroblastic cleavage condition (state 3) is a synapomorphy for the Onychophora Euarthropoda and is derived from the 'annelid' cross (state 2) in all minimal length trees (e.g. Fig. 4A).

Coelom. The transformation (one step) for the coelomic character in Fig. 4B (= tree shown in Fig. 1A), and all other minimal length trees, shows the presence of a schizocoelic coelom to be a synapomorphy for the

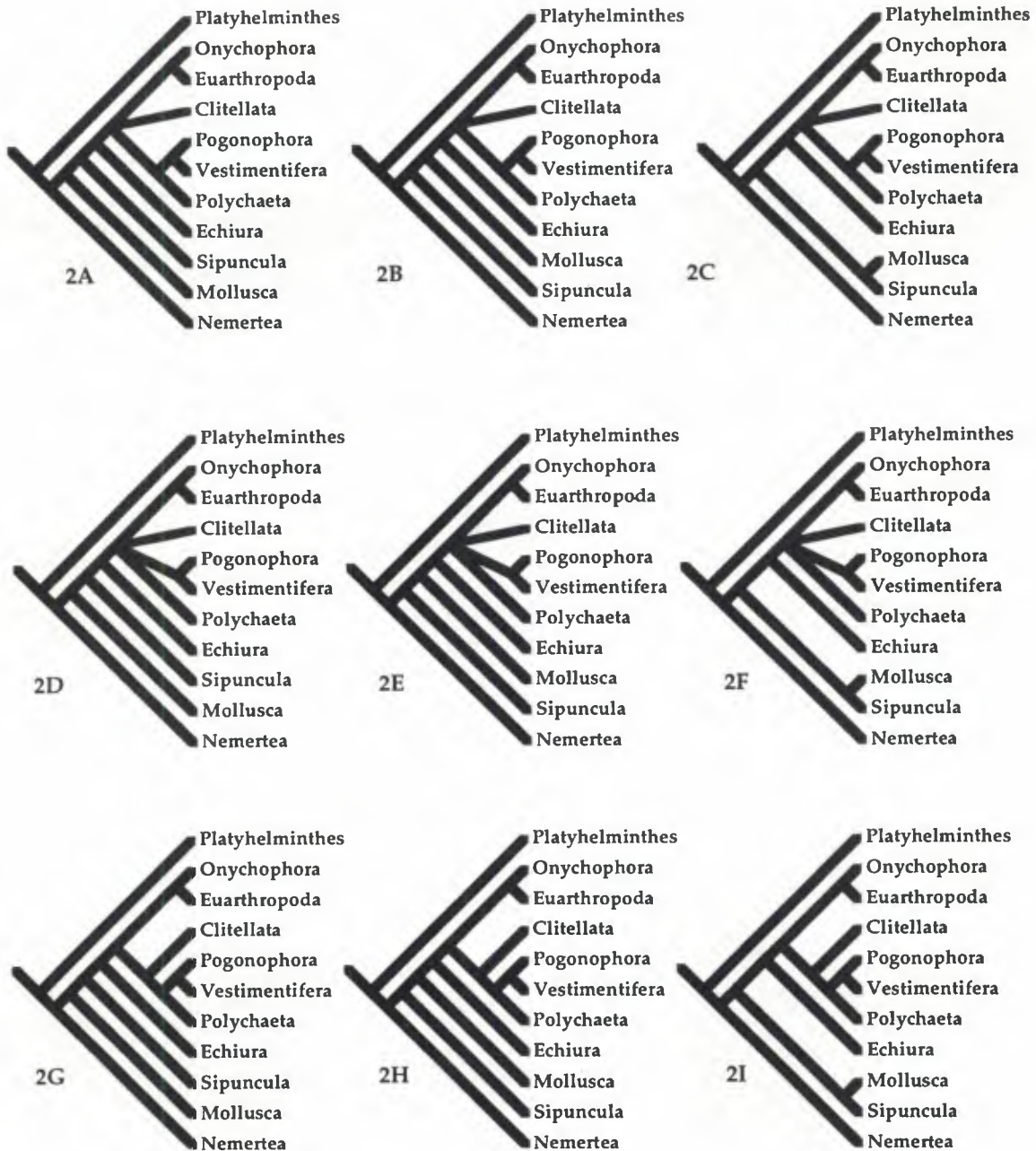


Fig. 2. The remaining nine of minimal length trees resulting from our search.

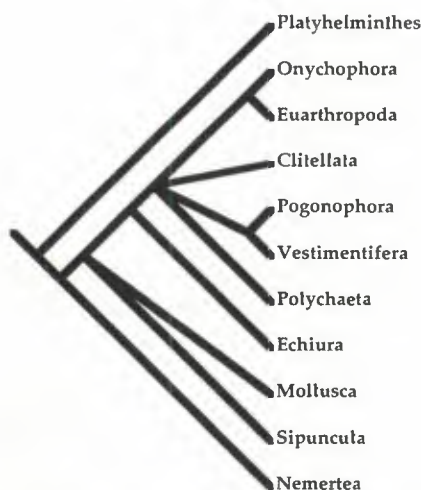


Fig. 3. Strict consensus tree of the 18 minimal length trees.

ingroup taxa and hence is uninformative in terms of resolving relationships amongst them (Fig. 4B).

Segmentation. In all minimal length trees, the presence of segmentation (one step) is a synapomorphy grouping the Clitellata, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera. The grade Platyhelminthes, Nemertea, Mollusca, Sipuncula, and Echiura show the plesiomorphic condition, body unsegmented (Fig. 4C).

Circumoesophageal ring. The presence of a circumoesophageal ring (one step) identifies the clade Mollusca, Sipuncula, Echiura, Clitellata, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera in Fig. 4D and in all other topologies.

Digestive system. The complete nature of the digestive tract (one step) is a synapomorphy for the ingroup taxa in

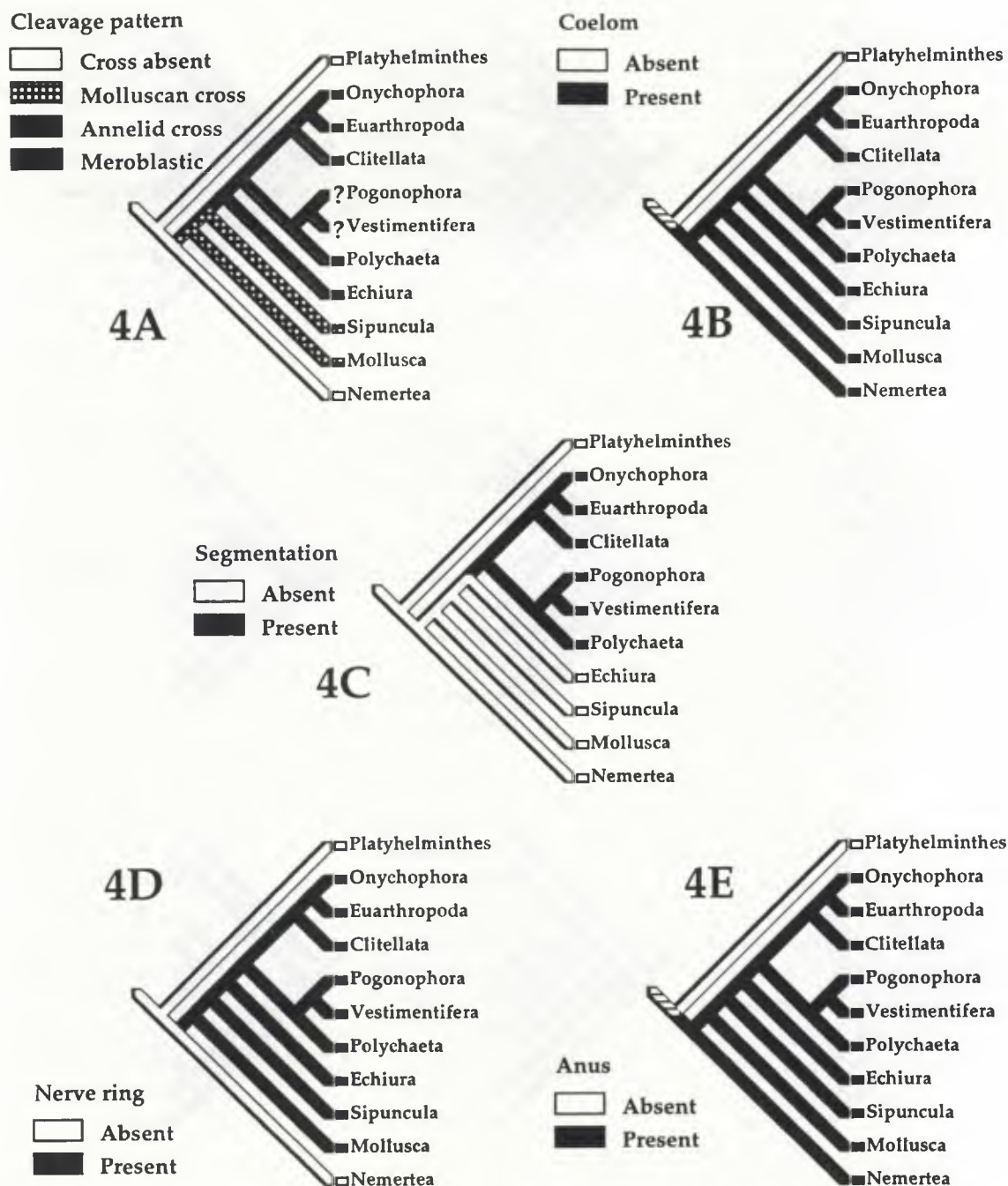


Fig. 4. Transformations of the first five characters used in our analysis onto the minimal length tree shown in Fig. 1A.—A. Transformation series for the character based on embryonic cleavage found in 12 of the 18 minimal length trees. Transformation series for the other six trees are discussed with reference to Fig. 7A. Note, pogonophores (scored with 0, 1, or 2) and vestimentiferans (scored with a '?') are indicated by a '?' to show this uncertainty. They are given the state for the annelid cross in this, and all other optimizations.—B. Found in all minimal length trees this is the only possible transformation for the coelomic character. Though uninformative for resolving relationships amongst the ingroup, the presence of a coelom is a synapomorphy for them as a whole. The 'equivocal' branch below the ingroup outgroup node is irrelevant.—C. Found in all minimal length trees this is the only possible transformation for the segmentation character. This is a synapomorphy for the members of the Articulata.—D. The only possible transformation for the circumoesophageal nerve ring. Found in all minimal length trees.—E. In all minimal length trees this is the only possible transformation for the nature of the digestive tract. Though uninformative for resolving relationships amongst the ingroup the presence of a complete gut (even if only transiently in Pogonophora and Vestimentifera) is a synapomorphy for them as a whole. The 'equivocal' branch below the ingroup outgroup node is irrelevant.

all minimal length trees (e.g. Fig. 4E) and hence is uninformative in terms of resolving relationships amongst them. Occlusion of the gut lumen (one step) is a synapomorphy for the pogonophores and vestimentiferans in all tree topologies (e.g. Fig. 5A).

Nephridia. In all topologies, protonephridia occur in the grade Platyhelminthes and Nemertea, with a reversal to this condition occurring in the Pogonophora (somewhat

questionably; see above, Character 7. Excretion). The character transformation involves four steps in all minimal length trees. For the six tree topologies shown in Figs 1A, 1D, 1G, 2A, 2D, and 2G, there are three possible transformations of this character on the branch indicated as equivocal in Fig. 5B. The molluscan condition could have been derived from a metanephridial condition, or independently of it from a protonephridial condition. The third possible alternative for the topology shown in Fig.

5B is that the metanephridial state (seen in the Clitellata, Echiura, Euarthropoda, Onychophora, Polychaeta, Sipuncula, and Vestimentifera) is derived from the molluscan condition. In the 12 remaining tree topologies, the molluscan nephridial condition unequivocally arises from the metanephridial condition. An example is shown in Fig. 7B that corresponds to the transformation seen in Figs 1B, 1E, 1H, 2B, 2E, and 2H. In the minimal length trees where the Mollusca are the sister group to the Sipuncula (Figs 1C, 1F, 1I, 2C, 2F, 2I), the molluscan nephridial system is also derived from the metanephridial condition.

Cuticle. In all topologies, 'cuticle with glycocalyx only' occurs in the grade Platyhelminthes and Nemertea. The character transformation involves three steps in all minimal length trees, but there are various equally parsimonious transformations of this character among the three tree basic topologies. However, in all cases, the arthropod condition 'cuticle chitinous' is derived from the 'cuticle collagenous' condition. In the tree topologies shown in Figs 1A, 1D, 1G, 2A, 2D, and 2G, there are three possible transformations of this character at the node above the branch indicated as equivocal in Fig. 5C; the molluscan 'cuticle with conchin' could have been derived from the 'cuticle collagenous' state; from a 'cuticle absent' condition; or the 'collagenous cuticle' state (seen in the Clitellata, Echiura, Sipuncula, Pogonophora, Polychaeta, and Vestimentifera) is derived from the molluscan condition. In the 12 other tree topologies, the molluscan 'cuticle with conchin' condition unequivocally arises from the 'cuticle with collagen' condition. In the trees in Figs 1B, 1E, 1H, 2B, 2E, and 2H, 'cuticle with collagen' appears at the node joining the Sipuncula with all other ingroup taxa (except Nemertea). In the trees where the Mollusca are the sister group to the Sipuncula (Figs 1C, 1F, 1I, 2C, 2F, 2I), the 'cuticle with conchin' condition is also derived from the 'cuticle with collagen' condition.

Chaetae. This character has a length of two steps but has differing transformations depending on the tree topology. In most minimal length trees (Figs 1A–1F, 2A–2F), chaetae appear once, at the node joining the Echiura and segmented taxa (Clitellata, Euarthropoda, Onychophora, Pogonophora and Polychaeta). Chaetae are subsequently lost in the arthropod clade. This transformation is shown in Fig. 5D for the tree shown in Fig. 1A. In the trees shown in Figs 1G, 1H, 1I, 2G, 2H, and 2I, the Clitellata, Polychaeta, and (Pogonophora Vestimentifera) form a clade. This clade is only supported by a transformation series where chaetae appear twice independently, once in the Echiura and again for the Clitellata, Polychaeta, and (Pogonophora Vestimentifera) clade. This transformation series also implies that the arthropod taxa never lost chaetae. Figure 7C shows this transformation for the tree shown in Fig. 2H.

Nuchal organs. The ambiguity in transformation series (one step in all cases) for nuchal organs allows for some of the variability in the topologies appearing for the members of the clade Clitellata, Euarthropoda, Onychophora,

Polychaeta, Pogonophora, and Vestimentifera. This is a result of coding the latter two taxa as unknown (?) for this character. Allowing the presence of nuchal organs to be a synapomorphy for the Pogonophora, Vestimentifera, and Polychaeta results in the topology shown in half of the 18 minimal length trees; Figs 1A, 1B, 1C, 2A, 2B, 2C, 2G, 2H, and 2I. The transformation of this character for the tree shown in Fig. 1A is shown in Fig. 5E. When nuchal organs are allowed for in polychaetes only, the topologies in Figs 1D–1I and 2D–2F are seen. For example the transformation series for nuchal organs for the tree shown in Fig. 1E is shown in Fig. 7D. When this character is not included in the analysis then nine minimal length trees of length 22 are obtained with the same topology as Figs 1D–1I and 2D–2F.

Longitudinal muscles bands. This transformation series has a length of two steps in all tree topologies. The presence of 'Longitudinal muscle bands' is a synapomorphy for the Clitellata, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera (e.g. Fig. 6A).

Circulatory system. In all minimal length trees, the transformation series for the character circulatory system takes four steps, though there is some variability among topologies. In the transformation series shown in Fig. 6B, the plesiomorphic state 'circulatory system absent' transforms to the 'open, chambered heart circulatory system' for the Mollusca and to the 'closed circulatory system' at the node uniting the Echiura and segmented taxa. Subsequently, there is the appearance of the 'open, ostiate heart circulatory system' in arthropods. As well as the tree shown here (= Fig. 1A), this transformation occurs in the trees shown in Figs 1D, 1G, 2A, 2D, and 2G. In the topologies shown in Figs 1B, 1E, 1H, 2B, 2E, and 2H, with the Mollusca as the sister group to the variously arranged Clitellata, Echiura, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera, there is only one possible transformation series for the circulatory system character that supports this basic topology. This transformation series has the 'closed circulatory system' being derived from the molluscan 'open, chambered heart circulatory system'. An example of this transformation is seen in Fig. 7E which has the tree topology found in Fig. 2E. In the six minimal length trees with the Mollusca as sister group to the Sipuncula (Figs 1C, 1F, 1I, 2C, 2F, 2I), the transformation series is basically the same as that shown in Fig. 6B with the 'open circulatory system' for the molluscs derived from the 'circulation absent' state.

Mitochondria in sperm. The transformation series for this character has a length of two steps in all minimal length trees. The six trees shown in Figs 1A, 1B, 1C, 1D, 1E, and 1F have the Clitellata as the sister group to the (Onychophora Euarthropoda). This clade is only supported by the transformation series where the apomorphic state for this character (state 1, 'mitochondria between the sperm nucleus and anchoring apparatus') appears at the node grouping the clitellates with the arthropods. The charac-

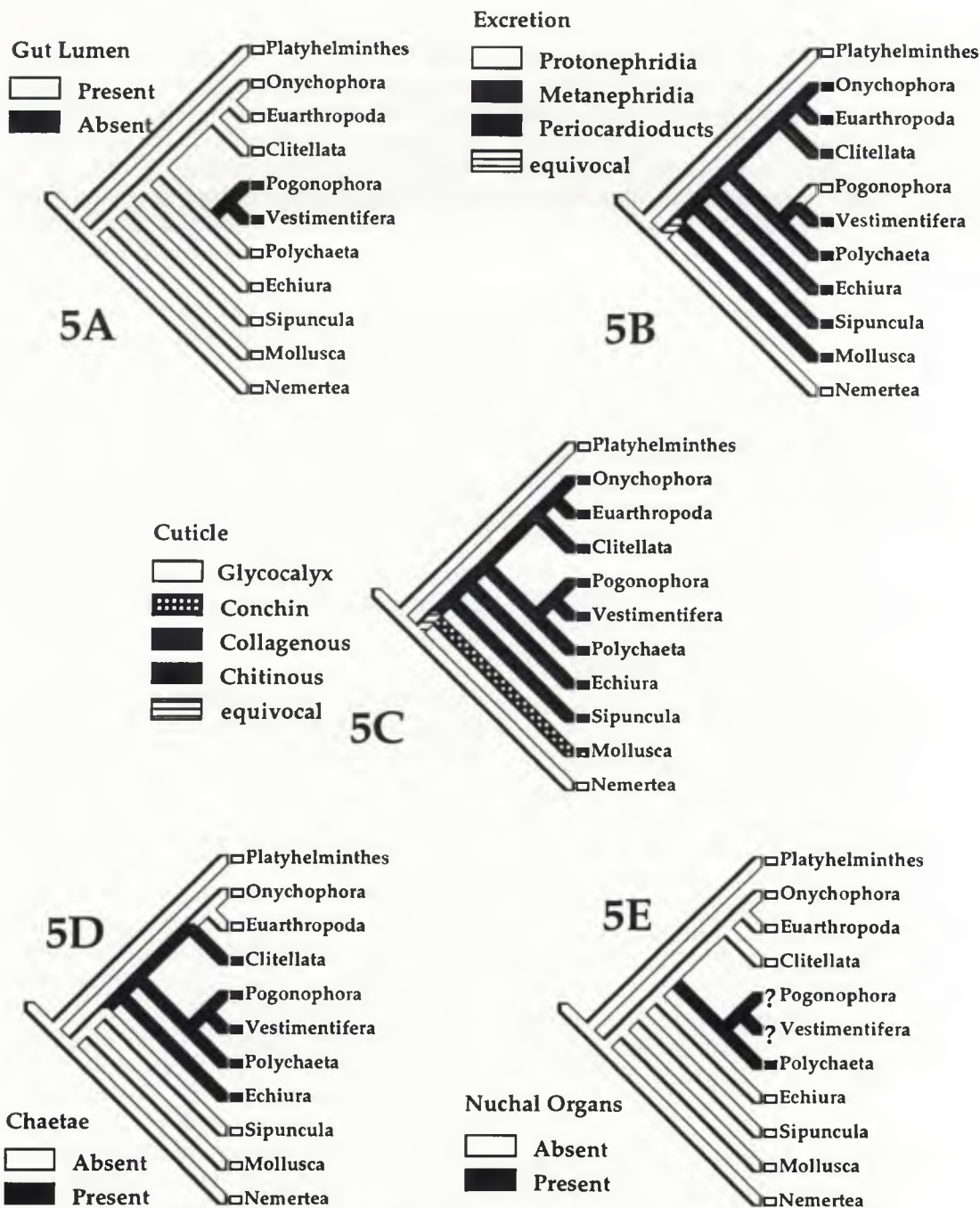


Fig. 5. Transformations of characters 6–10 on the minimal length tree shown in Fig. 1A.—A. The only possible transformation, in the minimal length trees, for the character based on gut lumen. This is a synapomorphy for the Pogonophora and Vestimentifera.—B. There are several possible transformations for the excretory character, depending on the topology of the minimal length trees. The node showing variation in transformations is the one above the branch indicated by 'equivocal' shading. The alternative transformations are explained in the text, and with reference to Fig. 7B. However, in all minimal length trees, the protonephridia of the Pogonophora is a reversal.—C. There are several possible transformations for the cuticle character, depending on the tree topology. That there are alternative transformations for this tree at the node joining the molluscs with the other ingroup taxa (except nemerteans) is suggested by the equivocal shading on the branch (see explanation in the text). The presence of a cuticle with chitin is a synapomorphy for the Onychophora and Euarthropoda.—D. One of the transformation series for the character based on chaetae found in the minimal length trees. In this case the state 'chaetae present' appears at the node joining Echiura and Articulata. A reversal subsequently occurs for the arthropods. Another possible transformation series is shown in Fig. 7C.—E. The only possible transformation for the character based on nuchal organs that would generate the topology is shown here (and trees in Figs 1B, 1C, 2A, 2B, 2C, 2G, 2H, and 2I). Note taxa optimized as being present for this character but are coded as unknown are indicated by a '?'. The presence of nuchal organs in pogonophores and vestimentiferans was allowed for in this case and this is the only synapomorphy with the Polychaeta. When nuchal organs are 'allowed' to be absent in the Pogonophora and Vestimentifera the remaining topologies, such as that shown in Fig. 7D occur.

ter subsequently reverses to state '0' for the euarthropods (Fig. 6C). In the remaining 12 minimal length trees, the state 'mitochondria between the sperm nucleus and anchoring apparatus' appears independently in the clitellates and onychophorans. An example of this transformation (Fig. 7F) is shown for the tree in Fig. 1H.

Discussion

Present transformation series and implications

While the Pogonophora and Vestimentifera were coded as uncertain ('0/1/2') and unknown ('?'), respectively, for

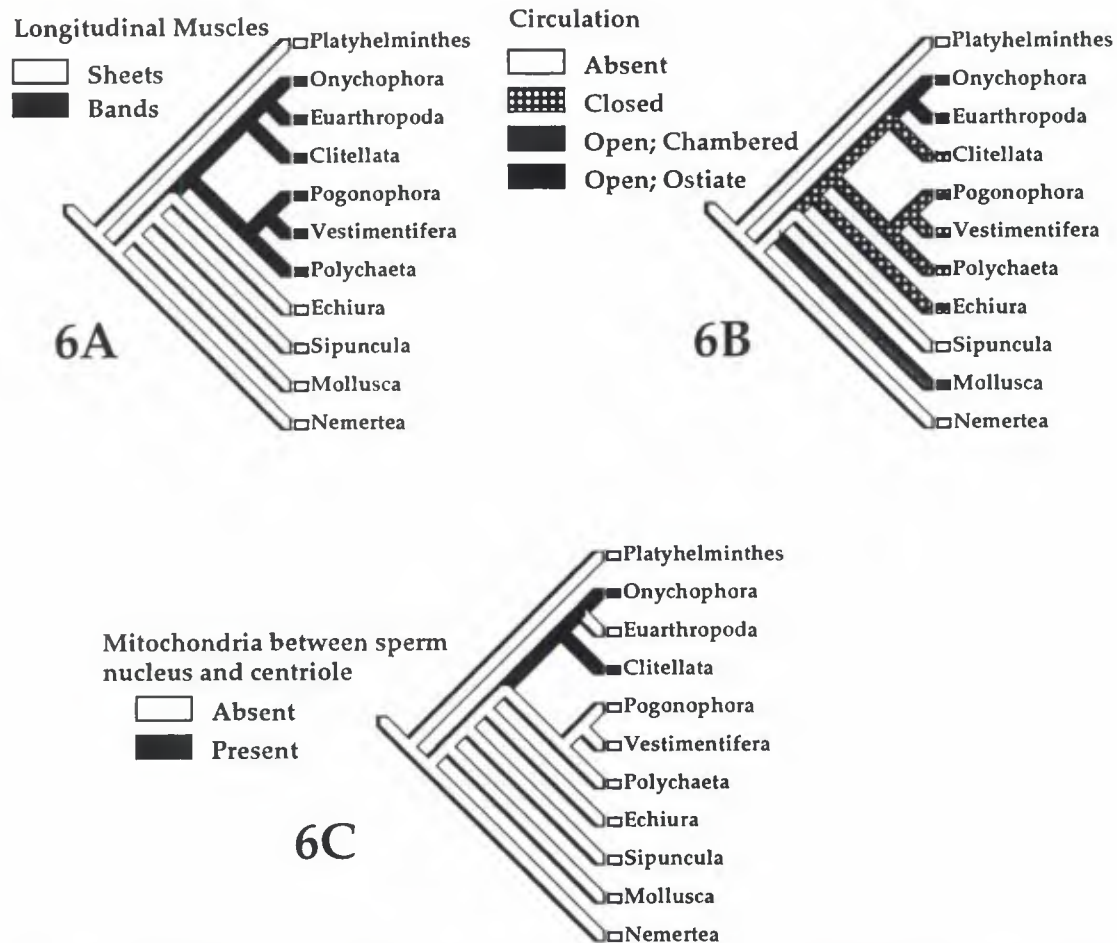


Fig. 6. Transformations of characters 11–13 on the minimal length tree shown in Fig. 1A.—A. The only possible transformation, in the minimal length trees, for the character based on longitudinal muscle. This is a synapomorphy for members of the Articulata.—B. One of several transformation series for the character based on circulation, depending tree topology. The plesiomorphic state 'circulatory system absent' transforms to the 'open, chambered heart circulatory system' for the Mollusca and to the 'closed circulatory system' at node uniting the Echiura and segmented taxa. Subsequently, there is the appearance of the 'open, ostiate heart circulatory system' in arthropods. Alternative transformation series are discussed in the text and one is shown in Fig. 7E.—C. One of the transformation series occurring among the minimal length trees for the character based on sperm mitochondria. This Clitellata/Arthropoda clade (also in Figs 1B, 1C, 1D, 1E, 1F) is only supported by the transformation series where the apomorphic state for this character (state 1, 'mitochondria between the sperm nucleus and anchoring apparatus') appears at the node grouping the clitellates with the arthropods. Subsequently, a reversal occurs for the euarthropods. In the other 12 trees (see Fig. 7F), the derived state appears independently in the clitellates and onychophorans.

the early cleavage of the embryo character, the other available evidence in our matrix predicts that the annelid cross pattern will be found in these taxa. It should be noted that in these two taxa, larvae are lecithotrophic, and this can obscure early cleavage patterns (Anderson, 1973). Hence, confusion arises over whether pogonophores have spiral or radial cleavage, as discussed in the section *Taxa included*. It has been observed that some vestimentiferans release eggs that are 100 μm in diameter, presumably after fertilization in the adult tube (Carey *et al.* 1989; Southward & Coates, 1989; Van Dover 1994). Some pogonophores are also presumed to have planktonic larvae (Southward 1988). These species may have embryos with cleavage patterns that could be revealing in terms of the 'cross' pattern. The meroblastic cleavage found in most onychophorans and euarthropods means that the issue of the presence or absence of a cross is inapplicable. Anderson (1973) has determined other similarities in the embryology of clitellates and onychophorans that deserve further investigation.

For the character based on the coelom, the possibility that the platyhelminths have lost the coelom has been

discussed and rejected by Smith & Tyler (1985) and is not of relevance to this paper. The debate about the nature of the coelom in the pogonophores and vestimentiferans (Jones 1985a; Southward 1988) was also not relevant to the scoring for these taxa. Both exhibit schizocelic coelom formation (Southward 1988; Gardiner & Jones 1993, 1994) resulting in a spacious coelom, a condition similar to that in sipunculids, echiurids, polychaetes, and clitellates. The limited coelomic spaces in arthropods, molluscs, and nemerteans may represent reductions (see Brusca & Brusca 1990), but this issue is not a focus of this paper, and any potential homology of these 'reductions' is unclear.

Two character states, the presence of segmentation and the presence of longitudinal muscle bands, group the arthropods, clitellates, polychaetes, pogonophores, and vestimentiferans. Descriptions of segment development in pogonophores, and vestimentiferans, clearly show that they were correctly scored the same condition as in 'annelids' (Southward 1988; Gardiner & Jones 1993, 1994). This grouping of arthropod and 'annelid-like' taxa is essentially similar to that of the Articulata proposed by

Cuvier (1812). Other recent authors (e.g. Ax 1984, 1987; Weygoldt 1986) have maintained the use of Articulata, and it is a name we accept for this clade (see below).

The absence of a gut lumen was the only synapomorphy for the Pogonophora and Vestimentifera in this analysis. However, the Vestimentifera are clearly closer to the Pogonophora than to any other group, and the proposition that the former should be regarded as a phylum (Jones 1985b), cannot be maintained. Pogonophora is the older name for the combined group and is here accepted as valid. The evidence for this conclusion is discussed in detail below (see **Discussion: Recent hypotheses with im-**

plications for articulate systematics: Evolutionary systematics).

Our results suggest that protonephridia have appeared more than once, a result that has support from various authors (see Smith & Ruppert 1988). Until more information is available on molluscs, little can be resolved regarding the various transformation for the excretory system we found. The finding by Reynolds *et al.* (1993) of podocytes in the Aplacophora lends support to the hypothesis that there is a link between the molluscan system and metanephridia, since podocytes are always associated with a metanephridial system (Smith & Rup-

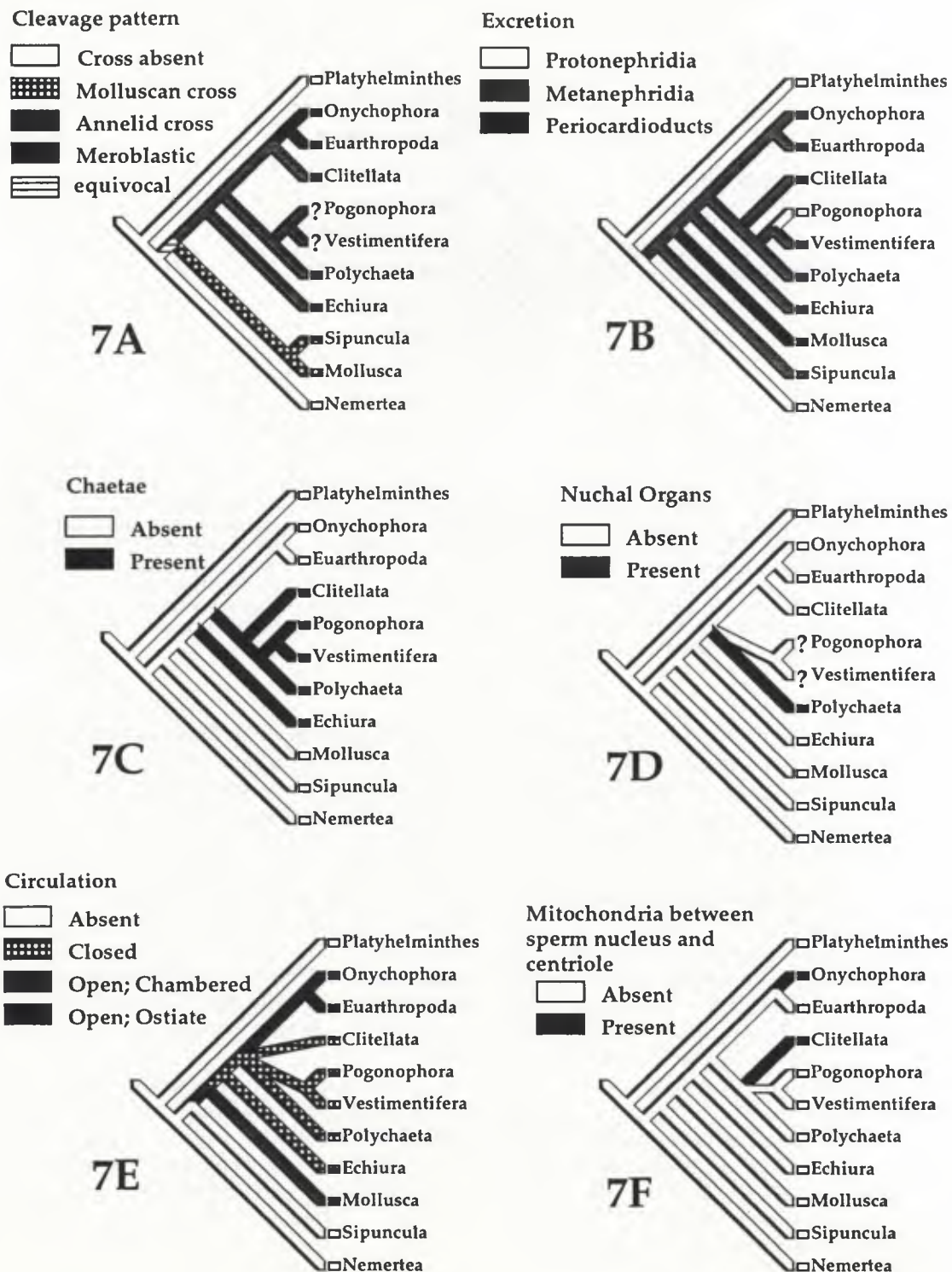


Fig. 7.

pert 1988). However, Salvini-Plawen (1988) has argued that the molluscan excretory system is mesodermal rather than ectodermal, i.e. nephridial. If the nephridial character is altered to make the molluscs have the metanephridial state, instead of their unique state, the number and topology of the resulting minimal length trees are unchanged in the analysis.

The various transformation series for the cuticle character all show that the state 'collagenous cuticle' is found in a grade containing the sipunculids, echiurids, polychaetes, clitellates, pogonophores and vestimentiferans. Previous coding suggests that there is a cuticle type unique to 'annelids' (e.g. Wheeler *et al.* 1993) are not supported by our results. The two alternative transformations for the chaetal character have major implications for the status of the taxa in the Articulata (see below). In six minimal length trees, the homoplastic presence of chaetae identifies a clade containing the clitellates, pogonophore, polychaetes, and vestimentiferans. The remaining trees show chaetae appearing once for the grade Echiura, Clitellata, Pogonophora, Polychaeta, and Vestimentifera before being lost in the arthropods. The suggestion that chaetae evolved twice means that, in the case of the ((Pogonophora, Vestimentifera) Clitellata Polychaeta) clade, chaetae appeared subsequent to the appearance of segmentation. The proposal by Brusca & Brusca (1990) of the (Annelida (Pogonophora Vestimentifera)) clade being supported by the presence of serially repeated chaetae is consistent with this scenario. The transformation series where chaetae appear once and are lost in arthropods suggests that segmentation is independent of, and arose after, the evolution of chaetae. It follows from this result that serially repeated chaetae are contingent on segmentation. This creates difficulty in identifying a clade based on serially repeated chaetae (e.g. Brusca & Brusca 1990) since chaetae are a symplesiomorphy with the Echiura, and segmentation merely repeats them. The only other taxa which has been proposed to have true chaetae are the brachiopods and juvenile cephalopods (Storch & Welsch 1972; Gustus & Cloney 1972; Orrhage 1973a; Storch 1979). We did not attempt any detailed assessment of other morphological features of the Brachiopoda. However, we find it of interest that analysis of molecular sequence data has

suggested a protostome relationship for brachiopods (Field *et al.* 1988; Halanych *et al.* 1995). Further investigation is needed in this regard.

Pogonophoran and vestimentiferan taxa may have nuchal organs since these structures can be small and difficult to locate, as in sabellid and serpulid polychaetes (see Orrhage 1980). Complete sectioning of the anterior ends of these organisms, especially larvae and juveniles, is required to determine the presence or absence of nuchal organs. Allowing for the presence of nuchal organs gave rise to the nine minimal length trees with the (Pogonophora Vestimentifera) being the sister group to the Polychaeta. Further evidence supporting a sister group relationship of this taxon with a group within the Polychaeta is discussed below.

In six of the minimal length trees, the Clitellata and Arthropoda formed a clade (Figs 1A, 1B, 1C, 1D, 1E, 1F), supported only by the derived state in character 13 (interpolation of mitochondria between the sperm nucleus and anchoring apparatus) appearing at the Clitellata/arthropod' node. Subsequently, a reversal occurs in Euarthropoda (e.g. Fig. 6C). Jamieson (1986, 1987a) accepted the possibility of arthropod polyphyly and, mainly using sperm structure, presented the topology ((Clitellata Onychophora) (Myriapoda Hexapoda)). This hypothesis, with the Onychophora closer to the Clitellata than to any 'arthropod', was not seen in our minimal length trees and would require an additional three steps. This requires the independent development of arthropod features in onychophorans (see Wheeler *et al.* 1993 for shared features in addition to the three synapomorphies and the loss of chaetae implied by our results), or loss of such features (and reappearance of chaetae) in clitellates. Jamieson (1987a: 35, Fig. 2.5A) also discussed a tree that is essentially similar to several of our minimal length trees with the clitellates and arthropods as sister taxa (e.g. Fig. 1A); the differences being our inclusion of the Pogonophora and Vestimentifera and considering the Euarthropoda instead of just the myriapods and hexapods. For this topology, Jamieson (1987a) argued that the transformation series for a character equivalent to our character 13 had to be homoplastic, with 'interpolation of mitochondria between the sperm nucleus and anchoring apparatus' arising independently in

Fig. 7. Alternative minimal length tree topologies to the one shown in Figs 4–6 used to show some of the different transformation series for six of the characters.—A. Tree (same as Fig. 1C) showing transformation series for embryonic cleavage (character 1). In this tree (and Figs 1F, 1I, 2C, 2F, 2I) the Mollusca and Sipuncula form a clade. The presence of the molluscan cross is the only synapomorphy supporting this topology. There are two possible alternative transformation series. The plesiomorphic condition for all ingroup taxa, except the Nemertea, can be the absence of a cross (state 0), or the 'annelid' cross (state 2). Either of these allow the molluscan cross to be a synapomorphy for the Sipuncula and Mollusca. Note, pogonophores and vestimentiferans, allocated the state 'annelid cross' though actually scored with a '?', are indicated by a '?'.—B. Tree (same as Fig. 1B) showing transformation series for the excretory system character. In contrast to Fig. 5B there is only one possible transformation series for this topology.—C. Tree (same as Fig. 2H) showing transformation series for the character based on chaetae. This is the only possible transformation series that supports a clade comprised of clitellates, pogonophores, polychaetes, and vestimentiferans (also for Figs 1G, 1H, 1I, 2G, 2I). This requires the homoplastic appearance of chaetae and that arthropods did not share an ancestor with 'annelids' that had chaetae.—D. Tree (same as Fig. 1E) showing transformation series for nuchal organs when the absence of nuchal organs is allowed for in pogonophores and vestimentiferans. Note, pogonophores and vestimentiferans, were actually scored with a '?', as indicated by a '?' at the terminal branch. The topologies in Figs 1D, 1F, 1I and 2D–2F are also seen when these two taxa are allocated the state absent for this character.—E. Tree (same as Fig. 2E) showing the only possible transformation series for circulatory system that supports this basic topology (also occurs for Figs. 1B, 1E, 1H, 2B, 2H). This transformation series has the 'closed circulatory system' being derived from the molluscan 'open circulatory system, chambered heart'.—F. Tree (same as Fig. 1H) showing the only possible transformation series for the character based on sperm morphology. In this, and 11 other minimal length trees (Figs 1F–1I, 2A–2G, 2I) the state 'mitochondria between the sperm nucleus and anchoring apparatus' appears independently in the clitellates and onychophorans. This should be compared with Fig. 6C.

clitellates and onychophorans. He rejected the reversal of this condition for the 'arthropod' taxa, as seen in our Fig. 5C, and stated 'reversal to sperm in which the midpiece is penetrated by the axoneme, as in insects, cannot be reasonably or parsimoniously envisaged'. (Jamieson 1987a: 35). Our findings are such that a reversal to the plesiomorphic state in the cuarthropods is necessary in order to support the clitellate/arthropod clade in the first place. The homoplastic occurrence of the derived state for this sperm character only appears in our minimal length trees when the clitellates are not the sister group to the arthropods (e.g. Fig. 6F).

Classifications

Various authors (e.g. de Queiroz & Gauthier 1992, 1994; Sundberg & Pleijel 1994) have discussed the flaws in the presently used Linnean system and suggested taxonomic systems, based on the cladistic pattern, to replace it. It is clear that the Linnean categories are too limited to adequately represent the hierarchical nature of the relationships amongst taxa with reference to cladistic pattern (or phylogeny) (Sundberg & Pleijel 1994). For this reason, applying a particular taxonomic level to a clade, e.g. phylum, is often a matter of personal preference or tradition. This can have various undesirable consequences (see Sundberg & Pleijel 1994), and we avoid discussion of the Linnean categories where possible. The issue of most importance is to attempt to use taxon names for clades only and we re-assess taxon names included in this study that result in paraphyly.

Articulata. As outlined in the introduction, we are most concerned with the concept of the taxon Annelida and associated taxa. According to the naming principles outlined by de Queiroz & Gauthier (1990, 1992: 465), the name Articulata should apply as the name of an 'annelid'/arthropod clade since this represents the first name that was ever used for this particular group (Cuvier 1812) and continues today (Ax 1984; Eernisse *et al.* 1992). We choose here to apply an apomorphy-based definition (de Queiroz & Gauthier 1992) of the taxon name Articulata. Hence, the name Articulata refers to the clade stemming from the first ancestor to show:

1. segmentation (i.e. repetition of homologous body structures derived by teloblastic growth); and
2. longitudinal musculature broken into bands.

Classification within the Articulata is somewhat problematic given the various tree topologies involved. The monophyly of the Arthropoda, Clitellata, Pogonophora (including Vestimentifera), and Polychaeta is accepted for the present discussion (but see below regarding the Polychaeta and Pogonophora). One way of classifying the taxa within the Articulata is to use the consensus tree topology (Fig. 2). The consensus tree corresponds, with respect to the Articulata, to three of the minimal length trees (Figs 2D, 2E, 2F). This gives four taxa of equal rank: Arthropoda, Clitellata, Polychaeta, and Pogonophora. Until relationships amongst these taxa are more resolved, this classification seems to be the most appropriate solution. Using the indented system developed by Nelson (1972, 1973), we provide an alternative (Fig. 8) to the

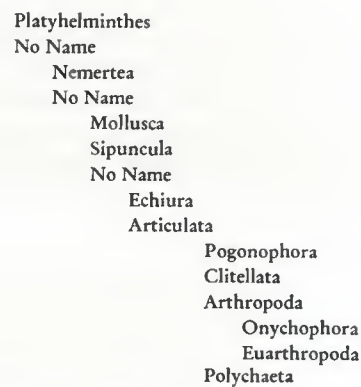


Fig. 8. Indented classification of the taxa included in this analysis. The name Annelida is not used because of uncertainty over whether it refers to a monophyletic group. The Articulata is comprised of the following clades: Arthropoda, Clitellata, Pogonophora, and Polychaeta. The relationships amongst these groups are unresolved. The name Pogonophora should be used for the Pogonophora and Vestimentifera, though they may be shown to belong within the Polychaeta (see text), and hence the name will revert to the original family name, Lamellisabellidae.

traditional Linnean categories which more accurately reflects the consensus tree topology for all taxa included in the analysis (Fig. 2).

Annelida and Arthropoda. There is nothing in our results that suggests that the Polychaeta and Clitellata, the traditional 'annelids', are more closely related to each other than to any of the other articulate taxa. The name Annelida should only be retained if the (Pogonophora Vestimentifera) are included in this taxon, since the Clitellata and Polychaeta never form an exclusive clade without them (Figs 1G, 1H, 1I, 2A, 2B, 2C, 2G, 2H, 2I). However, there are several additional complications involved in retaining the name Annelida:

1. The clitellates were the sister group to the arthropods in a number of minimal length trees (Figs 1A, 1B, 1C, 1D, 1E, 1F) resulting in a paraphyletic 'Annelida' by exclusion of arthropods. If this topology is supported in future analyses, the name Articulata should apply to this clade and the name Annelida should be eliminated.
2. The Arthropoda, Clitellata, (Pogonophora Vestimentifera), and Polychaeta formed a polytomy in three minimal length trees (Figs 2D, 2E, 2F). Under these circumstances the taxon Annelida is also not monophyletic. These factors clearly suggest that the name Annelida should not be used until the relationships amongst the Articulata clades are more resolved.

The monophyly of the Euarthropoda was assumed in this analysis, based on the results of Wheeler *et al.* (1993). The status of the Arthropoda, comprising the Onychophora and the Euarthropoda, is not challenged by any of our results. The finding that the Clitellata are possibly the sister group to the Arthropoda does raise the issue of a potential new name being required for this clade.

Pogonophora and Polychaeta. In this study, the Vestimentifera were found to be the sister group to the Pogonophora in all minimal length trees. Maintenance of the former group at the level of phylum contains no information, and minimally they should revert to being a group under the name Pogonophora (the older name). The reasons for the elevation of the Vestimentifera to the

status of phylum by Jones (1985b) are discussed in the section '*Recent hypotheses with implications for articulate systematics; Evolutionary systematics*'.

With reference to classification within what we will now refer to as the Pogonophora (= Pogonophora and Vestimentifera), several options are available. Webb (1969a) described *Lamellibrachia barhami* and erected the pogonophoran class Afrenulata and order Vestimentifera to contain this new species. The class Frenulata was erected by Webb (1969a) for the non-vestimentiferan Pogonophora. The names Obturata and Perviata, coined by Jones (1981a), were added as pogonophoran sub-phyla containing the classes Afrenulata and Frenulata, respectively. Vestimentifera became commonly used after van der Land & Nørrevang (1975) nominated this name for use at the class level, and was applied by Jones (1985b) at the phylum level. This name is usually used for the clade and the name Obturata can be considered obsolete. The name Perviata refers to the absence of an obturaculum and we recommend the use of Webb's (1969a) older term, Frenulata, which is based on the presence of a bridle. Other authors, such as Southward (1991), have also made suggestions which should be considered in a taxonomic revision of the group. It is very likely, however, that recognition of the Vestimentifera at the same hierarchical level as the Frenulata results in the latter group being paraphyletic. For instance, Southward (1993: 332) discusses one group of frenulates, the Sclerolinidae, as possibly being a 'link with the Obturata (Vestimentifera)'. Cladistic analysis of the relationships amongst taxa within the Pogonophora is warranted.

While, at present, we consider the Pogonophora as a clade of the Articulata with the same rank as Arthropoda, Polychaeta and Clitellata, the possibility that this makes the Polychaeta paraphyletic must be taken seriously. The issue of pogonophores belonging in the Polychaeta has been raised by Uschakov (1933), Hartman (1954), Liwanow & Porfirjewa, (1967), and van der Land & Nørrevang (1975). It should be noted that in half of the minimal length trees found in this analysis, the Pogonophora (and Vestimentifera) was the sister group to the Polychaeta. If this result is supported in further analyses, the status of the clade Pogonophora, and the name of the clade itself, should be altered. In forthcoming studies (Fauchald & Rouse in prep.; Rouse & Fauchald in prep.), we critically examine the possibility that the Pogonophora falls within the Polychaeta. We predict that the Pogonophora will be found to fall within the Polychaeta, close to the sabellid/terebellid clade of polychaetes. Potential synapomorphies between the Pogonophora and this clade include; chaetal types, nephridial distribution, internal septation, and structure of the head appendages. Under these circumstances then the whole pogonophoran clade should revert to the original family name erected by Uschakov (1933), the Lamellisabellidae.

Recent hypotheses with implications for articulate systematics

Evolutionary systematics. Jones (1985a) argued that the frenulate and vestimentiferan Pogonophora and Annelida (interpreted here as Polychaeta and Clitellata) share

a common ancestor that had schizocoely, giving rise to segments with the coelom divided by median mesenteries. Given Jones' (1985a) claim that the vestimentiferans are more closely related to the Annelida than to the frenulates, this hypothesis can only be interpreted to indicate that the mesenteries giving these paired coeloms in the Vestimentifera and Annelida are a symplesiomorphy, and that the segmented condition in the opisthosoma of the frenulate Pogonophora arose independently of the other taxa. Jones (1985a) did not consider the implications of this possible loss of mesenteries in the frenulate pogonophores, and thus (Jones 1985b), used a symplesiomorphy as an argument for erecting a separate phylum. This emphasis on differences in septation and development of the mesenteries in separating the Pogonophora and Vestimentifera was, in any case, erroneous. As pointed out by Southward (1988), mesenteries are present in early stages in both groups, since Southward (1975) demonstrated that they are later lost in the pogonophores such as *Siboglinum fiordicum*.

Jones (1985a) found difficulty in relating the vestimentiferans 'closely' with annelids, because of the nature of the first two 'segments' in the former, and hence also justified their status as a separate phylum (Jones 1985b, 1988). He argued that the first 'segment', the obturaculum, is schizocoelous and the second 'segment' bore 'branchiae', both of which never occur in annelids. In dismissing this argument it should first be noted that the obturaculum is actually derived from the 'second' segment (Southward 1988; Ivanov 1989). Southward (1988) reassessed Jones' division of the vestimentiferan body plan and found it to be identical to that of other pogonophores. We also believe difficulties disappear when Jones' (1985a) first two 'segments' are interpreted, not as segments, but as presegmental. Studies of larval development (Bakke 1980; Jones & Gardiner 1988, 1989; Southward 1988) indicate the cephalic lobe and tentacular apparatus in frenulates, and the tentacular apparatus of the vestimentiferans, correspond to the prostomium and peristomium of annelids. Peristomial appendages, i.e. those arising from behind the prototroch, as in frenulates and vestimentiferans, are common in polychaetes (see Rouse & Fitzhugh 1994). With reference to the schizocoelous nature of the pogonophoran head, similar coelomic spaces are known in polychaetes (Anderson 1959, 1966). Also, Jones (1981b, 1985a) was equivocal as to whether these spaces really are coelomic. In any case such features of the pogonophores do not contraindicate a relationship between pogonophores and 'annelids'.

In proposing the topology (Frenulata (Vestimentifera Annelida)), Jones (1985a, b) ignored a number of features that frenulate and vestimentiferan Pogonophora share. In addition to the synapomorphy used in this analysis, based on the collapse of the gut lumen and reliance on chemosynthetic bacteria for nutrition in a trophosome (Cavanaugh *et al.* 1981; Southward *et al.* 1981), we have identified at least eight other potential synapomorphies for vestimentiferans and frenulates. These include:

1. The presence of a posterior, clearly segmented region, the opisthosoma (Gardiner & Jones 1993, 1994; Southward 1993).

2. Chaetae with a unique dentition pattern. The trunk chaetae of the Frenulata are the same as the opisthosomal chaetae of the Vestimentifera (George & Southward 1973; Orrhage 1973a; Jones 1981a; Jones & Gardiner 1989).
3. At least one extremely elongate 'trunk' segment forming much of the body, with chaetae at the posterior end (Southward 1988). Note the trunk chaetae are only in larvae and juveniles of vestimentiferans (Southward 1988; Jones & Gardiner 1989).
4. A single pair of anterior nephridia for excretory purposes only (Gardiner & Jones 1993; Southward 1993).
5. Gonopores opening at the anterior end of the 'trunk segment' (Ivanov 1961; Webb 1977; Jones 1981b; Southward 1988).
6. Head appendages, or palps, called branchial filaments by Jones (1981a, b and elsewhere), developing from behind the prototroch (Southward 1988; Jones & Gardiner 1989; Bakke 1990). Ivanov (1989) and Selivanova (1989) have demonstrated the homology of the head appendages between both groups.
7. Various features of spermiogenesis and sperm ultrastructure can possibly be considered synapomorphies. These include the spiralling of mitochondria around the nucleus, and anterior spiralling of the nucleus (Franzén 1973; Gardiner & Jones 1985; Jones & Gardiner 1985; Southward & Coates, 1989).
8. A tube formed with a large chitinous component is found in vestimentiferans (Webb 1971) and frenulates (see Southward 1971), and is not a feature known in any polychaetes.

The implications of the hypothesis by Jones (1985a) can be seen when the characters outlined in the above paragraph are incorporated into his topology (Frenulata (Vestimentifera Annelida)). In addition to being numerous steps, longer than the ((Frenulata Vestimentifera) Annelida) hypothesis, the transformation series for each of these characters implies that 'annelids' have lost the features outlined above. Thus, the emphasis of one supposedly 'important' character, i.e. coelomic formation and mesenteries, results in an extraordinary hypothesis for the evolution of polychaetes and clitellates. Parsimony suggests that we must reject this hypothesis.

Cladistic hypotheses. Recently, some hypotheses about the relationships of metazoan groups have been postulated in a cladistic framework (Brusca & Brusca 1990; Schram 1991; Eernisse, *et al.* 1992; Backeljau *et al.* 1993; Wheeler *et al.* 1993; Winnepenninckx *et al.* 1995). Brusca & Brusca (1990: 882, Fig. 1) showed the Annelida as a sister group to a Vestimentifera/Pogonophora clade. This clade was then the sister group to the Arthropoda (*sensu lato*), based on the presence of teloblastic segmentation. The synapomorphies supporting the (Annelida (Pogonophora Vestimentifera)) were the presence of serially repeated chaetae and 'the unique annelidan head'. The Echiura have the same head construction as the Annelida in terms of having a prostomium and peristomium (Newby 1940), reducing the support for the clade to the presence of serially repeated chaetae, a character linked to segmentation. The presence of chaetae in the Echiura was not considered by Brusca & Brusca (1990). The

Pogonophora and Vestimentifera were identified as a clade on the basis of the opisthosoma. Given that Brusca & Brusca (1990) did not have the Annelida identified by synapomorphy, the topology shown by them is not inconsistent with six of our trees (Figs 1G–II, 2G–2I), since the two annelid classes would form a polytomy with the Pogonophora. Reconsideration of the Brusca & Brusca's (1990) chaetal character for the echiurans, 'annelids' (clitellates and polychaetes) and Pogonophora would probably result in a polytomy for the articulates, similar to our consensus tree.

Eernisse *et al.* (1992: Fig. 4) showed a topology that is somewhat similar to our results, for the taxa included in both analyses. The first difference is that they place the Pogonophora (including vestimentiferans) as the sister group to the Annelida (i.e. Polychaeta Clitellata). They also propose an interesting hypothesis that the Annelida is only distantly related to a monophyletic Arthropoda. However, there are some problems associated with the study, particularly in the nature of the characters and scoring. With regard to the latter, Eernisse *et al.* (1992) suffered from many coding errors, e.g. character 99 protonephridia: these are present in Nemertea, not absent. Further examples are discussed below. An additional problem is character linkage leading to differential character weighting. This issue is complex and was briefly discussed above in the Methods section (see also Pleijel *in press*).

Two forms of linkage are present in Eernisse *et al.* (1992) (see Table 1). First, for example, characters 9, 61, and 64 refer to the same condition, metamerism, just worded differently. Secondly, characters 15, 54 (and 56), 55, 57, 58, 59, are linked to the condition of metamerism, in the sense that, if an organism is metameric, it would have to be scored as having the apomorphic state for all these characters. Hence, all taxa coded as having metamerism in the first place will have additional character states unjustifiably grouping them together. Eernisse *et al.* (1992) argued for a distinction between metamerism and serial repetition of organ systems in their coding, but without serial repetition, what is metamerism? Serial repetition without metamerism occurs (e.g. in the Nemertea) but could have been coded as a single character, as should metamerism. There is often variability in the distribution of organ systems in metameric taxa, but the analysis by Eernisse *et al.* (1992) was at a hierarchical level ('class' 'phylum') where this information could not be utilised. The characters based on the nature of the cuticle described below also show a similar form of linkage. If the coding of Eernisse *et al.* (1992) represents an attempt at additive binary coding (a form of ordering characters), as was indicated for character numbers 5–8 in the matrix, this should have been made explicit, along with the reasons for such ordering.

A large amount of information can be contained within a cladogram, particularly when the analysis is as large as that undertaken by Eernisse *et al.* (1992). Often a topology is presented, and some general conclusions are drawn without going into great detail about the character transformations (e.g. Schram 1991; Schram & Ellis 1994). We will here discuss in detail a few of the nodes and characters in Eernisse *et al.*'s (1992) analysis that are of

Table 1. The various characters with states unequivocally supporting four of the nodes in Fig. 4 of Eernisse *et al.* (1992: Appendix 2). Character names are paraphrased

Characters supporting node 4 (Nematoda 'arthropods')	State	Comment
23. Pseudocoelom	Present	Homoplasy; reverses in 'arthropods'
28. Mitosis absent in epidermis	Present	Homoplasy; reverses in 'arthropods'
55. Serially repeated nerve ganglia	Present	Homoplasy; also in 'annelids'
82. Periodic ecdysis	Present	Unequivocal; mis-score for Priapulida?
119. Internal fertilisation	Present	Homoplasy; e.g. also scored clitellates, see text
Characters supporting node 9 (Spiralians)	State	Comment
11. Micromere cross	Present	Mis-scored; also errors in subsidiary character
32. Ventrum ciliated	Present	Homoplasy; 'lost' in many taxa
74. Cuticle	Absent	Homoplasy; present in 'annelids' etc.
76. Chitin in cuticle	Absent	Homoplasy; see text
110. 'Endon' (Beklemishev 1969)	Present	Homoplasy; poor character interpretation
112. Paired, preoral, olfactory fossae	Present	Mis-scored; see text
Characters supporting node 16 (Annelida Pogonophora)	State	Comment
9. Teloblastic segmentation	Present	Same as 61, 64. Homoplasy; in some 'arthropods'
15. Metameric coelom	Present	Linked-54 (+56), 57, 58, 59. In some 'arthropods'
62. Coelomic septa	Present	Linked to coelom and metamerism
65. Heart(s)/dorsal blood vessel	Present	Homoplasy; also in 'arthropods'
103. Orthogon	Absent	Homoplasy; mis-scored for Echiura
Characters supporting node 17 (Clitellata Polychaeta)	State	Comment
47. Paired ventral nerve bundles	Present	Homoplasy; in 'arthropods'. Mis-score Pogon.
54. Serially repeated muscle bundles	Present	Linked. Homoplasy; in 'arthropods'. Mis-score.
56. Serially repeated muscle bundles	Present	Replicate of 54.
57. Serially arranged nephridia	Present	Linked. Homoplasy. Mis-score for Pogon.?
58. Serially repeated respiratory surf.	Present	Linked. Miscore for polychaetes and clitellates
59. Serially repeated gonads	Present	Linked character. Mis-score for Pogon.
61. Schizocoelous metamerism	Present	Same as 9, 64. Mis-score for Pogon.
63. Branchioauricular sinuses	Present	Mis-scored
64. Metamerism in muscles, nerves, etc.	Present	Same as 9, 61. Mis-score for Pogon.
104. Subcutaneous neural plexus	Present	Mis-score for Pogon.

relevance to this paper. These are summarised in Table 1. Our concern is that cladistic hypotheses, such as the arthropods not being closely related to the annelids, can be taken at face value and the implications for the initial homology hypotheses (i.e. character coding) become hidden in the complexity of the tree topology.

The potentially most significant hypothesis in Eernisse *et al.*'s (1992) analysis was that the Nematoda are the sister group to a clade comprised of the Onychophora, Euarthropoda, Kinorhyncha, and Tardigrada (see Table I). Four of the five synapomorphies supporting this node were homoplastic, and either reverse in 'arthropods' or also appear in 'annelids' (Dales 1963), though the scoring of internal fertilization (character 119) as present, i.e. plesiomorphic, for the Clitellata is somewhat dubious (see Jamieson 1992: 296). This left character 82 (Ecdysis present) as the only non-homoplastic synapomorphy supporting node 4; an initial homology hypothesis open to some debate. For example, the Priapulida also show ecdysis (Shapeero 1961), yet were not scored with ecdysis present in the Eernisse *et al.* (1992) matrix.

Table I shows the six synapomorphies Eernisse *et al.* (1992: Appendix 2) presented in support of the monophyly of a clade of spiralian taxa (excluding arthropods), at node 9 in their Fig. 4. Character 11 (Cleavage micromeres form cross) had the following taxa scored with the state present: Acoelomorpha, Rhabditomorpha, Sipun-

cula, Polyplacophora, Conchifera, Echiura, and Polychaeta. Other relevant taxa were scored with '?'. The scoring of a cross present in flatworm taxa was incorrect; Salvini-Plawen (1985, 1988) clearly stated that a cross is absent. The Onychophora, and some euarthropod taxa, were correctly coded with a '?', since, as in many of the groups scored with this feature present, a micromere cross is not discernible in members with lecithotrophic development. Character 12 of Eernisse *et al.* (1992), while not appearing to identify any clades, is relevant to this discussion since it is related to the formation of a micromere cross, information used in our present analysis. In character 12, which was based on the nature of the 'cross' during cleavage (radiate or interradiate), the Cnidaria (the taxon used to root the tree) were scored with a question mark. Eernisse *et al.* stated that a dash '-' in the matrix represented the same state as in the outgroup taxon. Only the eight taxa scored with a cross present in character 11 were scored with 'radiate' (0) or 'interradiate' (1) for character 12; the remainder had a '-'. Presumably, all other taxa were thus scored with a '?' as in the Cnidaria, but this was not explained. The Acoelomorpha and Rhabditophora were scored as having the same state as the molluscan taxa and the Sipuncula, i.e. a cross with a radiate pattern. As discussed for character 11, no cross of either kind has been reported in these groups. Character 12 is linked to character 11 (absence or presence of a cross). The scoring

of '?' for the outgroup taxon is an appropriate way for dealing with such inapplicable characters (see Methods). However, this was not indicated with an N (admittedly equivalent for the computer to a '?') as Eernisse *et al.* (1992) did for supposedly inapplicable characters for the Cnidaria, such as those based on the coelom. Also, this methodology was inconsistently applied since characters such as 61, 62, and 98, which relate to a coelomate condition, were not given an N for the Cnidaria, but a 0. Ingroup taxa for which many characters were inappropriate, were often scored with a 0 rather than N. This can have the effect of grouping taxa on synapomorphies based on inappropriate absences as well as grouping via loss (homoplasy). For instance, the Rhabditophora and the Acoelomorpha were both scored absent for character 13, triploblastic tissue organisation, which was listed as an unequivocal synapomorphy for the clade through reversal. We interpret the condition triploblastic to mean mesoderm present, as well as ectoderm and endoderm. The Acoelomorpha were scored as absent for any mesoderm-contributing cells in characters 5–8, hence scoring them as absent for triploblasty was inappropriate, and probably erroneous for the Rhabditophora (see Brusca & Brusca 1990). As discussed above, this linkage problem is present throughout the paper.

Character 32 (ciliated ventral surface in adult) subsequently reversed to the absent condition in the Sipuncula, Echiura, Annelida, Vestimentifera, and Pogonophora. Character 74 (cuticle; continuously secreted, non-living external layer(s) containing protein) transforms to the state 'absent' below node 9 but subsequently reverses for the clade comprising the Sipuncula, Echiura, Annelida, Vestimentifera, and Pogonophora. With reference to the cuticle characters in general, it seems incongruous that the Onychophora, 'arthropod' taxa, and tardigrades were scored as having no cuticle (Character 74), and then scored as having chitinous proteins invested in the cuticle (Character 76), cellular secretion of chitinous proteins (Character 77), cuticular covering of entire external body surface (Character 78), and sclerotinisation of cuticle (Character 79). Interestingly, the polychaetes, clitellates, and pogonophores were scored as absent for character 78 after having been scored as present for character 74. Character 76 (chitinous proteins in cuticle) transforms below node 9 to the absent condition, though the Pogonophora were scored with this as present, presumably on the basis of chitin being a component in the tube or chaetae (Southward 1971; George & Southward 1973). Eernisse *et al.* (1992: 329) specifically did not score the Phoronida as having chitin, even though this is a component of their tubes. Thus, for consistency, the scoring of chitin as present in pogonophores cannot have been based on its presence in their tubes. This does then raise the question as to why the Echiura, Polychaeta, and Clitellata were not scored as having chitin since it is present in all chaetae (George & Southward 1973).

Character 110 of Eernisse *et al.* (1992), 'Endon; medial cerebral ganglion with adjacent aboral statocyst organ', was a character based on Beklemishev (1969). This character presumably referred to the condition found in some flatworm taxa where a single statocyst, located close to a cerebral ganglion, was called the 'endon' by Bek-

lemishev. Nearly all spiralian taxa (Pogonophora, Echiura, Sipuncula, Nemertea, and two molluscan groups) were scored with a question mark for this character, or absent in the case of clitellates. The gnathostomulids were scored as having an endon. In fact, it is absent (Ax 1987: 261). An endon was otherwise scored as present in the Acoelomorpha, Polyplacophora, Conchifera, and Polychaeta, and as polymorphic in the Rhabditomorpha. Beklemishev (1969: 161) specifically stated that such a structure is absent in the Amphineura (a taxon that includes the Polyplacophora). That the state found in flatworm taxa should be scored as homologous to the paired statocysts that lie away from the brain, found in some polychaetes and conchiferans, seems dubious, especially given the wide distribution of statocysts in the Metazoa.

Character 112 of Eernisse *et al.* (1992) 'Paired olfactory fossae of preoral lobes' was also based on the ideas of Beklemishev (1969). Beklemishev (1969: 157) regarded the cephalic olfactory fossae of 'turbellarians' to be 'astonishingly similar' to those of nematodes, nemerteans, and polychaetes. The nemerteans and nematodes were scored with question marks for this character. Presumably this character referred to the nuchal organs of polychaetes, which are absent in the Echiura, clitellates, and are unknown in Pogonophora (see above, **Methods Characters**). Eernisse *et al.* scored this character as present in these taxa. Furthermore, the structure is single, not paired in the Sipuncula (Hyman 1959), which was also scored as present. This character was also scored as being present in all four molluscan taxa, though Beklemishev (1969: 158) specifically states 'No certain homologues of cerebral olfactory fossae are known in molluscs.'

While not refuting the hypothesis proposed by Eernisse *et al.* (1992), the problems raised here cast doubt on the strength of any conclusions drawn from their analysis. A detailed analysis of all characters used in Eernisse *et al.* (1992) is required, particularly with regards to the initial homology hypotheses and the influence of linked (non-independent) characters, to properly assess the overall topology of their cladograms.

Leaving aside the larger issue of the relationships of arthropods and spiralian taxa, we will briefly examine the implications of the analysis by Eernisse *et al.* (1992) for the Annelida and Pogonophora. Table I shows the character states supporting the Pogonophora (including vestimentiferans) as sister group to the Annelida (i.e. node 16). All of the characters listed, with the exception of character 62 (coelomic septa), which is subsidiary to segmentation and the presence of a coelom, are scored the same way in the 'arthropods' (or given a '?'). As has already been discussed several of these characters are repetitive or linked.

Character 103 (orthogon; a diffuse neural plexus) reverses to absent, but why the Echiura were scored as present for this feature is not apparent in the quoted sources (this character also reverses in the arthropods and associated taxa).

Synapomorphies hypothesised by Eernisse *et al.* (1992) for the Polychaeta and Clitellata (node 17 of Fig. 4) are listed in Table I. With reference to the scoring of the Pogonophora, it can be argued that there was mis-scoring

Table II. Synapomorphies supporting the clades Articulata and Annelida in the morphological analysis of Wheeler *et al.* (1993). Character names are paraphrased. All characters are discussed more fully in the text

Articulata synapomorphies	Comment
50. Antennae and palps	Homology of pre-oral appendages uncertain
55. Order in fate maps	Symplesiomorphy with Sipuncula and Echiura
58. Teloblastic segmentation	Agrees with our results
59. Schizocoelic metamorphism	Linked to 58
60. Acranial protocerebrum	Linked to 58, 59?
61. Double ventral nerve cord	Varies in 'annelids'. Possible symplesiomorphy?
62. Longitudinal muscle bundles	Agrees with our results
63. Coelomoducts	Symplesiomorphy?
64. Dorsal blood vessel	Symplesiomorphy?
Annelida synapomorphies	Comment
7. Annelid head	Symplesiomorphy; not distinct from Echiura
9. Longitudinal muscle bundles	Same as 62? Also present in Onychophora
10. Annelid nephridial system	No unique 'annelid' system.

or poor interpretation for all characters that grouped the Polychaeta and Clitellata as sister taxa. For characters 47 and 104, pogonophores have paired nerve bundles (Jägersten 1956; see also Appendix III) as do polychaetes and clitellates. More or less diffuse nerve nets are present cutaneously or subcutaneously in all three groups (Southward 1971), so polychaetes and clitellates cannot be unequivocally scored with this character. Characters 54, 56, 57, 58, 59, comprise specific organ-systems that follow from the nature of segmentation. Serially repeated transverse muscles (character 54, repeated as character 56) are present in pogonophores (Southward 1975: 70, also 1993) as well as in other annelids. With reference to character 57, the condition found in pogonophores, a single pair of anterior excretory nephridia (Southward 1993), is in fact present in many polychaetes (Meyer 1888; Fauchald & Rouse in prep.) and the nature of the pogonophoran gonoducts has not been fully investigated. It is likely that there is possible nephridial involvement in the ducts, as occurs in many polychaetes (Goodrich 1945). Serially repeated respiratory structures (character 58) are not present in all polychaetes, and are absent in most clitellates (Cook 1971); when present, these structures may not be segmentally arranged, let alone homologous (Gardiner 1988). While most polychaetes have gonads present in many segments (character 59), all clitellates, and some polychaetes, have gonads limited to a few or single segments only. Pogonophoran gonads are present in only a single segment; hence the scoring should be the same for all three groups, unless one is willing to make *ad hoc* assumptions about the plesiomorphic condition for each 'clade'. Character 63 was mis-scored for the polychaetes and clitellates; they do not have branchioauricular sinuses with ctenidial pores.

Thus, given these problematic characters from Eernisse *et al.*'s (1992) analysis, we are left with no synapomorphies for the Clitellata and Polychaeta; the Annelida cannot be identified separately from the Pogonophora. We have not attempted a re-analysis after making corrections for the above errors. It is clear that there is no justification for suggesting that the clitellates and polychaetes are more closely related to one another than either is to the Pogonophora *sensu lato*. Similarly, it is

likely that the arthropods could move back as at least the sister group with the 'annelids'.

An analysis by Wheeler *et al.* (1993) investigated the issue of arthropod monophyly and concluded that the Onychophora and Euarthropoda formed a clade, Arthropoda, that was the sister group to a monophyletic Annelida (*Glycera* a polychaete, and two clitellates were used as 'annelids'). This conclusion was based on a parsimony analysis of combined morphological and molecular sequence data, rooted using molluscs. It is interesting to note that the separate molecular sequence data analyses for loci of 18S rDNA and Polyubiquitin (both separately and combined) did not support monophyly of the Annelida. Ubiquitin molecular sequence data supported the monophyly of the Articulata, and only the combined molecular sequence data supported the monophyly of the Arthropoda. Their morphological analysis, using 100 characters, resulted in monophyletic Articulata, Annelida, and Arthropoda, respectively. When the morphological and molecular data were combined, the monophyly of the Articulata, Annelida and Arthropoda was also supported. However, as discussed above with reference to the Eernisse *et al.* (1992), there are some problems with linkage of the morphological characters in the analyses by Wheeler *et al.* (1993) that cast doubts on the their support for annelid monophyly. Also, some of the proposed synapomorphies cannot be supported because of insufficient sampling of taxa.

We will limit our discussion here to the characters that were included as indicating monophyly of the Articulata and the Annelida. These are summarised in Table II. The proposed morphological synapomorphies for the Articulata were (character numbers are from Wheeler *et al.* 1993: Fig 5.):

50. Antennae and palps. This was an unordered multistate character with the states 0, nothing; 1, prostomial/preoral palps; 2, postoral antennae. Wheeler *et al.* (1993: 10) state that this character was coded deliberately to bias against arthropod monophyly, with state 1 being found in polychaetes and onychophorans and state 2 in all euarthropods, except for pycnogonids, *Limulus* and arachnids. The resulting transformation series has four steps.

Beyond the dubious homology assessment of polychaete head appendages (many polychaete groups have none) with those of the Onychophora, this character state provides little in the way of support for the monophyly of the Articulata. Under the optimization used ('deltran' is stated, but only 'acctran' will provide this result) in their Fig. 5, character 50: 1 arises below the (Annelida Arthropoda); reverses to state 0 for the clitellates; and transforms to state 2 for the euarthropods before reversing again to state 0 for the clade (Pycnogonida (*Limulus* Arachnida)). Four other equally parsimonious transformations are possible, with state 1 arising independently in the polychaetes and Onychophorans.

55. *Ordering of fate map tissues (anterior–stomodeum–midgut–mesoderm–posterior vs. anterior midgut–mesoderm–stomodeum–posterior)*. This character was homoplastic, with the state 1 (anterior–stomodeum. . .) arising below the (Annelida Arthropoda) changing to the outgroup condition below the Euarthropoda before reverting to state 1 for the (Diplopoda Chilopoda Hexapoda). Wheeler *et al.* (1993) coded this character to bias against arthropod monophyly, as was done for character 50. Some doubt can be expressed about the homology of molluscan fate map with those of chelicerates, xiphosurids, pycnogonids and crustaceans. For example, several molluscs seem to have similar fate map patterns to those of polychaetes, with the stomodeum anteriorly and the mesoderm posteriorly (MacBride 1914; Hadfield 1979; Pearse 1979). The homology assessment of fate maps amongst the chelicerates, xiphosurids, pycnogonids and crustaceans is also problematic (see Anderson 1973; Schram 1986). More importantly, the echiurids (Newby 1940) and Sipuncula (Rice 1975) show the same fate map, in the sense of this character description, as the 'annelids' and Onychophora etc., and this cannot reasonably be interpreted as a synapomorphy for the Articulata.

58. *Segment origin in caudal elongation or proliferation zone*.

59. *Schizocoelous metamerism between preoral acron (prostomium) and the non-metamerism (sic) telson (periproct)*. These two characters refer to the condition of segmentation and cannot be said to be independent as discussed above for characters 47, 54, 57, 58, and 59 in Eernisse *et al.* (1992). They correspond to our character 3. Segmentation, which was one of our two synapomorphies for the Articulata.

60. *Acronal protocerebrum serving the eyes and containing an association center connected with pedunculate bodies*. The acron, originally defined by Hatschek (1878a) to refer to the prostomium and peristomium of annelids, is now largely used to refer to the pre-segmental region in arthropods (Brusca & Brusca 1990). An acron, specifically stated to be absent in the Onychophora by Anderson (1973), is coded as present by Wheeler *et al.* (1993). Also, while nerve elements are present in the prostomium of polychaetes and clitellates taxa, they are not all associated with eyes. For example, in many clitellates, the brain is well away from the prostomium, and eyes are generally

absent (Jamieson 1992). The nature of the anterior end of platyhelminths, sipunculids, and nemerteans is such that there is innervation of eyespots from anterior extensions of the 'brain' (Brusca & Brusca 1990). Also, since the condition of the acron is linked with segmentation, i.e. they are pre-segmental structures, this seems to be a dubious separate synapomorphy for the Articulata.

61. *Double ventral somatic nerve cord*. We did not use a character based on the nature of the nerve cord because of uncertainty over homology. A double nerve cord is present in arthropods (Brusca & Brusca 1990), clitellates (Dales 1963), myzostomids (Prenant 1959: 745), pogonophores (Jägersten 1956; Ivanov 1959), and vestimentiferans (in the vestimentum region; Gardiner & Jones 1993). While some polychaetes show paired ventral nerve cords, in most cases, there is a single mid-ventral cord (Golding 1992). Similarly, some myzostomids have a single ventral nerve cord (Jägersten 1940). A single nerve cord is present in echiurids (Brusca & Brusca 1990) and sipunculids, though in the latter case, fusion of two cords has been seen in one species (Rice 1973). In the Nemertea, Mollusca and Platyhelminthes, there are a varying number of ventral cords. In 'turbellarian' platyhelminths there are one to several pairs of longitudinal nerve cords (Rieger *et al.* 1991). A pair of lateral nerve cords is present in nemerteans (Turbeville 1991) and a central ventral pair and lateral pair are present in molluscs (Brusca & Brusca 1990). Determining states given this variability in morphology was thought to be too problematic for our analysis, and we are unsure of its utility as a synapomorphy for the Articulata.

62. *Dorsal and ventral longitudinal muscle bundles*. We find this is also a synapomorphy for the Articulata, but it is difficult to explain how character 9. 'Longitudinal muscles broken into bands instead of sheets', can then serve as a synapomorphy for the Annelida (see below).

63. *Coelomoducts their vestiges and derivatives*. The vestigial nature of the coelomoducts and derivatives varies considerably amongst articulates and cannot be regarded as a synapomorphy for the Articulata. The gonads of the nemerteans have been interpreted as incipient or modified coelomoducts (Turbeville 1991). The 'nephridia' of the Echiura have also been interpreted as mixonephridia (Goodrich 1945: 232), and as such they have mesodermal components, as is found in the majority of polychaetes (Goodrich 1945). Clitellates have distinct, well developed coelomoducts separate from the nephridial system (Goodrich 1945). The components of the urinogenital system of the Sipuncula are generally referred to as metanephridia (e.g. Hyman 1959; Brusca & Brusca 1990; Rice 1993). The possibility that coelomoducts are incorporated into the 'metanephridia' and thus forming mixonephridia needs further investigation. Also, coelomoducts are possibly present in the molluscs (Brusca & Brusca 1990).

64. *Dorsal blood vessel with forward-going peristalsis*. While such a system is present in the members of the Articulata, it is also present in the Echiura (Pilger 1993)

Table III. Examples of characters used by Schram (1991). States are paraphrased somewhat

Character	'Primitive' state	'Derived' state	Comment
11. Mesoderm	Absent	Present	
19. Mesoderm	Ectomesoderm	4d mesoderm	Linked to 11
43. Mesoderm	Not segmented	Segmented or serial structures	Linked to 11, 19, 63
63. Mesoderm	No particular cell source	Teloblasts for mesoderm etc.	Linked to 11, 19, 43
42. Body cavity	No body cavity	Coelom or (metacoel)	
51. Coelom	Undivided	Archimeric	Linked to 42, 52
52. Coelom	Schizocoel, if present	Enterocoel, if present	Linked to 42, 51
64. Coelom	Large and pervasive	Around circulatory system	Linked to 42, 51, 52

and cannot be considered an articulate synapomorphy. This assessment of the proposed synapomorphies by Wheeler *et al.* (1993) illustrates the complexity of characters involved and in assigning homologies. While their analysis supports our conclusion that there is a monophyletic taxon Articulata, we see their finding of a monophyletic Annelida as more problematic.

The synapomorphies proposed by Wheeler *et al.* (1993) for the Annelida were shown in Table II. The nature of the annelid head was discussed above with reference to the analysis by Brusca & Brusca (1990), and it cannot be considered to be distinct from the condition seen in the Echiura (Newby 1940). Also, epidermal paired chaetae are present in the Echiura. The nature of the longitudinal muscles, i.e. broken into bands, is considered here to be similar in the Onychophora (Manton 1967) and was found to be synapomorphy for the Articulata. A separate form of banding of longitudinal musculature in the various 'annelid' groups cannot be discerned at this time. There is no unique condition of the annelid nephridial system that can be considered a synapomorphy for the group. The variability of polychaete nephridial systems is remarkable (Goodrich 1945; Schroeder & Hermans 1975), and a plesiomorphic polychaete condition has not been postulated. Serially repeated metanephridia that are separate from the genital system are present in the Clitellata and capitellid polychaetes (Goodrich 1945), as it is the Onychophora (Storch & Ruhberg 1993). As shown in our analysis above, the presence of a cuticle with collagen is a symplesiomorphy for the annelid groups, being also found in Sipuncula and Echiura. Thus, none of the proposed morphological synapomorphies for the Annelida *sensu* Wheeler *et al.* (1993) is valid. The addition of these characters to the combined morphological analysis suggested a monophyletic Annelida, and this result should now be questioned.

Two papers have used the matrix published by Schram (1991) and generated the same consensus tree, showing a polytomy for almost all ingroup taxa discussed here, as well as little resolution amongst major metazoan clades (Eernisse *et al.* 1992: Fig. 2a; Backeljau *et al.* 1993: Fig. 2B). The paper by Schram & Ellis (1994) is a response to Backeljau *et al.* (1993) and, seemingly, Eernisse *et al.* (1992) in which they correct a scoring error and remove the taxa 'ancestor' and the Pentastomida from the matrix of Schram (1991). They show a consensus tree of 30 minimal length trees (123 steps, with uninformative characters removed) with the topology of the taxa relevant to this discussion being (Nemertea (Arthropoda (Pogonophora (Annelida (Mollusca (Echiura Sipun-

cula)))). The 'deuterostomes' are the sister group to this clade with the Platyhelminthes (and gnathostomulids) sister group to this assemblage. This topology results in some novel transformations series but suffers from similar character coding problems to those seen above in Eernisse *et al.* (1992). Two examples are sufficient here and are summarised in Table III. Apart from the obvious, and unacknowledged, linkage problems involved with the characters that are subordinate to the presence of mesoderm or coelom, there are further errors in coding and logic. One example also occurs with reference to the suite of characters associated with mesoderm. Character 19 (already subsidiary to character 11) refers to the mode of mesoderm formation, ectomesoderm or 4d mesoderm. Taxa relevant for this discussion; Platyhelminthes, Nemertea, Annelida, Sipuncula, Echiura and Mollusca are scored for 4d mesoderm, whereas all other taxa, whether they have mesoderm or not, are scored with the state for ectomesoderm. Similarly, characters 43 and 63, which refer to the structure and formation of mesoderm and ectoderm (hence also linked to character 11, 19), have taxa that are justifiably scored for the states 'mesoderm not segmented' (character 43) and 'no particular cell source' (character 63) included with taxa having no mesoderm at all. Additionally, the Sipuncula, Echiura and Mollusca, scored with 4d mesoderm (character 19), are also scored with no particular cell source for character 63. This reversal, which is implied by the topology of Fig. 1 of Schram & Ellis (1994), serves as the only synapomorphy grouping these three taxa. This is erroneous, at least for the Echiura and Sipuncula, where there is no difference in the source of mesoderm formation from that seen in polychaetes and clitellates ('annelids'), except that the latter groups are segmented (Brusca & Brusca 1990).

Incidentally, we ran the matrix of Schram (1991), altered according to the parameters and corrections of Schram & Ellis (1994), and found 384 minimal length trees of length 124, with a consensus tree identical (given rooting differences, deletion of uninformative characters, and deletion of ancestor and Pentastomida) to fig. 2a of Eernisse *et al.* (1992) and fig. 2B of Backeljau *et al.* (1993). We then obtained Schram & Ellis's matrix (thanks to Dr Schram and to Dr H. ten Hove who ran the matrix for Schram & Ellis using Hennig86), and noted that their scoring for the Entoprocta for character 31 was different from Schram (1991). The 'derived' state (protonephridia) shown for entoprocts in Schram (1991) appears as the 'primitive' state '0' (no special excretory organ) in the unpublished matrix of Schram & Ellis (1994). Altering the matrix of Schram (1991) for character 31 to state '0'

then results in 30 minimal length trees with 123 steps, as found by Schram & Ellis (1994). This change is not actually justifiable since entoprocts do have protonephridia (Hyman 1951b; Brusca & Brusca 1990). While the scoring of character 31 for the entoprocts may simply be a typographical difference between Schram (1991) and the matrix used by Schram & Ellis (1994), the former matrix is correct on this issue. Thus, the 'correct' analysis should have been 384 minimal length trees (length 124) and the resulting lack of resolution of relationships amongst the taxa dealt with in this paper. We draw this to the attention of those wishing to repeat Schram & Ellis's (1994) result.

Winnepenninckx *et al.* (1995) used maximum parsimony analysis of 18S rRNA molecular sequence data to assess relationships among 'protostomes' and also included some deuterostomes (chordates and echinoderms). They found a single minimal length tree with a topology, rooted using a platyhelminth, that suggested the following: the Protostomata is paraphyletic by exclusion of the 'deuterostomes'; the Arthropoda is the sister group to a deuterostome/limited 'protostome' clade; the Annelida (a polychaete and a clitellate) is paraphyletic by exclusion of the Sipuncula; the Vestimentifera and Pogonophora form a clade that is the sister group to the Echiura; the Mollusca is paraphyletic by exclusion of the Nemertea, Vestimentifera, Pogonophora and Echiura; and that the Chordata is paraphyletic. This result is incongruent, to say the least, with our results. When we map our characters onto the tree topology of Winnepenninckx *et al.*'s (1995) fig. 2 (as far as possible, with deuterostomes deleted and 'mollusc' repeated to form a paraphyletic group with respect to the Nemertea, Vestimentifera, Pogonophora and Echiura), the various transformation series minimally total 41 steps, 18 steps longer than our minimal length trees. Winnepenninckx *et al.* (1995) conclude that further molecular sequence and anatomical data is needed to resolve discrepancies in hypotheses regarding the monophyly of the Mollusca and Annelida. We agree.

Conclusions

The aim of this paper was to consider the monophyly of the Annelida and to assess the relationship of taxa usually associated with annelids; the Pogonophora, Vestimentifera and Arthropoda. Our results show 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. We suggest that the name Annelida cease to be used, unless relationships within the Articulata are resolved to show a monophyletic Annelida. The Vestimentifera is the sister group to, or more likely a clade within, the frenulate pogonophores, and the name Pogonophora is retained for this group. The name Articulata is applied to the Clitellata, Euarthropoda, Onychophora, Pogonophora, Polychaeta, and Vestimentifera. The synapomorphies for the Articulata are the presence of segmentation and longitudinal muscle broken into bands.

The definition of the Articulata can be formulated as the clade stemming from the first ancestor to show repetition of homologous body structures derived by teloblastic growth and longitudinal muscles broken into bands. The Articulata is considered, based on current evidence and the consensus tree topology, to consist of four clades; the Arthropoda, Clitellata, Polychaeta, and Pogonophora, though the latter group may be a clade of polychaetes. If this is shown more conclusively, the Pogonophora should revert to the original family name, Lamellisabellidae Uschakov, 1933.

This analysis assumed the monophyly of the Polychaeta, a taxon that has never been identified by synapomorphy. The Clitellata, 'arthropods', and Pogonophora may well prove to fall inside the Polychaeta; use of these taxa as outgroups for an analysis of polychaete relationships is not justifiable at this time. Molecular systematic studies to date have only included at most one polychaete. We feel a more judicious selection of polychaete species will result in more powerful assessments of the membership of, and relationships within, the Articulata.

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Appendix I

Character list

1. Cleavage pattern
 0. Cross absent
 1. 'Mollusc' cross
 2. 'Annelid' cross
 3. Meroblastic cleavage
2. Coelom
 0. Absent
 1. Present
3. Segmentation
 0. Absent
 1. Present
4. Circumesophageal nerve ring
 0. Absent
 1. Present
5. Digestive tract with
 0. Mouth only
 1. Anus present (at least transiently)
6. Gut lumen
 0. Present
 1. Absent

7. Nephridia
 0. Protonephridia
 1. Metanephridia
 2. Pericardioducts
8. Cuticle
 0. with glycocalyx only
 1. with conchin
 2. with collagen
 3. with chitin
9. Chaetae
 0. Absent
 1. Present
10. Nuchal organs
 0. Absent
 1. Present
11. Longitudinal muscles
 0. Muscles in sheets
 1. Muscle broken into bands
12. Circulation system
 0. Absent
 1. Closed
 2. Open with chambered heart
 3. Open with ostiate heart
13. Sperm mitochondria
 0. Not interpolated between sperm nucleus and mitochondria
 1. Interpolated between sperm nucleus and mitochondria

Appendix II

Scoring matrix

Taxa	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Platyhelminthes	0	0	0	0	0	0	0	0	0	0	0	0	0
Clitellata	2	1	1	1	1	0	1	2	1	0	1	1	1
Echiura	2	1	0	1	1	0	1	2	1	0	0	1	0
Euarthropoda	3	1	1	1	1	0	1	3	0	0	1	3	0
Mollusca	1	1	0	1	1	0	2	1	0	0	0	2	0
Nemertea	0	1	0	0	1	0	0	0	0	0	0	0	0
Onychophora	3	1	1	1	0	1	3	0	0	1	3	1	1
Pogonophora	0/1/2	1	1	1	1	0	2	1	?	?	1	1	0
Polychaeta	2	1	1	1	1	0	1	2	1	1	1	1	0
Sipuncula	1	1	0	1	1	0	1	2	0	0	0	0	0
Vestimentifera	?	1	1	1	1	1	1	2	1	?	1	1	0

Appendix III

Sources for scoring taxa.

For each group one or more basic sources is given. For certain characters additional sources are listed where documentation from the primary literature appeared necessary, or where a feature was not clearly specified in the basic source.

Platyhelminthes

- Basic sources: Brusca & Brusca (1990); Rieger *et al.* (1991).
 Character 1, Salvini-Plawen (1985, 1988).
 Character 2, Smith & Tyler (1985).
 Character 5, Ax (1987).
 Character 7, Rieger *et al.* (1991).
 Character 8, Rieger (1984); Rieger *et al.* (1991).
 Character 11, Rieger *et al.* (1991).
 Character 13, Rieger *et al.* (1984).

Clitellata

- Basic sources: Cook (1971); Jamieson (1981, 1992).
 Character 1, Needham (1990).
 Character 8, Richards (1984).
 Character 9, Jamieson (1981).
 Character 11, Avel (1959).

Echiura

- Basic sources: Stephen & Edmonds (1972); Pilger (1993).
 Character 1: Newby (1940).
 Character 3: Newby (1940).

Character 4: The nerve ring is present in the proboscis; the ventral nerve cord is single in most of the body, but fused from a pair present anteriorly (Stephen & Edmonds, 1972).

Character 8, Storch (1984); Menon & Arp (1991).

Character 9, Orrhage (1971).

Euarthropoda

Basic sources: Brusca & Brusca (1990); Wheeler *et al.* (1993)

Character 1, Anderson (1973).

Character 2, Anderson (1973).

Character 3, Anderson (1973).

Character 7, Meglitsch (1972); Weygoldt (1986).

Character 11, Brusca & Brusca (1990); Wheeler *et al.* (1993).

Character 13, Jamieson (1987a).

Mollusca

Basic sources: Brusca & Brusca (1990); Scheltema (1993).

Character 1, Scheltema (1993).

Character 2, Reynolds *et al.* (1993); Morse & Reynolds (in press).

Character 7, Salvini-Plawen (1988); but see Reynolds *et al.* (1993)

Character 12, Reynolds *et al.* (1993)

Nemertea

Basic sources Hyman (1951a); Turbeville (1986, 1991).

Character 1, Salvini-Plawen (1985, 1988); Scheltema (1993).

Character 8, Rieger (1984).

Character 12, Bartolomaeus (1988).

Onychophora

Basic sources: Brusca & Brusca (1990); Storch & Ruhberg (1993).

Character 1, Anderson (1973).

Character 2, Anderson (1973).

Character 3, Anderson (1973).

Character 13, Jamieson (1986).

Pogonophora

Basic sources: Southward (1988, 1993).

Character 1, Bakke (1980).

Character 4, Gupta & Little (1975) reported no nerve ring present in the species they studied. Southward (1975) found three cords; Ivanov (1963) found two cords; the latter also reported a nerve net present. Caullery (1914a, b) and Jägersten (1956) both reported a nerve ring present anteriorly with the latter author reporting a paired nerve cord in parts.

Characters 5 and 6, Transitory anus and reduction of gut lumen reported by Flügel & Callsen-Cenic (1992), Southward (1993).

Character 7, Southward (1980) reported protonephridia from *Oligobranchia gracilis* and in *Siboglinum* (the latter as a personal communication from Nørrevang).

Character 9, Gupta & Little (1970) George & Southward (1973).

Polychaeta

Basic sources: Dales (1963); Brusca & Brusca (1990); Fauchald & Rouse (in prep.).

Character 1, Clark (1969); Salvini Plawen (1988).

Character 3, Anderson (1973).

Character 7, Metanephridia are assumed to be the plesiomorphic condition since protonephridia are restricted to small acoelomate forms and to a small group of phyllodocimorph taxa.

Character 8, Richards (1984); Storch (1988).

Character 9, Orrhage (1971, 1973a); George & Southward (1973).

Character 10, Brusca & Brusca (1990); Fauchald & Rouse (pers. obs.).

Character 11, Storch (1968).

Character 12, Gardiner (1992).

Character 13, Jamieson & Rouse (1989).

Sipuncula

Basic sources, Stephen & Edmonds (1972); Rice (1993).

Character 1, Clark (1969); Scheltema (1993).

Character 8, Storch (1984).

Character 10, Paired nuchal organs reported by Brusca and Brusca (1990); in reality the cephalic tubes leading into the deeply sunk cephalic organ are on occasion paired; the organ itself is always single as far as known. The nuchal organ may also be a protruding medial structure, sometimes bilobed or quadrilobate (Hyman, 1959: 616).

Vestimentifera

Basic sources, Jones (1985a, b); Gardiner & Jones (1993, 1994).

Character 3, Southward (1988), Jones and Gardiner (1988, 1989).

Character 4, Nerve cord ventral and paired, fusing in the trunk region. Brain is a ring shape (van der Land & Nørrevang, 1975).

Characters 5 and 6: Open digestive tract present for a short while in the juveniles Southward (1988), and Gardiner & Jones (1988, 1989).

Character 7, van der Land & Nørrevang (1975) found one pair of anterior nephridia in *Lamellibrachia barhami* and *L. luymeri* opening to the exterior with a single median dorsal nephridium. Each nephridium is open to the coelom; thus metanephridia of some form are present.

Character 13, Gaill *et al.* (1991)

Character 11, Jones (1985a: figs 19, 20) shows a ventral split in longitudinal muscle bands and refers to dorsal splits, but lateral splits have yet to be demonstrated.

