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Polychaete systematics: Past and present

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In this paper, we first demonstrate the historical background for the current unsatisfactory state of systematics of the polychaetes. We then briefly discuss our knowledge of internal and external structures. A review of the polychaete families makes up the third section; 81 families are treated in detail. Five families have been recently synonymized with others, and six families are too poorly known to be sufficiently characterized. Fossil polychaetes are briefly mentioned, with specific attention to problems associated with incorporating them in recent systematics.

The traditional separation in 'errant' and 'sedentary' polychaetes has increasingly become recognized as being unsatisfactory; however, the current trend towards grouping the polychaetes in many orders without specifying the relationships among the orders, is no more satisfactory. The lack of consistent morphological information is a major source of uncertainty. Intensive morphological studies should remove terminological ambiguities and alleviate some of the problems. © The Norwegian Academy of Science and Letters

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Contents

'It is impossible to separate the vast assemblage of families, except to ally certain groups.'

Hartman (1967)

'(O)f all the annelids, polychaetes present the most intractable problem of phylogeny'

Clark (1969)

Introduction

More than 20 years ago, one of us wrote a study of polychaete systematics (Fauchald 1974a) inspired by Dales (1962, 1963), Clark (1964, 1969) and Hermans (1969). He was also influenced by Hartman's (1968, 1969) attitude towards the families; to her, they appeared to be 'natural' units. A few years later, Fauchald (1977) issued a key to orders, families and genera in the spirit of his earlier paper. At the time, understanding polychaete phylogeny appeared to require knowledge of an ancestral annelid, a hypothetical organism, against which the recent families could be compared. Furthermore, an untested assumption behind all schemes was that evolution appeared to have tracked morphological differentiation from homonomous to heteronomous segmentation, perhaps along several lines, but certainly going from 'simple' to 'complex'.

Over the years, three factors have made it necessary to revise these attitudes. For one, many statements in Fauchald (1977) have turned out to be incorrect due mostly to new intensive studies. In addition, many new taxa have been described. Most important however, has been the change in systematic procedures from informal, evolutionary analyses to cladistics. The keys and diagnoses in Fauchald (1977) were based on an evaluation of differences between taxa; a cladistic analysis requires study of similarities. Cladistic analyses are still far from common in systematic publications on polychaetes; as a consequence, problems have accumulated at many hierarchical levels. A few examples demonstrate the kinds of situations we are facing.

Some recently recognized families are based on features not observed by previous workers (e.g. the hooks of the Uncispionidae, Green 1982); other families, however, represent previously unreported character–state combinations (e.g. Pseudocirratulidae, Petersen 1994; see below). Only rarely have new families been related to previously named ones through a consideration of synapomorphies, either formally or informally. In another case, the number of subfamilies in the Polynoidae has increased drastically. Four were recognized by Fauchald (1977); the latest count is 16 (Muir 1982; Hanley 1989); some new subfamilies represent previously undescribed taxa, but others are due to redescriptions of known taxa. These subfamilies may well represent monophyletic clades, but the relationships within the family have yet to be presented and tested. In the Capitellidae, new genera have been based on a combination of numbers of chaetigers with limbate chaetae and the total number of thoracic chaetigers (Fauchald 1972, 1977; Amaral 1980) without any strictly synapomorphic characters named. In the Dorvilleidae, increased description of small-bodied species has yielded many new genera (Westheide 1982; Westheide & Riser 1983; Westheide & Nordheim 1985; Nordheim 1987; Hilbig & Blake 1991). In addition, the synonymization of two families (Dinophilidae and Iphitimidae) with the Dorvilleidae (Eibye-Jacobsen & Kristensen 1994) have had consequences that have yet to be analyzed, perhaps mostly because many of the species-rich genera (e.g. *Ophryotrocha*) have yet to be completely studied.

Despite outstanding studies of internal structures of several families (e.g. Eisig 1887, 1914; Meyer 1887, 1888; Gustafson 1930), polychaete systematics is still based largely on external features. Many recently recognized families have been erected with little or no reference to internal structures (e.g. Aberrantidae, Wolf 1987; Alvinellidae, Desbruyères & Laubier 1986; Euniphysidae, Shen & Wu 1991; Hartmaniellidae, Imajima 1977; Laetmonectidae, Buzhinskaya 1986; Levidoridae, Perkins 1987; Uncispionidae, Green 1982; Yndolaciidae, Støp-Bowitz 1987). One recently erected family, Questidae (Hartman 1966) turned out to be of such interest that detailed anatomical investigations have been done (Giere & Riser 1981; Jamieson & Webb 1984). In small-bodied taxa, such as the Psammodrilidae (Swedmark 1952, Swedmark 1955) and Protodriloididae (Purschke & Jouin-Toulmond 1993), internal structures were detailed as part of the original descriptions. We are seeing a renaissance of detailed morphological studies (e.g. studies by Orrhage, Purschke, Smith and Tzetlin among many others) but even so, descriptions remain largely limited to external features, especially in the species-rich, large-bodied families. Recently, SEM pictures have become included as standard illustrations (e.g. Jamieson & Webb 1984; Rouse 1990, 1992*a*, *b*, 1993, 1994; Pleijel 1991, 1993) adding information about structures not previously well illustrated, such as ciliary bands.

Lack of information about internal structures may not in itself be a problem in that families may be well characterized on external morphology alone, but the additional information gained for example in studies of terebellid nephridia (Meyer 1887; Hessle 1917; Smith 1988) has demonstrated a polymorphism that potentially could be important for understanding the relations among the studied taxa.

More than 80 families of polychaetes are currently recognized. Some are known only through a single original report and not all authors recognize all families; for example, compare the treatment of eunicicds (*sensu lato*) and scale-worms in Day (1967) with Fauchald (1977). Twenty-three families have been named after 1960; most others were described before the end of the 19th century; the mid-late 1860s were the most active in terms of naming new families (see overview of taxa below).

A few polychaete families and groups of families have been analyzed cladistically (i.e. Nereididae, Fitzhugh 1987, Sabellidae Fitzhugh 1989 and Rouse & Fitzhugh 1994; Phyllodocidae, Pleijel 1991; superfamily Nereididacea, Glasby 1993; Pilargidae, Licher & Westheide 1994; Alciopidae, Wu & Lu 1994; Terebellidae, McHugh 1995); however, an overall analysis has yet to be performed on the group.

This paper is the second of three papers exploring the relations within Annelida and Polychaeta. The first paper suggested that Annelida can be a monophyletic taxon only by assuming that chaetae arose independently in the Echiura and the 'Annelida'. Polychaeta and Clitellata both belong to the clade Articulata together with the Arthropoda (*sensu lato*) and Pogonophora (Rouse & Fauchald 1995). We suggested in that paper that the Polychaeta may be monophyletic and that the relation between Polychaeta and Pogonophora was unresolved.

The third paper in the series (Rouse & Fauchald 1997) is a cladistic analysis of morphological information here presented and partially expanded upon in that paper.

Historical overview

While known from antiquity (Ashworth 1912), the first descriptions of polychaetes accepted for taxonomic purposes can be found in Linné (1758). Linné recognized the class Vermes for soft-bodied worm-like organisms. Vermes contained, in addition to organisms now recognized as polychaetes and clitellates, also various molluscs and a few crustaceans, nematodes, sea urchins, starfish and cnidarians. The next few decades saw a gradual acceptance of Linnean binomial nomenclature. Parallel with penetration of this system, and at least partially as a consequence of its presence, many new polychaete taxa were described between 1760 and 1800 by O.F. Müller, O. Fabricius, P.P. Pallas and J.-C. Savigny and others. In a manuscript available in 1809 (with plates completed in 1812), Savigny described many new species and reorganized the worms; this paper was not published until 1822 (ICZN Opinion 1461, 1987). Both Cuvier (1816) and Lamarck (1818), quoted Savigny's manuscript in detail, especially at the generic and species level, even if they had their own ideas as to the major groups of annelids to be recognized.

Lamarck (1801) placed all polychaetes, earthworms and echiurids into a single subgroup, 'Vers exterieurs avec des organes exterieurs' (Appendix I). A year later, Lamarck (1802) coined the name Annélides for segmented worm-like organisms. Cuvier (1812) grouped the 'annelids' with what is now referred to as the arthropods into the group Articulata. The segmented worms were referred to as 'Annélides' or 'Vers a sang rouge', a term Cuvier had originally proposed in 1795 (Cuvier 1795). Cuvier's 'annelids' included polychaetes, earthworms, leeches, echiurids and sipunculids. He recognized three subgroups: 'Dorsibranchiata', 'Tubicoles' and 'Abranches' (Appendix I). The Dorsibranchiata, as the name indicates, had dorsally distributed branchiae; the tubicoles, if they had branchiae, had these associated with the anterior end only. Cuvier's 'tubicoles' included also scaphopods and the green alga, *Penicillus*. Cuvier (1816) repeated the same classification with enhanced descriptions.

Lamarck (1818) presented a new scheme. The 'Annélides' was divided into three subgroups, 'Apodes', 'Antennées' and 'Sédentaires' (see also Lamarck 1815, 1816; Appendix I). The 'Apodes' lacked parapodia and chaetae; the 'Antennées' had anterior antennae, dorsal branchiae, parapodia and were essentially free-living. The 'Sédentaires' corresponded largely to Cuvier's 'tubicoles' with a few notable differences; the arenicolids were listed among the 'dorsibranches' in Cuvier, but among the 'sédentaires' in Lamarck. A new term, Chaetopoda, was introduced by Blainville (1825, originally proposed in its French form 'Sétipodes' in 1816 and used in the text of Blainville 1825; Appendix I); it included all worms with distinct chaetae. This phase of annelid classification terminated with two of Cuvier's students, Audouin & Milne Edwards (1832, 1833*a–d*); re-issued as a book in 1834) giving a major overview of the French fauna; the only new name of importance introduced in the higher classification was Errantia; a change from 'Antennées' or 'Dorsibranchiata' of previous authors to be a companion-term to Sedentaria.

Grube (1850: 274–276; Appendix II) who introduced the term Polychaeta, presented a new classification of the Annelida (as Annulata). The order Appendiculata Polychaeta contained only groups which today are still called polychaetes. *Tomopteris* was placed in a separate order, Gymnocopa. The third order was Onychophora for *Peripatus*, which he listed among the annelids, as did Audouin & Milne Edwards (1834). The order Oligochaeta contained earthworms and related taxa, and the order Discophora contained the leeches. Thus, Grube, for the first time, separated both clitellate groups from the polychaetes. Appendiculata Polychaeta was divided into two suborders, Rapacia and Limivora. Named for the modes of feeding, Grube's diagnoses also included reference to head appendages, jaws, branchiae and chaetal structures. Rapacia included most of what elsewhere had been called errant polychaetes; Grube's Limivora included the sedentary polychaetes (Audouin & Milne Edwards 1832).

Quatrefages (1849, 1865) divided worms into two series, 'Vers dioique' and 'Vers monoique' to use the terminology that he presented in 1865. The polychaetes were all included in the 'Annélides'. In a handbook, Quatrefages (1866,

Appendix II) divided the polychaetes in two major groups, 'Erraticae' and 'Sedentariae', defined on the absence or presence of distinct body-regions. Each of the two groups was divided into 'aberrantes' and 'propriae'. The 'erraticae aberrantes' included the scale-worms; all other 'errant' polychaetes were included among the 'erraticae propriae'. Quatrefages included the cirratulids, some spionids as 'Nériniens' and some opheliids as 'Polyophthalmiens' in the 'erraticae'. The aberrant sedentary family was Chaetopteridae. The remaining families were listed among the 'sedentariae propriae', including the tomopterids. The Sternaspidae was listed as a member of the Gephyrea which otherwise included Echiura, Sipuncula and Priapulida. The separation of polychaetes into errants and sedentaries is still in use (e.g. Barnes 1987) with diagnoses similar to those formulated by Quatrefages (1866).

Ehlers (1864, 1868*a*) contains extensive descriptions of a selection of polychaete families (Appendix II). His major classification, which he based on Savigny (1822), did not become influential, but his detailed descriptions of morphology and anatomy of members of his order Nereidea are still among the best, sometimes the only, sources of information for the families that he covered. Johnston's (1865, Appendix II) overview had little influence on the subsequent authors. Levinsen (1883) grouped spionids with syllids as perhaps the most unusual feature in a system which has subsequently been disregarded, probably, as Ashworth (1912) remarked, because he did not diagnose his groups. Some of the terms Levinsen coined (e.g. Aphroditiformia, Phyllodociformia) have been used as suborders by later authors (e.g. Uschakov 1972; Fauchald 1977).

Hatschek (1888–1891) issued the three first sections of a textbook in zoology; his overall scheme for the invertebrates was issued in 1888 and has been widely quoted. However, the book stops in the middle of a presentation of chaetopod morphology, and the rest was never published. The annelid portion of his system was issued as Hatschek (1893, Appendix II). He first listed the Archiannelida, a group that he had named in Hatschek (1878), as a separate class to include two families, Polygordiidae, in which he included *Protodrilus* as well as *Polygordius*, and Dinophilidae. The counterpart to the Archiannelida was the class Chaetopoda, which was separated into Protochaeta, Polychaeta and Oligochaeta. Protochaeta included a single family, Saccocirridae. The polygordiids and saccocirrids are now considered distinct polychaete families (cf. Fauchald 1974*a*, 1977; Rouse & Fauchald 1995); *Dinophilus* and similar genera are currently considered dorvilleids (Eibye-Jacobsen & Kristensen 1994).

Hatschek divided the polychaetes into two groups, Cirrifera and Acirra. Among the Cirrifera, he listed three major groups, Spiomorpha, Amphinomorpha and Rapacia; for the latter, Hatschek gave the name Nereimorpha in parenthesis, presumably as a synonym. Spiomorpha included spionids and orbiniids (as Ariciidae) as members, with chaetopterids, flabelligerids (as Pherusidae) and opheliids as 'appendices'. Amphinomorpha contained only the amphinomids, which, at this time, also included the euphrosinids. Rapacia included the scaleworms, nereidids, phyllodocids and related taxa and the euniceans. Hatschek listed the myzostomids as an 'appendix' to the Rapacia. The Acirra was divided into Drilomorpha, Terebellomorpha and Serpulimorpha. Drilomorpha included cirratulids, arenicolids, capitellids and maldanids; the oweniids were considered maldanids. As appendices to Drilomorpha, he listed sternaspids and ctenodrilids. Terebellomorpha included terebellids (presumably including the ampharetids) and the pectinariids (as Amphictenidae). Finally, Serpulimorpha included sabellariids (as Hermellidae) and serpulids (presumably including the sabellids). Hatschek's treatment is unfortunately very brief, since many of his higher taxa have been in use since they were first proposed.

Hatschek's (1893) system was tied to his ideas of evolution in the polychaetes leading from bipalpate archiannelids (polygordiids) via saccocirrids to bipalpate spionids. Consequently for Hatschek, the most primitive polychaetes were the spionids. As the next most primitive group, Hatschek listed families with similar segments along the body, for example the phyllodocids and nereidids. Most of these taxa also have dorsal and ventral cirri, and Hatschek used the presence or absence of these cirri as unique features for one of his main groups (Cirrophora vs. Acirra). Hatschek was forced to consider the spionid notopodial and neuropodial postchaetal lobes as corresponding to the dorsal and ventral cirri of what he considered the most closely related taxa (e.g. nereidids and phyllodocids). The spionid parapodial structures were well known at the time (cf. Claparède 1870), and Hatschek's redesignation did not receive any support. Hatschek added the chaetopterids, in which the segments are more highly differentiated than in any other polychaete taxon, to the Cirrophora as an appendix, i.e. he listed them as part of the most primitive group of polychaetes; he did not discuss this decision. Most authors agree that the chaetopterids are related to the spionids (cf. Fauvel 1927; Hartmann-Schröder 1971; Fauchald 1977), but have refrained from claiming that either the spionids or the chaetopterids are 'primitive.'

Another interesting system with limited long-term consequences was proposed by Benham (1894, 1896). Cryptocephala was defined as having the prostomium overgrown by the expanded peristomium and usually completely hidden (Appendix II); note that the list of contained families, but not the definition, differs between the two papers. In the Phanerocephala (called Eucephala in Benham 1894), the prostomium was distinct, and the peristomium did now overgrow the prostomium. The Nereidiformia included the orbiniids (called Ariciidae) in addition to the nereidids, syllids and other families usually listed with the nereidids. The Capitelliformia included the capitellids only. The Scoleciformia included the Opheliidae, Maldanidae, Arenicolidae, Scalibregmatidae, Flabelligeridae (called Chloraemidae) and Sternaspidae. Scoleciformia was taken up by Sedgwick (1898) in a widely used textbook, and by Goodrich (1895, 1945) in his surveys of the polychaete nephridia, but in both cases expanded to include the capitellids as well as the other families listed. Perrier (1897, Appendix II) presented a variant of the classical separation into errants and sedentaries.

During this century, the single most commonly used system was derived from Quatrefages (1866), as codified in widely used monographs by Fauvel (1923, 1927, 1953), Hempelmann (1937), Uschakov (1955), Day (1967) and Hartmann-Schröder (1971). The concepts of Errantia and Sedentaria were used even when the authors complained about the inadequacies of the system. For example, Uschakov (1955: 25) pointed out problems with Quatrefages' diagnoses; he did not propose any solution to the problem, but remarked that "the names 'Errantia' and 'Sedentaria' are firmly established in both the Russian and other literature". Day (1967: 19) considered the two orders as an 'arbitrary grouping' used for 'practical purposes'; he did not recognize any taxonomic levels between orders and families. Hartman (1967, 1968, 1969) had come to the same conclusion (cf. the quote given at the head of the paper), but issued her atlas of California polychaetes in two volumes, errantiates in one, and sedentariates, archiannelids and myzostomes in the other. Hartman (1968: 3, see also 1969) listed 71 families. Of these, 33 belonged to the Errantia, 32 to the Sedentaria, three to the Myzostomida (called 'a small parasitic group' by Hartman) and three to the 'very aberrant' Archiannelida. As indicated by the quote at the head of the paper, Hartman did not consider it possible to organize the polychaete families into coherent higher taxa.

Hartmann-Schröder (1971) divided the polychaetes into orders along the same lines as Uschakov (1955), except that she included the euniceans as a distinct subgroup of the Nereimorpha. Her treatment of the sedentaries is the same as in Uschakov (1955). Hartmann-Schröder considered Errantia and Sedentaria as orders rather than as subclasses, consequently shifting the taxonomic level of the subsidiary groups down one level. Uschakov and Hartmann-Schröder thus combined Quatrefages major subdivisions with the system proposed by Hatschek (1893); their diagnoses followed traditional paths.

A system proposed by Dales (1962, 1963, 1977) used structural relations of the stomodaeum and nephridia to furnish criteria for an analysis of the polychaetes at the family level. Families with axial pharynges were separated into three orders. Phyllodocida had strongly muscular pharynges; Capitellida and Spionida lacked muscularized pharyngeal walls. Subdivision of the Phyllodocida was based on the distribution of nephridial structures (protonephridia and metanephridia, nephromixia and mixonephridia). Families with ventral pharyngeal structures were grouped into nine orders partially based on the development of this structure. A ventral proboscis was present in three orders (Eunicida, Amphinomida and Magelonida), a non-eversible buccal organ was found in five orders (Ariciida, Cirratulida, Oweniida, Terebellida, Flabelligerida and ?Psammodrilida), and finally in one order (Sabellida), the buccal organs had been lost. Dales' findings were criticized by Orrhage (1973), partially on theoretical grounds, but also for incorrect observations.

Dales (1977) corrected some of his earlier statements about the stomodeal structure in certain 'spioniform' families; however, he also reviewed developments in phylogeny studies since his earlier publications. As a general principle, Dales found that while "all of the families of the Class Polychaeta are distinct,... some show obvious resemblances while others appear to be isolated.... The grouping of families into larger groups presents some difficulties, therefore, and while some groups of families or orders emerge, there remains a series of families with no close affinities with any other group. My own view is that it is better to leave such families in isolated orders until their affinities are understood than it is to reduce the value and coherence of natural orders by including such families in one or another group on tenuous evidence."

Dales (1977) went on to discuss some striking developments in the study of polychaetes over the 14-year time span since his book came out. He discussed the position of the pogonophorans, concluding that whereas the pogonophorans were more related to annelids than to the deuterostome groups, the relationship was not a very close one. He tentatively suggested retaining the Archiannelida, but argued that, in contrast to proposals made by Bubko (1973), the oweniids were better considered polychaetes rather than becoming transferred to the Archiannelida. Dales also concluded that similarities in the ultrastructure of chaetae of pogonophorans, brachiopods and annelids (as studied by, among others, Gustus & Cloney 1972, Storch & Welsch 1972 and Orrhage 1973) demonstrate that the ability to secrete chitin was a feature shared among the protostomians, rather than showing any particularly close relationship among these three groups.

Storch (1968) concluded, tentatively, that the scale-worms (Aphroditacea) have the most primitive arrangement of muscles and that the other (errant) families could be derived from the scale-worm condition by reductions. Mettam (1985) pointed out that Storch had not explained how the scale-worms, with their complex musculature, came into being; for Mettam, it appeared more likely that the scale-worms had a derived, rather than a primitive position. Dales (1977: 532–533) also discussed Storch's findings and concluded that "the relative isolation of the eunicid group and the serpulimorphs could be held to support the hypothesis that stomodaeal structure is phyletically important. It seems more likely that the amphinomids, the chrysopetalids and the scaleworm group were all separately derived from polychaete stock and that each has retained certain primitive features". Dales' statement illustrates that a diagram such as the one presented by Storch could be read in more than one direction.

In general, Dales (1977) re-stated his finding that the stomodaeal modifications are of major importance for understanding polychaete phylogeny, and that other features, also considered in his earlier publications such as nephridia, musculature and chaetae, add importantly to phylogenetic interpretation. In discussing the importance of the variability of stomodaeal structures in the maldanids and spionids, he concluded that: "We are left with two alternatives. Either that the variability of the pharyngeal structure in the maldanids and spionids demonstrates that the region is too plastic to have any phyletic value and that apparently similar structures have arisen by convergence, or that the ventral muscle organs are primitive and have been converted or, replaced by, various lip and proboscis structures in adaptation to different styles of feeding".

Pettibone (1963) presented a key to the class Polychaeta leading directly to families, without reference to orders. She later (1982) recognized 25 orders, including one for each of the five traditional 'archiannelidan' families in addition to the orders defined by either Dales (1963) or

Fauchald (1977), often with emphasis on different morphological structures than in the latter two publications.

Fauchald (1977) included 17 orders; his diagnoses did not focus on any single morphological feature, but showed a preference for features of the anterior end for major subdivisions. While defined differently, the orders contained roughly the same taxa as those listed in Dales (1963). The new orders added by Dales, Fauchald and Pettibone were mostly for morphologically unusual families (e.g. Spintheridae, Sternaspidae, Oweniidae). Dales (1977: 526) gave a justification for recognizing higher taxa for these 'isolated' families.

George in George & Hartmann-Schröder (1985) divided the polychaetes into 22 orders resembling the groupings suggested by Fauchald (1977) and Pettibone (1982), but recognizing more intermediate categories between the orders and families than either of the latter two authors (Appendix II). Uschakov (1985) reviewed previous systems and proposed a system of 26 orders, including four orders for the 'archiannelidan' families. He split what George had called Spionida into four orders, including separate orders for the chaetopterids, magelonids and cirratulids in contrast to George who had kept these together in the Spionida. He also listed the poeobiids in a separate order. The sequence in which the families are listed in Uschakov (1985) differs somewhat from the sequence in George's publication, presumably reflecting Ushakov's views of the phylogeny of the group.

Orensanz (1990) reviewed the eunicean families and incorporated for the first time the scolecodonts (fossil polychaete jaws and jaw-assemblages) in overall schemes for the group. His analysis consisted mainly of a set of schemes arranging the jaw assemblages by similarity. Orensanz named unique structures for each of his groups where these were present. His schemes have yet to be tested.

The relations among the classificatory schemes and phylogeny, and various problems with the major groups of schemes will be explored below (see Discussion).

Polychaete morphological structures

The intent of our series of studies is to obtain a better understanding of annelid and polychaete systematics. While discussion of the morphology is focused on features to be used in our analysis (Rouse & Fauchald 1997), we also review a few structures not there scored, usually because they have been used in systematic studies elsewhere. We comment on postulated relations between polychaete morphological structures and those of the Sipuncula, Echiura, Clitellata, Frenulata, Vestimentifera, and on occasion, Onychophora and Arthropoda where appropriate.

Polychaetes consist of three basic regions. The presegmental region is ontogenetically derived from the episphere, the prototroch and the area surrounding the mouth in the larvae; it makes up the prostomium and peristomium in the adults. The episphere gives rise to the prostomium (Anderson 1973; Schroeder & Hermans 1975). The prototroch, the area around the mouth including the metatroch posterior to the mouth gives rise to the peristomium (Schroeder & Hermans 1975). The next region is the segmented trunk. Each segment is, in principle, limited by septa from neighboring segments. The septa may be more or less complete. They correspond externally to the intersegmental grooves, but each segment may be divided into two or more rings (e.g. glycerids, Fauvel 1923; scalibregmatids, Fauvel 1927). Each segment usually carries parapodia and chaetae in addition to various segmentally arranged internal organs, but especially anteriorly, parapodia or chaetae or both may be missing. The third region is the postsegmental pygidium which also includes the growth zone from which new segments are derived by growth along its anterior edge (Anderson 1973; Schroeder & Hermans 1975).

Head and head structures

The head is composed of the prostomium, peristomium and, if present, anterior fused segments and anterior segments in which the parapodial structures clearly differ from those present in the rest of the body.

The prostomium contains at least part of the brain, and often carries eyes and antennae (Fauvel 1959 and Fauchald 1977). The prostomium is often a distinct structure marked by an external groove from the next section of body, which may be either the peristomium or the first segment. Prostomia vary a great deal in shape, including but not limited to, simple conical structures (e.g. some spionids, capitellids, many orbiniids), square or pentagonal (e.g. nephtyids), T-shapes (some spionids and scalibregmatids) or inverse T-shapes (nereidids).

The prostomium may be fused to the peristomium. In some groups, such as the maldanids and paraonids (Pilgrim 1966a; Strelzov 1973), the joint structure is well separated from the rest of the body as a distinct head. In other taxa, the joint structure may be modified to form a tentacular crown, and the prostomium proper is no longer identifiable as a separate entity (e.g. sabellids and serpulids, Fitzhugh 1989; Rouse & Fitzhugh 1994).

In terebellids and trichobranchids, the prostomium is located directly on top of the peristomium with the free frontal edge fused (Holthe 1986); the joint structure may be foliose with a folded margin (e.g. polycirrins and some trichobranchids) or it may be restricted to a short saddle-shaped structure (e.g. some amphitritins).

In Echiura, the structure called the proboscis in the identificatory literature (Stephen & Edmonds 1972: 344, fig. 42A) is often a flattened, tongue-shaped structure, but also may be rolled up laterally into a more or less closed tube. It is pretrochal in origin (Newby 1940) and contains a greatly elongated circumesophageal loop (Stephen & Edmonds 1972: 344, fig. 42A) and thus may be homologous with the polychaete prostomium.

The anteriormost region of the Arthropoda is called the acron (Schram 1986: 25–26); it contains the anteriormost part of the brain (protocerebrum) and may carry eyes (Brusca & Brusca 1990: 558). It is homologous with the polychaete prostomium, but differs from this in that it is invariably imbedded in the rest of the head. It is separated from the mouth by a ring that contains the deuterocerebrum; this ring is a true segment carrying appendages in

Crustacea, Myriapoda and Insecta. It lacks appendages in Chelicerata, Pycnogonida and Trilobita, according to Schram (1986). The acron is absent in Onychophora (Anderson 1973).

The polychaete peristomium varies a great deal in shape in adults. In many polychaetes, the only adult peristomial structure visible is the area immediately surrounding the mouth and in some cases including the roof of the mouth (e.g. terebellids, trichobranchids). The facial tubercle of the scale-worms is a ridge stretching from the lower side of the prostomium to the upper lip; this structure is presumably peristomial in nature, but this assumption has not been tested. The relationship between facial tubercles (or lobes) of other polychaetes (e.g. poecilochaetids, Hartman 1969) and the structure present in scale-worms has not been examined. Grooved palps are often extensions from the larval prototroch and thus peristomial in origin. Polychaetes with well-developed peristomial palps (e.g. spionids, Söderström 1920) may otherwise have the peristomium limited to the lips. Other than the prototroch, the region giving rise to the peristomium is mostly situated ventrally in the larva (Anderson 1973); even so, in some polychaetes, the peristomium is one (or two) complete rings separating the prostomium from the first segment (e.g. euniceans, Åkesson 1967; Eibye-Jacobsen 1994). In sabellids and serpulids, the peristomium is also a complete ring, but in these two families with their terminal mouth, a section of the peristomium is folded forwards outlining the lips surrounding the mouth (Nicol 1930).

The frenulate and vestimentiferan 'tentacles' are attached to the second part of the body which is an elongated peristomium; this is demonstrated by the larval development (illustrations in Ivanov 1963; Southward 1988,1993; Gardiner & Jones 1993).

The echiurans have a peristomium limited to the region immediately surrounding the mouth. In onychophorans, this region is missing, since the acron is absent. In the arthropods, the second part of the acron is located wholly in front of the mouth, rather than surrounding the mouth as in the polychaetes and is not considered homologous with the peristomium (Schram 1986).

Head appendages include antennae, palps, peristomial cirri and, associated with one or more cephalized segments, tentacular cirri.

Antennae are always located on the prostomium and are sensory (Fauchald 1977); three antennae may be present including a pair of lateral antennae and one median antenna. Most common are simple, tapering or digitiform antennae (e.g. phyllodocids, Pleijel 1991; nephtyids, Rainer 1984, 1989) but they may be articulated (e.g. eunicids, Fauchald 1992*a*) or consist of a basal ceratophore and a distal ceratostyle (e.g. polynoids, Fauvel 1923). The lateral antennae may be located at or near the frontal edge of the prostomium (nereidids, Fauvel 1923, fig. 127a). The median antenna is usually located behind the frontal margin (phyllodocids, Pleijel 1991; some hesionids, Pleijel 1993; syllids, Malaquin 1893: 35; Fauvel 1923, figs 95a and e). Pleijel (1991) reported that the median antenna of some phyllodocids is homologous to the nuchal papilla of other phyllodocids based on innervation patterns. Nuchal papillae and the nuchal organs are different structures (the latter being paired sensory organs present in most polychaetes, see below) linked by the use of the adjective 'nuchal' meaning neck. In some cases, the lateral antennae are missing, leaving a single median antenna (e.g. aphroditids, Fordham 1926; Fauvel 1923). Some spionids have a single median antenna emerging from a posterior prolongation of the prostomium (Foster 1971); we consider this structure as a homolog to the median antenna in other polychaetes despite the different position.

In antenniferous euniceans, except in Dorvilleidae, the antennae are located along the posterior edge of the prostomium; they vary in number from a single median to three antennae in a straight or curved row (Fauchald 1992*a*). These antennae are the same as the paired lateral and median antennae of other polychaetes. The outer (or outer lateral) 'antennae' (*ex auctores*) of some euniceans are paired ventro-lateral palps (Orrhage 1995). Antennae of onuphids and eunicids are usually distinctly jointed with a basal ceratophore and a style; either ceratophore or style or both may be articulated (e.g. onuphids, Paxton 1986*a*; eunicids, Fauchald 1992*a*). In the Dorvilleidae, the paired antennae are more or less frontal (Fauvel 1923). The innervation of eunicean antennae is similar to that in other polychaetes (Orrhage 1995). The frontal, tapering antenna-like structures, sometimes referred to as frontal palps (Paxton 1986*a*) in onuphids, are dorsal lips (Orrhage 1995).

The term 'antennae' is used for very different structures in the Arthropoda. Antennae in three arthropod subgroups (Crustacea, Myriapoda and Insecta) are located on the second presegmental ring (Schram 1986) and are jointed with a distinct exoskeletal cover. Usage of the term 'antennae' is deeply ingrained and would be difficult to change. It is, however, important that the presence of 'antennae' in both arthropods and polychaetes not be considered a statement of homology (Rouse & Fauchald 1995).

All palps, whether emerging from the prostomium or the peristomium, are similarly innervated from the middle (or posterior) part of the brain, or partially or wholly from the circumesophageal ring (Orrhage 1966, 1978, 1980, 1990, 1991, 1993, 1995, 1996) and are considered homologous structures. In the euphrosinids, only the characteristic innervation is present (Gustafson 1930), but the external palps are missing; this is also the case in scalibregmatids and paraonids (Orrhage 1993). Palps can be divided into two structurally different groups, grooved feeding palps and ventral, tapering sensory palps (e.g. Orrhage 1980). In all but one family, the feeding palps have ciliated longitudinal grooves as, for example, in the spionids (Söderström 1920), terebellids (Dales 1955) and acrocirrids (Banse 1969). The exception is the family Magelonidae, in which the palps lack a longitudinal ciliated path and are studded with papillae; they emerge at the corners of the mouth ventrally, rather than dorsally as in the spiomorphs with which the magelonids are usually compared (Jones 1968). Despite these differences, they are homologous with the grooved palps (Orrhage 1966). A single pair of grooved palps is present in many polychaetes (e.g. flabelligerids, Spies 1975; spionids, Dauer 1994). The detailed structure of these palps varies somewhat, but in most cases, the cross-section of a palp is U-shaped or V-shaped with a ciliary tract running along the groove. Groups of cilia are also usually present at the junction of the convex and concave surfaces. These palps are nearly always attached on the dorsum at or near the junction of the pro- and peristomium, but in the flabelligerids, they are located at the outer corners of the terminal mouth (Spies 1975).

In terebellids and trichobranchids, the prostomium and peristomium are fused marginally, and multiple, usually grooved, palps are attached along the fusion line. These are produced from the latero-posterior corners of the fusion line and migrate with the growth of the worm into increasingly more dorsal positions. The palps can also be replaced directly *in situ* in many taxa (Dales 1955; Holthe 1986) and in some terebellids. In the sabellids and serpulids, the grooved palps form a prostomial branchial crown (Orrhage 1980; Fitzhugh 1989; Rouse & Fitzhugh 1994). The prostomial derivation is visible in developing juveniles in which the buds for the crown appear in front of the prototroch (Rouse 1993). In adults, the crown consists of three or more pairs of radioles that may carry a large number of pinnules. The whole crown has a complex ciliary pattern (Nicol 1930) similar in principle to the ciliated grooved structures present in, for example, the paired palps of spionids (Dauer 1994). In many sabellids, the crown is supported by an internal skeleton. In one genus of oweniids, *Owenia*, the grooved palps are prostomial ciliated lobes. These differ from the branchial crown described above in that they are flattened, often distally bifurcated marginally ciliated structures, and lack the support structures present in the sabellids (Dales 1957). Another oweniid genus, *Myriowenia*, has paired grooved palps, and some oweniids lack palps altogether (see Hartman 1969 for illustrations).

Buccal tentacles are multiple peristomial palps; they are always ciliated and in some cases are grooved (ampharetids, pectinariids, Holthe 1986). In the ampharetids, they are located on a fold of tissue located dorsally in the buccal cavity and can be flipped out as a group or retracted; in the alvinellids and pectinariids, while they are structurally very similar, they are permanently exposed.

Cossurids have dorsally attached buccal tentacles contained in the buccal cavity (Tzetlin 1994); these tentacles lack the musculature needed for active motion and are exposed by retraction of the lower lip; they are not considered palps (see Rouse & Fauchald 1997).

The frenulate and vestimentiferan 'branchiae' are peristomial grooved palps, located dorsally and usually ciliated. In some cases, they carry rows of papillae arranged in one or two rows, but most often papillae are absent (Ivanov 1963 in illustrations; Webb 1964; Southward 1988). The numbers of branchiae may vary from a single coiled structure such as in *Siboglinum* (Ivanov 1963 in illustrations) through multiples as in Lamellisabellidae (Uschakov 1933; Ivanov 1963). In large vestimentiferan pogonophorans, the individuals' palpal filaments are partially fused to sheaths and are present in very large numbers with the free ends of the filaments forming a thick brush-like structure on the side of the obturaculum (Jones 1985).

Ventral sensory palps are morphologically somewhat more uniform; in most cases they are tapering or digitiform and relatively short compared to the grooved palps. Sensory palps of the amphinomids are slender, tapering structures located on the prostomium in a ventrolateral position (Gustafson 1930). In the euniceans, the palps (traditionally called outer, or outer lateral, antennae) are located dorsolaterally and are relatively slender, tapering structures. The ventral inflated pads located in front of and lateral to the mouth previously referred to as palps (von Haffner 1959; Fauchald 1970, 1977, 1992*a*, *b*) represent lips (Orrhage 1995). Most commonly ventral palps are tapering with digitiform or pointed tips (e.g. acoetids, Pettibone 1989; phyllodocids, Pleijel 1991). The ventral palps are bi-articulated in some taxa (some hesionids, Pleijel 1993; nereidids, Fauvel 1923). The term 'articulated' may be a misnomer, as indicated by Harper (1979); he demonstrated in one nereidid species that the outer article can be completely everted and represents a distal section of the palp that can be pulled back by muscles attached in a ring to form the appearance of an articulation. In other nereidids, the articulation appears to be a permanent feature (Ehlers 1864).

A third kind of head appendages, peristomial cirri, are present in some euniceans (Paxton 1986*a*; Fauchald 1992*a*). The peristomium forms either one or two complete rings in these families, and the peristomial cirri are attached dorsolaterally near the anterior edge of the ring in onuphids, or in a similar position on the second ring in eunicids. Peristomial cirri are often referred to as tentacular cirri (Fauvel 1923); peristomial cirri are associated with the pre-segmental peristomium, whereas tentacular cirri are located on one or more cephalized anterior segments. The tentacular cirri of certain families (e.g. nereidids, pilargids and syllids) were considered as pre-segmental and thus as peristomial cirri by Glasby (1993). The cirri of these families are located laterally, rather than dorsolaterally, and resemble the structures present in hesionids closely and are here considered to be tentacular cirri. They will be discussed below since they appear to be parapodial in nature.

Sensory organs

Only three kinds of sensory organs are considered here. These include nuchal organs, lateral organs and a newly described sensory structure, called a dorsal cirrus organ (Hayashi & Yamane 1994), which so far appears to be present only among euniceans. Many other sensory structures, such as eyes and statocysts, are present. Eyes are morphologically diverse (Eakin & Hermans 1988) and highly characteristic of certain taxa (e.g. alciopids, Rice 1987; acoetids, Pettibone 1989) and tend to vary in development with sexual maturity (e.g. nereidids, Schroeder & Hermans 1975). Arranging this morphological cornucopia into an organized pattern is difficult and requires detailed study.

Nuchal organs are paired sensory ciliated structures that may be innervated directly from the posterior part of the brain, from a pair of nerves emerging from the brain or from one of the dorsal posterior commissures (Storch & Schlötzer-Schrehardt 1988; Orrhage 1991). Nuchal organs are present only in polychaetes. In most of these taxa, they are relatively simple structures in terms of overall morphology. They may be ciliated patches (e.g. potamodrilids, see illustrations in Bunke 1967, who did not consider these sensory patches nuchal organs), folds (flabelligerids, Spies 1975), pits (nephtyids, Racovitza 1896), sometimes with eversible folded or finger-shaped structures (nephtyids, Fauchald 1968; opheliids, McConnaughey & Fox 1949) or grooves (syllids, Malaquin 1893). In some cases, the nuchal organs are posterior projections (epaulettes) attached basally (e.g. some syllids, Rullier 1951). Some nuchal organs are paired ciliated folds on each side of a posterior prolongation of the head (spionids, Söderström 1920; Schlötzer-Schrehardt 1991). Söderström (1920, 1930) claimed that the longitudinal ciliated tracts present dorsally on some, but not all spionids (dorsal organs) are continuous with the nuchal organs. Schlötzer-Schrehardt (1991) found that in *Pygospio elegans*, dorsal organs were only present in the males and did not contain any sensory elements; she suggested that at least in this species, the dorsal organs are associated with transportation of spermatophores. In a few cases, a pair of dorsal crests is the only evidence of nuchal organs (e.g. pectinariids, Nilsson 1912). These have been assumed homologous to the dorsal crests present in the spionids (Söderström 1930); in view of Schlötzer-Schrehardt's (1991) findings, the structure of these organs should be re-examined. In sabellids and serpulids, the nuchal organs have become internalized (Orrhage 1980).

The caruncles of amphinomids and euphrosinids are also nuchal organs, according to Storch & Welsch (1969). The caruncles are projecting or attached structures with four to eight ciliated ridges. The 'epaulettes' present in some syllids have ciliated edges (Malaquin 1893); in the caruncles, the ciliated nuchal structures are minimally duplicated, more usually eight or more tracks of cilia are present (Gustafson 1930). The term 'caruncle' is also used about a posterior prolongation of the prostomium proper (e.g. spionids, Sigvaldadóttir *et al.*, 1997); this appears to be a different structure, even if it is similar in position.

Because the nuchal organs were proposed as a synapomorphy for the Polychaeta in the first section of our analysis (Rouse & Fauchald 1995: 281, 285), a brief overview of similar structures in related organisms may be useful. Nuchal organs are absent in Clitellata (Bullock & Horridge 1965; Mill 1978) and in Echiura (Pilger 1993). Various cephalic sense organs are present in the nemerteans (called cephalic grooves, slits or pits, Turbeville 1991) and platyhelminths (Rieger *et al.* 1991); ultrastructural comparisons have not yet been made between these and the polychaete nuchal organs. Sipuncula have a single median sensory organ associated with the cephalic pit (Rice 1993); this organ may have single or paired openings and may be variously lobulated and folded (Stephen & Edmonds 1972; Rice 1993; Cutler 1994). Nuchal organs are absent in Onychophora and Arthropoda (Schram 1986).

Lateral organs are internally ciliated pits or ciliated papillae present segmentally between the notopodia and neuropodia (or dorsal to the neuropodia when notopodia are missing). Eisig (1887) described lateral organs in capitellids; lateral organs have been reported in many other families (e.g. opheliids, orbiniids, and scalibregmatids, Rullier 1951; paraonids, Strelzov 1973). Ultrastructural details were summarized by Storch & Schlötzer-Schrehardt (1988). Lateral line organs have been described in certain clitellates, but appear to be structurally different, even if they are positionally comparable to those in the polychaetes (Jeener 1928).

Hayashi & Yamane (1994) described a probable sensory structure, which they called the dorsal cirrus organ. It is a ciliated structure on the lower side of the notopodia in eunicean polychaetes. It is sometimes a pendant lobe as in *Euniphysa*, but more usually a thickened and ciliated patch on the ventral side of the dorsal cirrus near the base. A similarly structured organ is present in a nephtyid, but in this case as one of many similar structures scattered over the body (Hayashi & Yamane 1994). Dorsal cirrus organs or similar organs may be more widespread among the polychaetes, but most families have yet to be examined for their presence. No similar organs have been reported from any of the non-polychaete groups here considered.

Trunk structures

The trunk of the polychaetes is the segmented region between the prostomium/peristomium and the pygidium. Segmentation, defined as "repetition of homologous body structures derived by teloblastic growth" (Brusca & Brusca 1990; Rouse & Fauchald 1995), is present in all but a few groups here considered. In most clitellates and polychaetes, segmentation is visible externally; in a few cases, only the presence of internal septa reveals the segmented condition (e.g. poeobiids, Heath 1930; Robbins 1965). Onychophora and Arthropoda are also segmented (Brusca & Brusca 1990). We regard Echiura as lacking segmentation (Newby 1940; Rouse & Fauchald 1995); however, this is by no means uniformly accepted. Nielsen (1995: 142) referred to evidence of segmentation in the Echiura as 'inconclusive'.

The longitudinal muscles are grouped in four, sometimes five distinct bundles in the polychaetes (e.g. acoetids, Storch 1968; ampharetids, Meyer 1887; Fauvel 1897) and in the clitellates (Stephenson 1930; Rouse & Fauchald 1995). In echiurans, the longitudinal muscles form a continuous sheath instead (Pilger 1993).

The first segment(s) often differ(s) in size and shape from the following ones; in addition, the parapodial structures are often different in anterior segments. One or more anterior segments, which can be recognized as segments by being innervated from ganglia of the ventral nerve cord, may be cephalized and their ganglia more or less associated with the circumesophageal ring (e.g. Orrhage 1991). Appendages of cephalized segments may be parapodia or resemble some of the parapodial structures present in other segments. Dorsal or ventral cirri of cephalized segment(s), which differ obviously in length or structure or both from dorsal or ventral cirri of other segments, are called tentacular cirri (Fauchald 1977; e.g. nereidids, Glasby 1991; phyllodocids, Pleijel 1991). Tentacular cirri may be present on a segment in which the rest of the parapodial structures are similar to those found elsewhere in the body. For example, in some phyllodocids with four body follow distinct patterns (Pettibone 1963,1989); elytrigerous segments may alternate with segments in which the dorsal cirri are well-developed, or dorsal cirri may be absent in non-elytrigerous segments. In the phyllodocids and some morphologically similar families, the dorsal cirrus is also flattened to a foliose structure (Pleijel 1991), but in this case, the attachment point is at one margin of the flattened structure. In lumbrinerids and oenonids, well-developed dorsal cirri, when present, are foliose structures supported on short, truncate notopodia; however, in most taxa of both families, the dorsal cirri are truncate structures barely projecting above the surface. In the apistobranchids, a series of mid-body segments carry long, slender notopodia terminating distally in narrow elongate dorsal cirri.

Ventral cirri are usually tapering or digitiform (e.g. nereidids, Fauvel 1923), but they may be flattened and foliose (phyllodocids, Banse 1973). In the euniceans, they may be inflated and glandular at least in a number of median segments (Fauchald 1992*a*,*b*); in other euniceans, such as the oenoniids and lumbrinerids, the ventral cirri are thickened and pad-like throughout the body (Orensanz 1990).

Both dorsal and ventral cirri are absent in many polychaete families.

External gills (branchiae)

Gills are extensions from the body wall containing a loop of the vascular system and with inter-epidermal capillaries (Gardiner 1988). Storch & Alberti (1978) recognized three additional morphological arrangements, the most common of which had the branches of the vascular loop connected to each other through intra-epidermal capillary vessels. Recognition of a structure as a branchia as defined here requires the presence of a circulatory system; thus, the extensions from the body wall in some glycerids and capitellids (Arwidsson 1899; Eisig 1887) are not considered gills since, in both these families, the circulatory system is absent (see below). Similarly, the notopodial ligules of the nereidids and the dorsal cirri of the phyllodocids may have obvious vascularization (Fauvel 1923), but lack the characteristic capillary loops and are not considered homologous with the gills of other polychaetes (Gardiner 1988).

Gills are absent in many taxa, including most small-bodied taxa (e.g. aeolosomatids, Bunke 1967), but also in some large-bodied taxa such as most maldanids (Fauvel 1927) and oeononiids (Orensanz 1990). In many taxa, the gills are associated directly with dorsal cirri or the notopodial parapodial lobes (e.g. some scalibregmatids and opheliids, Fauvel 1927; euniceans, Fauchald 1992*a*). These parapodial gills may consist of single filaments (opheliids, Fauvel 1927), or may be tufted (amphinomids, Gustafson 1930) or pectinate (eunicids, Fauchald 1992*a*). Alternatively, gills may emerge from the dorsum between the notopodia and the dorsal midline of the body, usually separately from the notopodia, but they may fuse longitudinally to a varying degree to the notopodial postchaetal lamellae (e.g. spionids, Foster 1971). Dorsal gills may take a variety of shapes. The simple kinds may be digitiform or tapering; they may have a circular cross-section or be flattened. The latter are often heavily ciliated along the narrow edges. Dosal simple gills may be present on many segments (e.g. cirratulids, Fauvel 1927) or may be limited to a few segments anteriorly (e.g. ampharetids, Holthe 1986). Dorsal branched gills often have a stalk and a distal group of filaments. Each filament may be dichotomously branching (certain terebellids, Holthe 1986), they may be flattened and foliose (e.g. pectinariids, Holthe 1986), or they may simply be irregularly branching and tufted (certain terebellids, Holthe 1986). In the trichobranchid, *Terebellides*, the stalk is median and single, but the distal, foliose filaments are arranged in two groups side by side revealing the original bilateral structure of the gills. In some terebellids and trichobranchids, the stalks are short or missing, and the filaments may appear as groups of sessile gills on each side of the dorsum (thelepodin terebellids, Hutchings & Glasby 1987). However, the feature that the terebellid gills have in common is their position: they are dorsal and limited to a few anterior chaetigers. The terebellomorph gills are segmental; however, especially in the ampharetids (Meyer 1887), alvinellids (Desbruyères & Laubier 1986) and trichobranchids (Wirén 1885), the gills may appear to be located on one or two anterior segments. The blood vessels show the segmental origin of the gills.

In some taxa in which the dorsal gills are strongly tapering and anteroposteriorly flattened, the gills can be seen as double-rows of triangular structures, sometimes starting out very short, increasing rapidly in length (e.g. some orbiniids, Hartman 1957) or decreasing rapidly in size posteriorly (e.g. certain paraonids, Strelzov 1973).

The gills of the flabelligerids and a few similar taxa (Spies 1973, 1975) are located on a fold of the peristomium called the gill membrane; however, morphologically, these gills are segmentally arranged and dorsal in position. Spies (1973) demonstrated that the gills vessels are organized in a series on each side, corresponding to the first few segments. Each gill is simple, usually digitiform, and agrees structurally with other kinds of gills in having the distinctive interepidermal vascular loops. A minimum of four pairs of gills may be present; other taxa may have multiple gills. Spies (1975) illustrated the varying structure of the gill membrane and the position of this structure in relation to other anterior structures in the flabelligerids.

Interramal gills are unique to the nephtyids; they are suspended from the notopodial ramus between the well-developed parapodial rami (illustrations in Hartman 1950). They are tapering and curved in various ways and usually ciliated along both edges.

The single median structure located dorsally on an anterior segment in cossurids has been demonstrated to be a gill (Fournier & Petersen 1991).

Epidermal papillae

Many polychaetes have epidermal rugosities and various forms of papillar structures. The epidermis is thick and rugose in some taxa (e.g. arenicolids, Ashworth 1912; capitellids, Eisig 1887; scalibregmatids, Ashworth 1902). The rugosities may be present only anteriorly such as in many capitellids or may be present throughout the whole body as in most scalibregmatids. Small papillae are often scattered over the whole body (some syllids, Fauvel 1923; pilargids, Pettibone 1966). Many sphaerodorids may have papillae of two kinds, some very large, and others smaller. The large, spherical sphaerodorid papillae (macrotubercles *sensu* Fauchald 1974*b*), located on the body-wall immediately above the base of the neuropodia, are dorsal cirri; the other papillae that are structurally different are here considered a characteristic class of papillae unique to the sphaerodorids. In sigalionids, elongated skintabs, referred to as stylodes, are often present (Pettibone 1970*a*). The complex papillae present in acrocirrids, some fauveliopsids, flabelligerids and poebiids have a common, unique structure and have been considered as homologous (Mesnil 1899; Robbins 1965; Banse 1969; Fauchald 1972).

Pygidial cirri

The postsegmental pygidium may be a small structure, essentially just carrying the anus (e.g. the opheliid genus *Travisia*, Fauvel 1923) or it may be a larger structure on which the anus is present, centrally or on one side (e.g. the opheliid genus *Ophelina*, Fauvel 1927, as *Ammotrypane*; maldanids, Fauvel 1927). The pygidium may be smooth, or may carry one or more pairs of pygidial cirri that may resemble the dorsal cirri or even the tentacular cirri in structure and length. The margin of the anus may be smooth or scalloped or may have short papillar structures. These anal structures have been confused in the literature with pygidial cirri (see especially Fauvel 1927), and it is currently difficult to sort out the available information. Pygidial cirri are absent in many, especially small-bodied taxa (e.g. aeolosomatids, Bunke 1967; parergodrilids, Karling 1958) and in the clitellates.

In one distinct pattern of pygidial cirri, one pair is present (e.g. nereidids, Uschakov 1955; Day 1967), and sometimes a very short, peg-like additional pair may be present (e.g. eunicids, Fauchald 1992*a*); when two pairs are present, the ventral pair is always short and peg-like, the dorsal pair is longer and much more noticeable (e.g. eunicids, Fauchald 1992*a*). In the nephtyids, a single median cirrus is present (Uschakov 1955, Day 1967). In another group of taxa, the pygidium is ornate with groups of cirri of varying lengths (e.g. maldanids, Hartman 1969; cossurids, Jones 1956) or may be a hood-like structure carrying a variable number of cirri (e.g. *Ophelia* Brown 1938; *Ophelina*, Fauvel 1923, Uschakov 1955, in both as *Ammotrypane*). In most groups, only one or a few kinds of pygidial cirri are present; however, in some groups, the pygidial cirri vary; for example, the spionids may have a simple funnel, four pads or tapering papillae or multiple slender cirri (Sigvaldadóttir *et al.*, 1997).

In many small polychaetes, the pygidium may have adhesive papillae carried either on a single structure or on paired 'toes' (e.g. polygordiids, Westheide 1990; protodrilids, Purschke & Jouin 1988 and saccocirrids, Westheide 1990).

Stomodaeum

The larval structure, called the stomodaeal invagination, which is ectodermal in origin (Schroeder & Hermans 1975), may give rise to a variety of structures in the adults. Generally, the adult structure corresponding to the stomodaeum is the buccal cavity, so these features could also be referred to as buccal features. A variable, but often complex set of folds, musculature and glands present on the ventral side of many polychaetes is usually referred to as the ventral buccal organ (Purschke 1988*a*). Note that the modifier 'buccal' is associated also with structures not derived from the stomodaeal invagination, such as 'buccal tentacles', which are modifications of the palps. Stomodaeal structures were used as basic criteria for grouping the families by Dales (1962, 1963).

Dorsolateral ciliated folds in the roof of the buccal cavity have recently been demonstrated to be present in many polychaetes (Purschke & Tzetlin 1996). These folds are longitudinal or oblique structures covered with ciliated cells and usually with associated gland cells. The folds do not contain any intrinsic musculature, but may be everted when the pharynx is everted. These folds are absent in taxa with muscular axial pharynges, and in sabellids, serpulids, sabellariids and in many, but not all, of the terebelliform families. Otherwise, Purschke & Tzetlin (1996) demonstrated the presence of such folds in members of 16 families.

The stomodaeum may lack obvious differentiation, by which is meant that the wall of the buccal cavity remains without any obvious large glands or additional muscular layers. In Clitellata, the dorsal wall of the stomodaeum has a differentiated, muscularized pad (Cook 1971).

Many polychaetes have variously ventrally differentiated pharynges. In the eunicean families (*sensu* Fauchald 1977, except Ichthyotomidae), the ventral and lateral walls of the involuted stomodaeum is muscular, and the lining of the stomodaeum is sclerotinized into a varying number of jaw pieces (Ehlers 1868*a*; Kielan-Jaworowska 1966; Hartmann-Schröder 1967; Wolf 1976; Imajima 1977; Wolf 1980; Orensanz 1990). The jaws are separated into a pair of ventral mandibles (Orensanz 1990, fig. 2) and two or more pairs of lateral maxillae (Orensanz 1990, fig. 1). Ehlers (1868*a*: 273–274) recognized two patterns of maxillae, labidognaths and prionognaths. He defined the labidognaths as having highly differentiated jaws situated in such a fashion that when the jaw apparatus is withdrawn, the larger pieces are located in a pocket with the smaller pieces arranged in semi-circles at the anterior end of the pocket. The prionognaths, however, were defined as having more or less similar jaw-pieces located in two rows on longitudinal ridges. In most recent euniceans, the maxillae are either supported basally by a pair of carriers (e.g. eunicids), which may be fused medially (e.g. certain dorvilleids), or carriers may be absent (e.g. some dorvilleids, Fauchald 1977). In addition to the features mentioned, labidognath jaws also have the carriers and MxI closely linked (Hartmann-Schröder 1967; Wolf 1976, 1980), and the jaws are calcified (Colbath 1986); in contrast, in the prionognaths, there is little linkage between carriers and MxI, and the jaws are heavily sclerotinized with small amounts of various metal-ions included, but without distinct calcification (Colbath 1986). Labidognath families include Onuphidae, Eunicidae and Lumbrineridae; prionognaths include the Oenonidae and Histriobdellidae and possibly the Hartmaniellidae (Wolf 1976, 1980; Szaniawski & Imajima 1996; pers. obs.). Characteristically, labidognath patterns are conservative in terms of numbers of jaw pieces. The number of teeth on each jaw-piece may vary, however, as demonstrated by Kielan-Jaworowska (1966). However, the oenonids have very variable numbers of jaw pieces, and even the symmetry relationships vary, also within single species (Crossland 1924; Orensanz 1990; see taxonomic section). Kielan-Jaworowska (1966) added two additional terms for maxillary assemblages, placognaths and ctenognaths. The former have exclusively been reported from fossils; they have asymmetrically developed large posterior jaws and symmetrically developed anterior denticles; carriers are absent. Ctenognath jaws, defined as consisting of relatively large basal maxillae and symmetrically arranged rows of numerous anterior denticles in longitudinal series without carriers, are present in some dorvilleids and various extinct taxa. Maxillae of juvenile onuphids and eunicids (Hsieh & Simon 1987; Kristian Fauchald, pers. obs.) have the ctenognath arrangement, but are far less differentiated than the denticles present in dorvilleids. Another term, xenognath, was introduced by Mierzejewski & Mierzejewska (1975) for an Ordovician fossil; the xenognath pattern consists of a series of small, symmetrically developed maxillary pieces with minimal differentiation. Orensanz (1990) explored relations between the fossil and recent families of euniceans based mainly on the jaw structures; he referred to his system as a 'synthetic phylogeny'. It is a useful conceptual frame-work not least since it has allowed an integration of the fossil taxa with the recent ones; much, however, remains to be tested for his suggested relationships to become fully accepted. Further discussion of the varying kinds of eunicean jaws is in the taxonomic section.

In amphinomids and euphrosinids (Gustafson 1930), the ventral wall of the stomodaeum is also muscularized and eversible, and the cuticular lining is sclerotinized. The sclerotinization is less obvious than in the euniceans, so, instead of forming distinct jaws, the whole ventral lining forms reinforced ridges and papillae in a file-like structure.

Purschke (1984, 1985*a*,*b*, 1987*a*,*b*, 1988*a*,*b*) and Purschke & Jouin (1988) demonstrated that ventral buccal organs may vary a great deal in ultrastructure. Despite these differences, the ventral buccal organs resemble each other more than they resemble any other form of stomodaeal differentiation. Ventral buccal organs may be eversible or non-eversible.

Ventral eversible sac-like or lobulated, poorly muscularized pharynges are present in some taxa (e.g. orbiniids, Hartman 1957). The outer end of these pharynges may be frilled and densely ciliated. The paraonids have the lateral walls of the eversible pharynx folded and broadly connected ventrally to a deep buccal organ (called the pharyngeal sac by Strelzov 1973). This pharyngeal structure resembles in cross-section the one present in the euniceans, but lacks the heavy musculature. The paraonid structure is here considered a ventral eversible poorly muscularized pharynx similar to the one in the orbiniids.

Tzetlin (1994) described the feeding apparatus of the cossurids. It consists of a series of feeding tentacles attached dorsally and posteriorly in the buccal cavity. They are poorly equipped with muscles and can be everted only by pulling the lower lip posteriorly. Each tentacle is marginally heavily ciliated; there is no buccal organ.

The psammodrilid stomodaeum has a unique structure. The buccal cavity, within the first peristomial ring, is simple; but the second peristomial ring has a massive musculature forming a pair of diaphragms (Swedmark 1955, fig. 12); these diaphragms are continued as short muscular sleeves covering the gut at each diaphragm. The two diaphragms are linked by two large muscles, one above and one below the digestive tract, apparently running free through the coelom. The whole structure appears to be a strongly muscular pump (Swedmark 1955, fig. 14).

An axial, sac-like eversible pharynx is present in certain taxa (e.g. arenicolids, Ashworth 1904, 1912; maldanids, Pilgrim 1966*a*,*b*; opheliids Brown 1938). Everted, usually through the contraction of a gular membrane and the anterior body-wall musculature, the outer surfaces of these sacs are often papillated and well-equipped with glands.

In many polychaetes, the stomodaeum is an axial eversible pharynx with thickened, strongly muscular walls. This pharynx may be retracted into a sheath, especially in taxa with large jaws (e.g. nereidids) or very heavy musculature (e.g. hesionids and nephtyids). In other cases, the pharynx can be partially retracted and partially inverted (e.g. glycerids, goniadids and phyllodocids). The external opening seen when the pharynx is fully retracted is often referred to as the mouth (i.e. Fauvel 1923; Hartman 1968), but is more accurately referred to as the opening to the pharyngeal sheath. The mouth proper is located at the tip of the pharynx when fully everted. The mouth may be surrounded by terminal papillae (sometimes called buccal papillae), or may be ciliated or smooth. Phyllodocidae (Pleijel 1991) and Alciopidae (Rice 1987) have jaw-less muscular eversible pharynges with the mouth opening fringed with terminal papillae. The phyllodocid pharynges are very long and slender; in the Alciopidae, the pharynges are shorter and more stiffly muscular. In two pelagic families, Tomopteridae (Åkesson 1962) and Typhloscolecidae (Uschakov 1972), the eversible muscular pharynges lack both jaws and papillae. The typhloscolecids have a dorsal retort organ that is partially everted with the pharynx (Greeff 1879; see also glossary in Pleijel & Dales 1991). Subterminal papillae in various patterns are present in some of these families (e.g. phyllodocids, Pleijel 1991).

In axial muscular pharynges, jaws may be present as a bilaterally arranged pair, as one or two dorsoventrally arranged pairs, as two pairs forming a cross, or as a circlet of smaller or larger pieces. Bilaterally arranged jaws may be well-developed and obvious (nereidids, Fauvel 1923), other jaws may be rather poorly developed (e.g. some hesionids, Fauvel 1923) and even wholly internalized at all times (nephtyids, Kirkegaard 1970). The surface of the nereidid pharynx when everted usually has groups of either papillae or sclerotinized paragnaths in characteristic patterns (Hartman 1968; Fauchald 1977; Glasby 1991), and subterminal papillae of various kinds are present in several families (e.g. nephtyids, Hartman 1950; Fauchald

1963; Rainer 1984, 1989; pontodorids, Fauvel 1923). The chrysopetalids have a pair of lateral stylets in the same relative position as the nereidid jaws (Perkins 1985; Glasby 1993). Most scale-worm families (e.g. Acoetidae, Pettibone 1989) have one or two pairs of dorsoventrally arranged jaws, and the mouth opening is bordered by terminal papillae. Similar jaws are present also in the Pisionidae (Åkesson 1961; Stecher 1968). In the Aphroditidae, the jaws are poorly developed and often irregular (Day 1967) but are still in the dorsoventral position, rather than being bilateral as in the nereidids and related taxa. Glycerids and goniadids have very long, axial eversible pharynges, covered externally with pharyngeal papillae and tipped with strongly sclerotinized jaws (Hartman 1950; Wolf 1976). In the glycerids, four jaws arranged in a cross and four accessory jaw pieces (ailerons) are present; in the goniadids, paired larger pieces (macrognaths) are in lateral positions, linked dorsally and ventrally by two arches of smaller jaw pieces (micrognaths) forming a somewhat irregular circlet. The pharyngeal papillae in the glycerids are mostly of one or two kinds in each species and are rather soft, but with a characteristic structure (Hartman 1950). In the goniadids, the pharyngeal papillae may be sclerotinized and differentiated into a variety of shapes (e.g. *Glycinde*, Hartman 1950). A completely sclerotinized lining, such as the one present in some taxa with ventrally muscularized pharynges (e.g. amphinomids) appears to be absent in all taxa with axial muscularized pharynges.

In the syllids, the stomodaeum is highly differentiated; the eversible structure may be sclerotinized, forming a circlet of stiffened crown-like structure (a trepan); behind the mouth opening, but usually projecting forward sufficiently to reach the mouth when fully everted, is a single dorsal, pointed tooth. The syllid eversible structure is followed by a strongly muscularized proventricle in which the muscle fibers are arranged radially. Glasby (1993) suggested a sequence of differentiation of an originally evenly muscular eversible pharynx into the eversible tube and proventricle present in the syllids; detailed documentation for this suggestion is not yet available. A proventricle has been reported also in the pontodorids (Greeff 1879). The sphaerodorids also have a proventricle (Reimers 1933), but differ from most syllids in lacking trepans and teeth. Miura & Laubier (1989) suggested that proventricles were present also in the nautiliniellids, but this has been rejected (Blake 1990; Glasby 1993).

In Vestimentifera and Frenulata, a stomodaeum is absent in the adults, since the digestive tract is closed anteriorly (and posteriorly); a strand of tissue running through the brain might be considered a remnant of the stomodaeum, but this relationship has yet to be accurately traced and must await detailing of the structure of the larval stomodaeum (Jones & Gardiner 1988; Southward 1988; Callsen-Cencic & Flügel 1995) and the fate of the various tissues of the anterior end during ontogenesis.

The structure of the stomodaeal invagination in the onychophorans and euarthropods is related to the presence of cuticular modifications characteristic of these two groups. Musculature, if present, is attached to the stomodaeal lining on one side and to apodemes on the body-wall on the other side, as are the promoter and retractor muscles in polychaete pharynges (Dales 1962; Brusca & Brusca 1990), but the arthropods lack the characteristic musculature present in the pharyngeal wall itself. Jaws derived from the pharyngeal lining are always absent, replaced by grasping and chewing surfaces on segmental appendages attached entirely outside the stomodaeal invagination.

Gular membrane

In most polychaetes, the septa are similar throughout the body or change slowly in shape and composition along the body. A gular membrane is a complete or nearly complete, usually muscularized, septum (often called the *diaphragm* in older literature; Meyer 1887), present anteriorly and differing distinctly from other septa in the same region of the body. The presence of a gular membrane is often associated with anterior eversible structures, either an eversible pharynx or a set of very extensible grooved palps. The septum dividing the middle part of the body in the frenulates could be considered a gular membrane (see illustration in Southward 1988). This is consistent with our interpretation of the segmentation in the frenulates (Rouse & Fauchald 1995). The presence of a gular membrane in the vestimentiferan pogonophorans has not been demonstrated; we consider the potential presence of gular membranes in these two groups as unproven.

The gular membrane may be present in front of the first segment (e.g. flabelligerids, Spies 1975), or, alternatively, between two successive anterior segments (e.g. arenicolids, Ashworth 1904; maldanids, Pilgrim 1966*a*; cirratulids, terebellids, ampharetids, Meyer 1887).

Digestive tract

In most polychaetes and clitellates, the gut is essentially a simple tube, supported by at least a dorsal mesentery and by partial to complete septa at each end of every segment. The gut can be longer than the body, such as in cirratulids, in which it zig-zags through the body cavity, passing through the septa at the midline, but forming alternating loops at the side of the segments. In many polychaetes, the gut is distended in each segment with narrow openings at each septum. In ampharetids and pectinariids (Wirén 1885; Hessle 1917; Holthe 1986), the gut is much longer than the body and may form one or two loops in the anterior part of the body. The presence of looped guts is associated with absence or near absence of septa, at least in the anterior end, so that the gut lies more or less free in the body-cavity.

The gut may be distinctly branching with branches leading out to the sides and sometimes dorsally into the bases of the dorsal cirri and other appendages (aphroditids, Fauvel 1959; polynoids, Dales & Pell 1971). Dales & Pell (1971) demonstrated that these side branches show physiological differentiation in scale-worms.

The vestimentiferans and frenulates have the gut occluded anteriorly and posteriorly (Gardiner & Jones 1993; Southward 1993). Normally, the gut lumen is said to be missing, but Southward (1988) reported the presence of unknown, presumably present in most segments. Circulatory system unknown, presumably closed; heart body presumably absent. Aciculae present. Chaetae variously ornamented capillaries and spines (Pettibone 1989, in descriptions and illustrations). Notopodial spines present; other notochaetae fine silken strands released and woven to form tubes (Pflugfelder 1934; Pettibone 1989).

The microscopic structure of the acoetid 'gills' is unknown; thus, they are not considered gills in the sense of the term is used in this paper.

ACROCIRRIDAE Banse, 1969

Main reference: Banse 1969.

Evidence for monophyly: None known.

The acrocirrids were originally described as cirratulids with compound chaetae (Fauvel 1927; Day 1967). Okuda (1934) added important information on internal structures and Banse (1969) diagnosed a new family for *Acrocirrus* and *Macrochaeta*. The family shares features with the flabelligerids such as the structure of the epidermal papillae and the compound hooks.

Prostomium either rounded and distinct (*Macrochaeta*) or a narrow keel between compressed anterior segments (*Acrocirrus*). Peristomium lips only (Okuda 1934, fig. 2b). Antennae absent. One pair of grooved dorsolateral peristomial palps present (easily lost; omitted in many early descriptions). Nuchal organs present (Okuda 1934, fig. 8d). Organization of longitudinal muscles unknown; segmentation distinct. First segment dorsally reduced, without parapodia and chaetae, with first pair of gills (Banse 1969, fig. 1b). In other segments, parapodial rami similar, small, truncate cones; notopodia larger than neuropodia in some parapodia of some taxa (illustrations in Banse 1969). Dorsal and ventral cirri absent. Paired dorsal gills present on anterior segments, usually four pairs in total (Banse 1969). Lateral organs and dorsal cirrus organs not observed. Epidermal papillae similar to flabelligerid papillae (Mesnil 1899). Stomodaeum a ventral buccal organ; presumably eversible (called proboscis by Banse 1969). Gular membrane absent; gut a straight simple tube. Metanephridia present (Okuda 1934: 201); description matches mixonephridia of cirratulids. First pair of segmental organs excretory (Banse 1969: 2597); others presumably gonoducts. Numerous segmental organs may be present in anterior region (Okuda 1934; observation needs confirmation). Circulatory system closed; heart body present (Mesnil 1899). Aciculae absent. Compound chaetae unusually large with expanded joints consisting of superficial grooves or folds. Other chaetae variously ornamented or smooth capillaries.

The narrow keel-shaped prostomium in *Acrocirrus* may appear like a short median antenna in dorsal view, but is actually just the upper end of a ridge running down the prostomium very nearly to the upper lip (Banse 1969, fig. 1b). Some of the many epidermal papillae scattered or densely covering the body may mimic dorsal or ventral cirri; however, none of them appears to have differentiated from the other body papillae. According to Banse (1969), not only the first segment, but the first two or three segments are achaetous.

AEOLOSOMATIDAE Beddard, 1895

Main references: Bunke 1967, 1988.

Evidence for monophyly: None known.

The aeolosomatids were for more than 100 years considered an isolated family of oligochaetes (Stephenson 1930). Brinkhurst (1971: 176 in Brinkhurst & Jamieson 1971) found that the aeolosomatids, while resembling the clitellates, could not be included in that group (see also Bunke 1967, 1988). Timm (1987), recognizing the isolated position of the family, proposed a new order for them within the oligochaetes. However, nuchal organs are present, and the aeolosomatids are, for that reason, here considered polychaetes. Aeolosomatids are small, slender flattened worms that mostly reproduce asexually by forming chains. Most species occur in freshwater, but marine species have been described (Westheide & Bunke 1970). We suspect that the long association of the aeolosomatids with the clitellates is due partially to their simple overall body-structure, but also to their most common habitat: they are found in an environment investigated for their content of clitellates, not for their content of polychaetes.

Prostomium and peristomium fused to single unit [Bunke's (1967: 196) 'Pharynxabschnitt' peristomial part of unit]. Antennae, palps and tentacular cirri absent. Nuchal organs transverse ciliated slits (Bunke 1967, fig. 1b). Longitudinal muscle banding apparently absent (Marcus 1944, fig. 23); segmentation present. First segment is similar to all other segments. Parapodia and parapodial appendages are absent, as are external gills, epidermal papillae and pygidial cirri (Bunke 1967). Lateral organs and dorsal organs not observed. Stomodaeum with ventral, eversible buccal organ (Bunke 1967: 196–197). Gular membrane absent; gut a simple tube. Nephridia metanephridia; ciliophagocytic organ absent. Segmental organs apparently mixonephridia (Bunke 1994: 257). Segmental organs present in most segments (at least in some taxa). Circulatory system closed; heart body absent (Baskin 1928; Marcus 1944; Bunke 1967, fig. 32). All chaetae variously ornamented capillaries.

The structure and distribution of the segmental organs are somewhat uncertain. Bunke (1967: 297 and 1988: 345) reported that sperm was discharged through metanephridia. Bunke (1988: 345) stated that metanephridia were not present in all segments; however, male gonads may be present anterior and posterior to female ones, and, since the sperm is voided through 'metanephridia' segmental organs, must be present in many segments, relative to the total number of segments present. The sigmoid chaetae present in some taxa are short, distally truncate, with teeth or rugosities, and might qualify as spines, but differ only slightly from the rest of the chaetae in thickness and are here considered capillary.

ALCIOPIDAE Ehlers, 1864

Main references: Rice 1987; Wu & Lu 1994.

Evidence for monophyly: Large camera-type eyes present.

The first described alciopids were related to the phyllodocids, which they resemble closely in parapodial structures; these pelagic worms are still often considered a subgroup of phyllodocids (Fauvel 1923; Pleijel 1991). The Phyllodocidae is probably paraphyletic without inclusion of this family. The main feature in which alciopids differ from phyllodocids is the presence of enormous eyes, which structurally distort the whole anterior end.

Prostomium small, more or less quadrangular between huge eyes (Rice 1987, figs 1–3); eyes complex, with camera-type construction (Hermans & Eakin 1974). Peristomium is limited to the lips. One pair of lateral and a median antenna present. A pair of slender, tapering ventral palps present (usually considered a ventral pair of antennae; see Rice 1987). Nuchal organs present as ciliated patches posterior to eyes (Claparède 1870). Organization of longitudinal muscles not observed; segmentation present. First segment dorsally incomplete with tentacular cirri; three to five pairs of tentacular cirri present on maximum three segments. Parapodia biramous with well-developed neuropodia and notopodia represented by foliose dorsal cirri attached to cirrophores on edge; ventral cirri present. Gills and epidermal papillae absent. One pair of pygidial cirri present in most taxa; others with a single anal cirrus (Uschakov 1972). Lateral organs and dorsal cirrus organs not observed. Stomodaeum eversible, muscular pharynx without jaws; with at least one pair of terminal papillae. Gular membrane absent; gut a straight tube. Protonephridia present in adults; ciliophagocytic organs absent (Goodrich 1945). Segmental organs protonephromixia present in most segments; those in anterior segments sterile (Claparède 1870). Circulatory system limited to main stems only (Smith & Ruppert 1988, table 14; Ehlers 1864: 179); heart body absent. Aciculae present. Compound chaetae present in many taxa (presence assumed plesiomorphic, Wu & Lu 1994) with slender, tapering appendages; joint with single ligaments. Other chaetae capillary.

ALVINELLIDAE Desbruyères & Laubier, 1986

Main references: Desbruyères & Laubier 1980, 1986, 1989, 1991.

Evidence for monophyly: Stomodaeum with characteristic dorsal modification (Desbruyères & Laubier 1991).

The type genus was originally described in Ampharetidae (Desbruyères & Laubier 1980); later, it and one additional genus, *Paralvinella*, were moved to a separate family (Desbruyères & Laubier 1986).

Prostomium folded and curved separated by distinct groove. Peristomium forming roof of mouth and lips (Desbruyères & Laubier 1991, fig. 3c). All antennae absent. Palps multiple grooved buccal tentacles external to mouth (Desbruyères & Laubier 1991: 32). Nuchal organs ciliated transverse patches. Organization of longitudinal muscles not observed; segmentation present. First two or three segments more or less fused, separated from pro- and peristomium by distinct groove (Desbruyères & Laubier 1991, fig. 3c) without appendages and chaetae but with gills. Notopodia short, slender cylinders; neuropodia are tori. Dorsal and ventral cirri absent (but see below). Four pairs of dorsal gills present on anterior segments; each branched from distinct stalk. Epidermal papillae absent. Pygidial cirri absent. Lateral organs absent; dorsal cirrus organs not observed; presumably absent. Stomodaeum with non-eversible buccal organ and characteristic dorsal glandular modification. Gular membrane present between two anterior segments; digestive tract probably looped as in ampharetids (pers. obs.). Segmental organs one pair of anterior excretory metanephridia with strictly nephridial function followed by three pairs of gonoducts (Zal *et al.* 1994: 43); apparently mixonephridia. Circulatory system present; apparently closed (pers. obs.: capillary beds in gills); heart body not seen. Aciculae absent. Chaetae notopodial capillaries and neuropodial uncini. One anterior segment with notopodial spines (Desbruyères & Laubier 1991: 32).

Desbruyères & Laubier (1991: 31–33) described dorsal cirri in *Paralvinella*; these may be homologous to the dorsal cirri of other polychaetes, but positionally they are more likely to be autapomorphic structures in the alvinellids since they are part of the neuropodia rather than the notopodia. The dorsal stomodaeal pad present in the alvinellids has a different composition from the one present in the clitellates and is here considered an autapomorphy.

AMPHARETIDAE Malmgren, 1866

Main references: Day 1964; Holthe 1986.

Evidence for monophyly: Motile buccal tentacles located on an eversible lip-like structure (Hessle 1917; Holthe 1986).

The ampharetids resemble the terebellids in many structures and were included among the terebellids until Malmgren's (1866) revision.

Prostomium relatively small, elongated, rounded, or pointed; located on top of a larger unit consisting of fused first and second segments. Peristomium limited to lips and roof of mouth. Antennae absent. Palps short, slender peristomial buccal tentacles attached to dorsally located curtain within the buccal cavity; occasionally supplemented by one or two very much larger grooved ones (Hartman 1969: 548–549, fig. 2, see also 570–571, fig. 1). Nuchal organs comma-shaped located lateral to prostomium. Longitudinal muscles in four bands; segmentation present. First segment completely fused to pro- and peristomium, apodous and achaetigerous; gills may be present. Short cylindrical notopodia present in thorax; neuropodia tori throughout. Dorsal and ventral cirri absent. Up to four pairs of gills present on anterior segments; tapering in most taxa, but structurally different gills occur. Epidermal papillae absent. Pygidium unadorned or with many cirri. Lateral organs present; dorsal cirrus organs not observed, presumably absent. Stomodaeum with non-eversible buccal organ (Fauvel 1897; called food-sorter by Dales 1963). Gular membrane present between two anterior segments (Meyer 1887; Hessle 1917). Gut straight in some taxa, looped in others; looped apparently most common condition (Wirén 1885: 30–31). Segmental organs mixonephridia (Goodrich 1945); first pair excretory; others gonoducts; only few anterior pairs present. Circulatory system closed (Wirén 1885); heart body present (Kennedy & Dales 1958). Aciculae absent. Chaetae notopodial thoracic capillaries and neuropodial uncini; slender, peg-like chaetae in anterior neuropodia present in some taxa. Paleae present in some taxa; others with paired large hooks dorsally in paleal positions; many taxa without either paleae or hooks.

In ampharetids, the feeding apparatus consists of protrusible buccal tentacles; in terebellids and trichobranchids, the feeding palps, which are homologous with the buccal tentacles, are wholly external to the mouth. Day (1964) reviewed the construction of the ampharetid anterior end, concluding that the paleal segment (when paleae are present) is the third segment (see also Fauvel 1927: 225 and Holthe 1986: 29); consequently, the first and second segments are achaetigerous and completely fused to the head. Holthe (1986: 44) discussed buccal tentacles among the terebellomorphs; the dorsal curtain to which these are attached in the ampharetids is an autapomorphy for the family. The usual statement, that the buccal tentacles are retractable into the mouth (cf. Fauvel 1927: 225 and Fauchald 1977: 121) is easily misunderstood: the buccal tentacles, while they have considerable individual mobility, are protruded as a group, rather than individually. In the closely related alvinellids, similarly constructed buccal tentacles are grouped around the mouth and are not located on a dorsal curtain. The cirri attached to the upper edge of the neuropodia in the abdomen of some ampharetids (Holthe 1986, fig. 8b) appear to be *de-novo* structures not related to dorsal cirri associated with notopodia (compare the description of the alvinellids).

AMPHINOMIDAE Savigny in Lamarck, 1818

Main reference: Gustafson 1930.

Evidence for monophyly: Caruncle (nuchal organ) with four or more rows of ciliary bands (cf. Gustafson 1930: 446).

The caruncle, which is an unusual development of the nuchal organ, is a synapomorphy shared with the Euphrosinidae. The two families are also the only polychaetes with calcified chaetae (Gustafson 1930). The pharyngeal structure with the sclerotinized, rugose eversible lower lip is another unusual feature shared by the two families. The family may be paraphyletic by the recognition of the euphrosinids. One major difference between the families lies in the structure of the notopodia, which are short, truncate cylinders or cones in the amphinomids and elongated crests in the euphrosinids. The gills are single tufts associated with the notopodia in the amphinomids and are spread out along the crests as smaller, less branching, groups in the euphrosinids. The description of a new family (Archinomidae Kudenov 1991; see Euphrosinidae and later) based on the new genus, *Archinome* for a species originally described as a euphrosinid complicated the issue in that it has the caruncular structure of a euphrosinid and the notopodia of an amphinomid.

Prostomium with two parts, overall a frontally rounded triangle widest anteriorly. Peristomium limited to lips (illustrations in Hartman 1951). Paired lateral antennae on anterior prostomial lobe; median antenna on posterior lobe (Gustafson 1930, fig. 38). Ventrolateral palps slender; located on anterior prostomial lobe. Nuchal organs complex structure usually consisting of several folds and ciliated tracts; attached to dorsum posterior to prostomium (Storch & Welsch 1969). Longitudinal muscles grouped in four bundles (Storch 1968, fig. 21); segmentation present. First segment curved around prostomium with parapodia similar to those elsewhere. All parapodia biramous; notopodia truncate cylinders; neuropodia tapering, project beyond notopodia; tentacular cirri absent. Dorsal and ventral cirri present. Gills branching structures attached to notopodial bases. Epidermal papillae absent. Pygidial cirri absent (Marsden 1963: 177). Lateral organs and dorsal cirrus organs not observed. Stomodaeum with thick, muscular eversible lower lip covered with rugosities and usually with thickened cuticle (Dales 1962). Gular membrane absent; gut a straight tube. Segmental organs mixonephridia (Goodrich 1945); assumed present in most segments. Circulatory system closed; heart body absent. Aciculae present. All chaetae more or less calcified (Gustafson 1930: 324). Chaetae variously ornamented capillaries and spines, often dentate, usually very brittle.

APHRODITIDAE Malmgren, 1867

Main references: Darboux 1899; Fordham 1926.

Evidence of monophyly: None known.

The dorsal felt chaetae attached to the notopodia (Hutchings & McRae 1993: 283) are present in most, but not all taxa (Day 1967: 31). Aphroditids were among the first polychaetes described and, as mentioned above (in the section on the acoetids), the family is sometimes defined to include all scale-worms; recently, the scale-worms have been split into six families (Acoetidae, Aphroditidae, Eulepethidae, Polynoidae, Pholoidae and Sigalionidae). The aphroditids are most closely similar to the acoetids; these two families share the presence of fine, silken notochaetae. In acoetids, these are used to form the tube; in aphroditids, only some of which are capable of producing these chaetae, they form a felt attached to the notopodia covering the dorsum. Fordham (1926): 129, text fig. 1 considered the first segment part of the peristomium.

Prostomium a frontally rounded double lobe. Peristomium limited to lips. Lateral antennae absent; median antenna present. Facial tubercle prominent in most taxa. Ventral, tapering, unarticulated palps present; fused to medial side of first pair of parapodia. Nuchal organs present (Rullier 1951: 309). Longitudinal muscles in four bundles (Storch 1968); segmentation distinct. First segment curved around prostomium with parapodia similar to others. Two pairs of tentacular cirri present. Notopodia always shorter than the neuropodia. Dorsal cirri alternating with elytrae throughout; ventral cirri present. Gills absent. Complex epidermal papillae of the kind present in flabelligerids absent; simple papillae present on ventrum and parapodia in many taxa. Pygidial cirri present (Fauvel 1923: 34; absent according to Fordham 1926). Lateral organs and dorsal cirrus organs not observed. Stomodaeum an eversible muscular axial pharynx with two pairs of dorsoventrally arranged jaws; poorly developed in some species (Day 1967); terminal pharyngeal papillae present. Gular membrane absent; gut with paired side-branches in most segments. Segmental organs mixonephridia present in most segments. Circulatory system closed; heart body absent. Aciculae present. Chaetae variously ornamented capillaries and spines. Notochaetae spines and capillaries and fine silky fibers forming a dorsal felt in many taxa (i.e. spinning glands present).

Elytrae are absent in *Palmyra* (Watson Russell 1989). Fordham (1926: 153) described 'heart-bodies' associated with the nephridia, rather than as inserts in dorsal blood-vessels. Fordham's structures are here considered 'glomerulus'-like structures differing positionally and structurally from heart-bodies present in other polychaetes.

APISTOBRANCHIDAE Mesnil & Caullery, 1898

Main references: Orrhage 1962, 1974.

Evidence for monophyly: Slender dorsal appendages supported by aciculae on many chaetigers (Orrhage 1962, fig. 8).

The first apistobranchid was described as *Aricia tullbergi* Théel (1879) in the Orbiniidae (as Ariciidae) and moved to its own genus within that family by Levinsen (1883). Mesnil & Caullery (1898) recognized that the genus was more closely related to the spionids than to the orbiniids and erected a new family for it among the spionid-related families where it still remains. The most detailed studies of the family were made by Orrhage (1962, 1974).

Prostomium rounded, diamond-shaped. Peristomium limited to lips. Antennae absent. Paired grooved palps are dorsolateral to prostomium. Nuchal organs present; located outside palpal bases. Longitudinal muscle bands present; segmentation distinct. First segment with uniramous parapodia, interramal cirus present (Orrhage 1962: 430, figs 2–4; fig. 8, segm. 1). Most neuropodia with flanged postchaetal lobes similar to those in spionids. Notopodia more or less flask-shaped, narrowed distally into distinct dorsal cirri (Orrhage 1962, fig. 8); ventral cirri absent. Gills absent. Epidermal papillae absent. Multiple pygidial cirri present. Lateral organs present; dorsal cirrus organs not observed. Stomodaeum possibly eversible and axial (Orrhage 1974); ventral pharyngeal organs absent (Purschke & Tzetlin 1996). Gular membrane absent; gut a straight tube. Metanephridia present; anterior ones presumably excretory; posterior ones gonoducts. Circulatory system closed; heart body absent. Notopodial aciculae present in many segments (Orrhage 1962, fig. 8 1974); other aciculae absent. Chaetae all variously modified capillaries.

In Orrhage (1962, fig. 8) several segments are shown to have a small cirrus-like structure ventral to the neuropodia; this may be a high point along the flanged postchaetal lobe similar to those present in magelonids (see below). Orrhage (1974) described the buccal pouches without mentioning that the structure was eversible; however, in his treatment of the musculature, he mentioned protractors and retractors for the anterior part of the digestive tract. The structure of the segmental organs is poorly understood; the anterior nephridia are assumed to be strictly excretory, and the more posterior ones function as gonoducts since gametes are found only from chaetiger 13 and backwards (Orrhage 1974). Orrhage (1974: 20) did not illustrate the segmental organs; the structure of nephridia in related taxa (e.g. poecilochaetids and spionids) is also poorly understood.

ARENICOLIDAE Johnston, 1835

Main references: Ashworth 1904, 1912; Wells 1959.

Evidence for monophyly: Glandular caeca along esophagus (Wells 1959).

Arenicolids were among the first described polychaetes, being mentioned also in pre-Linnean publications (Ashworth 1912). They are easily recognized, but surprisingly difficult to characterize; the evidence for monophyly suggested here is tentative: glandular caeca are present in all arenicolids but are not known to be unique to this taxon. The characteristic thick, rugose epidermis is not unique to this family; similarly structured if not quite as thick, epidermis is present in some scalibregmatids (Ashworth 1902) and capitellids (Eisig 1887). The structure and distribution of gills is uniform in all arenicolids, except *Branchiomaldane*, and potentially an apomorphy for the family. Arenicolids are usually considered related to maldanids and capitellids; these three families are grouped together in the order Capitellida in several recent reviews (Dales 1963; Fauchald 1977; Pettibone 1982).

Prostomium small, rounded or conical. Peristomium limited to lips. Antennae and palps absent. Nuchal organs paired dorsolateral pits. Longitudinal muscles in four distinct bands (Storch 1968); segmentation distinct. First segment similar to other segments; without any parapodial structures in adults; tentacular cirri absent. Notopodia short, distally truncate cylinders or cones; neuropodia tori. Dorsal and ventral cirri absent. Gills branching tufts associated with notopodia in middle part of the body in most taxa; as simple, tapering structures in *Branchiomaldane*. Epidermal papillae absent. Pygidial papillae absent. Lateral organs absent (Rullier 1951); dorsal cirrus organs not observed, presumably absent. Stomodaeum an eversible sac-like pharynx covered externally with large papillae. Gular membrane present; gut a straight tube. Segmental organs mixonephridia (Goodrich 1945); only few pairs present anteriorly; first one purely excretory. Circulatory system closed; heart body absent. Aciculae absent. Chaetae variously ornamented notopodial capillaries and distally dentate, unprotected neuropodial hooks.

The hearts described by Dales & Cummings (1987) are not homologous with the heart bodies of other polychaetes.

CAPITELLIDAE Grube, 1862

Main references: Eisig 1887; Hartman 1947.

Evidence for monophyly: Distally multidentate hooks with full, enclosing hoods in tori of both rami in posterior chaetigers (Eisig 1887; Hartman 1947; Thomassin & Picard 1972).

The first capitellids were described in the clitellate genus *Lumbricus*; the genus *Capitella* was recognized early (Blainville 1828), and the capitellids were recognized as a distinct family among the polychaetes from 1862. The family has always been considered related to the arenicolids and the maldanids. Capitellids are frequently encountered, but characters useful in comparing taxa remain poorly understood. The counts of segments with differing equipment of soft structures and chaetae frequently used to identify genera and species (Fauchald 1977) have to be interpreted with care, since the distribution of various features is related to size and may change ontogenetically (Ewing 1982).

Prostomium a short, blunt cone. Peristomium limited to lips. Antennae and palps absent. Nuchal organs a pair of dorsolateral pits. Longitudinal muscles in distinct bundles; segmentation present. First segment longer than next following; without parapodia and chaetae. A variable number of anterior chaetigers with short, truncate parapodial lobes sometimes deeply recessed in the body wall in both rami; replaced by tori in both rami in more posterior chaetigers. Dorsal and ventral cirri absent. Gills absent. Epidermal papillae absent. Pygidial cirri absent in many taxa; varying numbers of cirri present in others. Lateral organs present; dorsal cirrus organs not observed, presumably absent. Stomodaeum with simple axial eversible proboscis. Gular membrane present between chaetigers 4 and 5. Gut a straight tube. Metanephridia present; the nephridia and coelomoducts entirely separated; coelomoducts appearing only at sexual maturity (Goodrich 1945); number of segmental organs variable. Circulatory system and heart body absent. Aciculae absent. Chaetae include capillaries and hooded hooks. Anterior chaetigers with capillary chaetae in a variable number of chaetigers in both rami; posteriorly both rami with hooks. Hooks small and in single row in each torus (Fauchald 1977).

Some, otherwise apparently unrelated, species have respiratory extensions from the body wall; however, since a circulatory system is absent, these contain coelomic extensions rather than loops from the circulatory system and are here considered a *de-novo* feature of the capitellids. Anterior end of body is often rugose (Eisig 1887, pl. 2), but epidermal papillae are absent. Capitellids have a shunt that opens into the digestive tract anteriorly and posteriorly (Eisig 1887: 14); this may be a another unique feature of the family, but the presence or absence of such a structure has not been recorded for most polychaete families so this feature cannot yet be used as a character. The number of segmental organs tend to be restricted, but not in any pattern similar to those of other polychaetes.

CHAETOPTERIDAE Audouin & Milne Edwards, 1833d

Main references: Joyeux-Laffuie 1890; Gitay 1969; Barnes 1965.

Evidence for monophyly: Body with three characteristic body regions with sequentially differentiated parapodia.

The first chaetopterid was described by Renier (1804) with the generic name added by Cuvier (1830) and the concept of the family (incorrectly named) by Audouin & Milne Edwards (1833*d*). Original descriptions of many species are poor or based on incomplete material. As a consequence, it is not known how many of the many descriptions in the larger genera (*Chaetopterus*, *Phyllochaetopterus*) refer to valid species; for example, Fauvel (1927) and Hartman (1969) considered the genus *Chaetopterus* to be monotypic with a single, very widely distributed species.

Usually considered related to the spionids or the spioniform families, the external morphology of the chaetopterids is very complex and they have for that reason often been considered as having an isolated position among the polychaetes.

Prostomium small rounded or quadrangular. Peristomium limited to lips. Antennae absent (see below). One pair of long, grooved peristomial palps present. Nuchal organs on sides of prostomium. Longitudinal muscles in distinct bands; segmentation distinct. First segment similar in size to next following ones and, like these, with notopodia present. Tentacular cirri absent. Parapodia unusually differentiated; anterior end with notopodia only; mid-body parapodia biramous with large achaetous flap-shaped notopodia and neuropodial tori; posterior parapodia biramous with either both rami pointed or notopodia pointed and neuropodia tori. Dorsal and ventral cirri absent. Gills absent. Epidermal papillae absent; pygidial cirri absent. Lateral organs unknown; dorsal cirrus organs absent. Stomodaeum a simple tube without vestige of a proboscis (Dales 1962: 417). Gular membrane absent. Gut straight, but often with distinct pouching in each segment; gut wall often dark green. Segmental organs metanephromixia; anterior segmental organs excretory; posterior ones fertile. Circulatory system closed; heart body absent. Acicula absent. Chaetae lancet-shaped anterior chaetae; a pair of large spines in chaetiger 4 and neuropodial uncini.

A pair of small 'antennae' are present posterior and external to the palps in *Phyllochaetopterus* (Barnes 1965, fig. 4); positionally, these structures are not homologous to the antennae of other polychaetes; they are not present in other members of the family. In *Chaetopterus*, small cirri are present above the superior edge of posterior neuropodia (Joyeux-Laffuie 1890); positionally, these cirri appear to be interramal and are not homologous with the ventral cirri. Joyeux-Laffuie's (1890: 318–332) description of the segmental organs matches well with Goodrich's (1945: 294) generalization: "The whole of the Spiomorpha" (which includes the chaetopterids)"should probably be included in Section I"..."which includes families with open nephridiostomes, but at sexual maturity become large-funneled metanephromixia acting as gonoducts in the fertile segments". Some chaetae are deeply imbedded; they are not aciculae since they outreach the tip of the parapodia by a considerably distance and are here considered capillaries (Joyeux-Laffuie 1890: 257–271, pl. 15, figs 4, 6–9).

CHRYSOPETALIDAE Ehlers, 1864

Main references: Perkins 1985; Watson Russell 1986, 1991; Dahlgren & Pleijel 1995.

Evidence for monophyly: Paleal notochaetae of characteristic structure (Butterfield 1990; Westheide & Watson Russell 1992).

The first chrysopetalid was described by Ehlers (1864); the family was quickly linked to the 'palmyrids', which have similar appearing notochaetae in rosettes (e.g. Day 1967). However, Watson Russell (1989) demonstrated that *Palmyra* is a member of the scale-worm family Aphroditidae. The chrysopetalids have otherwise been considered related to the nereididoid families (Glasby 1993).

Prostomium quadrangular. Peristomium limited to lips.

Nuchal organs present (Racovitza 1896). Organization of longitudinal muscles unknown; segmentation present. First segment curved around prostomium with parapodia resembling other parapodia. Two pairs of tentacular cirri present (Watson Russell 1986, figs 2–3). Neuropodia relatively short compared to large notopodia in most taxa but project laterally. Dorsal and ventral cirri present. One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum axial muscular eversible pharynx with one pair of laterally arranged jaws. Terminal papillae absent. Gular membrane absent; gut a straight tube. Segmental organs metanephromixia (Fage 1906); distribution undocumented. Circulatory system closed; heart body absent. Aciculae present. Neuropodial compound chaetae with single ligaments in joints; appendages falcate. True capillaries possibly absent in adults (Perkins 1985: 859), but present in larvae (Greg Rouse, pers. obs.). Most species with expanded paleal notochaetae, members of one genus have spine-like notochaetae.

Jorge (1954, figs 1–2) showed the prostomium as completely fused to the rest of the body; Perkins (1985) and Watson Russell (1986, fig. 2) demonstrated that it is distinct from the first segment, but retractable under a nuchal fold formed by the dorsal side of the first chaetiger. Ehlers (1864) illustrated the digestive tract as if it had side branches; however, the gut appears only to be pouching in each segment (Thomas Dahlgren, pers. commun.). Segmental organs have been reported as metanephromixia; however, Goodrich (1945) discussed the possibility that they might be mixonephridia.

CIRRATULIDAE Carus, 1863

Main references: Caullery & Mesnil 1898; Day 1967; Blake 1991.

Evidence of monophyly: None known.

The cirratulids were either considered related to the spionids (Levinsen 1883), presumably due to the presence of grooved palps; or they were considered drilomorphs and listed with other taxa without antennae and with simple chaetae (Hatschek 1893). Most recent studies group the cirratulids with the spiomorphs (Appendix B).

Prostomium pointed or bluntly conical; peristomium limited to lips. Antennae absent. Paired grooved peristomial palps present in juveniles and adults of many species (but see below). Nuchal organs paired dorsolateral pits. First segment apodous and achaetous. Both parapodial rami similar, papillar or short cones. Dorsal and ventral cirri absent. Slender dorsal gills present (Fauvel 1927: 89; Caullery & Mesnil 1898). Epidermal papillae absent. Pygidial cirri absent (but see Caullery & Mesnil 1898: 12). Lateral organs and dorsal cirrus organs not observed. Stomodaeum with eversible ventral buccal organ. Gular membrane present; gut a straight tube (Meyer 1887). Segmental organs mixonephridia; a single anterior pair excretory; others more posteriorly gonoducts (Meyer 1887; Goodrich 1945). Circulatory system closed; heart body present (Mesnil 1899; Kennedy & Dales 1958). Aciculae absent. Chaetae smooth or ornamented capillaries and falcate or distally dentate spines.

All cirratulids studied have paired grooved palps as juveniles. In some taxa (e.g. *Cirratulus*), the palps become longitudinally split and are located in two patches at the posterior edge of a posteriorly projecting fold of the peristomium and sometimes appearing even further back. Two or more patches of multiple palps are characteristic especially of large-bodied cirratulids, but in many genera (e.g. *Chaetozone*), a single pair of grooved palps is present throughout life; we assume that the presence of a single pair is plesiomorphic for the family. The first visible segment that appears as half a segment in many taxa because of the overlapping dorsal extension of the prostomium is apodous and achaetous (Caullery & Mesnil 1898: 12). The spines may be curved and are sometimes called hooks, but are more similar to the spines than to hooks present in other polychaetes.

COSSURIDAE Day, 1963

Main references: Fournier & Petersen 1991; Tzetlin 1994.

Evidence for monophyly: A single median gill present on one anterior chaetiger (Fournier & Petersen 1991: 70–71).

Cossurids resemble the cirratulids in having no prostomial appendages and only capillary chaetae; they were removed from the cirratulids by Day (1963) mainly due to the presence of median single 'tentacle'; all cirratulid appendages, whether 'tentacular' or gills, are paired. Tzetlin (1994) has also demonstrated the highly unusual nature of the feeding apparatus; he compared it to the structures present in the orbiniids, but it appears to be unique to the cossurids.

Prostomium bluntly conical. Peristomium a distinct ring. Anterior appendages absent (Laubier 1963; Fournier & Petersen 1991: 65). Nuchal organs are dorsolateral ciliated short grooves. Longitudinal muscles are grouped in bundles (Tzetlin 1994); segmentation is distinct. First segment similar to next segments with parapodia and chaetae; tentacular cirri absent. Parapodial rami often nearly confluent in first or first few segments. Both notopodia and neuropodia low, ridge-like or papillar structures; dorsal and ventral cirri absent. A single median gill present dorsally on one anterior chaetiger (Fournier & Petersen 1991: 70–71). Epidermal papillae absent. Three or more pygidial cirri present in some taxa (Uschakov 1955; Jones 1956). Lateral organs and dorsal cirrus organs not observed. Stomodaeum with dorsally attached buccal tentacles. Gular membrane absent; gut a straight tube. Nephridial and reproductive system poorly documented. Circulatory system closed; heart body not seen. Aciculae absent. Chaetae limbate and slender capillaries, spines in posterior end in one genus (Ewing 1987).

The peristomium is sometimes confused with the first segment (see Fournier & Petersen 1991: 70). The structure referred to as a tentacle in the descriptive literature is a gill (see above). Tzetlin (1994) described the feeding apparatus as consisting of heavily ciliated buccal tentacles attached posteriorly to the roof of the buccal cavity. These buccal tentacles are applied to the substrate when the mouth is opened. Tzetlin (1994) suggested that the paired muscle cells internally in each buccal tentacle were more likely to function as a skeletal rod than as a true motile element. In structure and position, the cossurid buccal tentacles appear unique and not homologous with the similarly named structures in ampharetids and alvinellids (Tzetlin 1994).

CTENODRILIDAE Kennel, 1882

Main references: Caullery & Mesnil 1898; Wilfert 1973; Gelder & Palmer 1976; Purschke 1988*b*; Petersen & George 1991.

Evidence for monophyly: None known

The ctenodrilids were described in detail by Caullery & Mesnil (1898); they were considered part of the Cirratulidae (Fauvel 1927: 90; Day 1967: 501), which they resemble in lacking antennae and in having poorly developed parapodia with simple chaetae. Dales (1963: 186) considered them a separate family within his order Cirratulida. Hartmann-Schröder (1971) treated them as a separate family within the Drilomorpha. Fauchald (1977) considered them as belonging to a separate order together with the Parergodrilidae. The ctenodrilids share with the parergodrilids a small body size, a simple body construction with a limited number of segments and no anterior appendages. Recognition of Ctenodrilidae may make it difficult to characterize Cirratulidae in that the filiform gills present in the Cirratulidae are also present in one subfamily of the Ctenodrilidae.

Prostomium short and frontally truncate. Peristomium limited to lips. Antennae and palps absent. Paired nuchal pits are present (Petersen & George 1991, fig. 6b–c). Longitudinal muscles grouped in bundles (Sokolow 1911); segmentation present. First segment similar to other chaetigers; tentacular cirri absent. Parapodia and parapodial cirri absent. Paired filiform, dorsal gills present in some taxa. Epidermal papillae and pygidial cirri absent. Lateral organs absent; dorsal cirrus organs not observed, probably absent. Stomodaeum with eversible ventral buccal organ. Gular membrane absent; gut a straight tube. Segmental organs mixonephridia; only one excretory pair present; gametes exit through more posterior ducts (Caullery & Mesnil 1898). Circulatory system closed; heart body present. Aciculae absent. Capillary chaetae present in Raphidrilinae; other chaetae distally dentate, unprotected hooks.

The chaetae have been referred to as proteinaceous (Wilfert 1973); if verified, it would be unique among the polychaetes.

DIURODRILIDAE Kristensen & Niilonen 1982

Main references: Kristensen & Niilonen 1982; Westheide 1990; Kristensen & Eibye-Jacobsen 1995.

Evidence for monophyly: None known.

The genus *Diurodrilus* Remane 1925 was described as a dinophilid. The Dinophilidae was synonymized with the dorvilleids by Kristensen & Eibye-Jacobsen (1995); however, they retained Diurodrilidae as a distinct entity. Diurodrilids are very small, interstitial worms that resemble small dorvilleids.

Prostomium distinct and frontally rounded. Peristomium a distinct ring. All anterior appendages absent. Nuchal organs not observed. Organization of longitudinal muscles undocumented; segmentation distinct. First segment similar to other segments. Parapodia, dorsal and ventral cirri absent. Gills absent. Epidermal papillae absent. One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with ventral, probably eversible, buccal organ (Kristensen & Niilonen 1982; Purschke & Tzetlin 1996). Gular membrane absent; gut a straight tube. Protonephridia present; gonoducts unknown (Westheide 1990); distribution of segmental organs unknown. Circulatory system and heart body absent. Chaetae absent.

We interpret the 'toes' of the diurodrilids as a pair of pygidial cirri (cf. Kristensen & Niilonen 1982, fig. 17).

DORVILLEIDAE Chamberlin, 1919

Main references: Ehlers 1868*a*; Jumars 1974; Eibye-Jacobsen & Kristensen 1994.

Evidence for monophyly: Highly sclerotinized ventrolateral jaws divided into series of jaw pieces on each side in a muscularized ventral eversible pharynx.

The two invalid generic names *Staurocephalus* and *Stauronereis* were applied to various relatively large-bodied dorvilleids through the 19th century until Chamberlin (1919) demonstrated the validity of the name *Dorvillea* and consequently the family based on that generic name; however, the dorvilleids were recognized as early as 1850 as a distinct group of taxa related to the eunicids. Recent benthic investigations have found many small species (Jumars 1974; Hillbig and Blake 1991). Eibye-Jacobsen & Kristensen (1994) demonstrated that taxa previously included in Dinophilidae and Iphitimidae formed a single clade with the dorvilleids; in their cladogram, *Dorvillea* and related genera are plesiomorphic. Where characters are variable within the family, the characterization here is based on the plesiomorphic states in the publication cited; other states are suggested where appropriate.

Prostomium truncate, often quadrangular. Peristomium usually two, rarely one ring. One pair of lateral and a median antennae present. Palps dorsolateral, often articulated. Antennae and palps may be small, often wholly missing in small-bodied taxa. Paired nuchal pits present dorsolaterally at boundary between pro- and peristomium. Longitudinal muscles in bundles (Clark 1962, fig. 26). First segment similar to other segments with parapodia similar to those in other segments. Parapodia biramous with notopodia smaller than neuropodia. Dorsal and ventral cirri present. Gills associated with notopodia in some taxa. Epidermal papillae absent. One pair of pygidial cirri present. Lateral organs not observed; dorsal cirrus organs present. Stomodaeum with muscularized ventral eversible pharynx. Heavily sclerotinized ctenognath maxillae and mandibles present in most plesiomorphic dorvilleids (Eibye-Jacobsen & Kristensen 1994, fig. 9). Jaws completely absent in several taxa. Gular membrane absent; gut a straight tube. Metanephridia present in larger-bodied taxa; protonephridia reported from small-bodied taxa (Westheide & Riser 1983); relation between nephridia and coelomoducts poorly known. Segmental organs probably present in most segments. Circulatory system assumed closed in larger taxa but reduced or absent in smaller taxa (Smith & Ruppert 1988); heart body absent. Aciculae present. Compound chaetae present; joints with double ligaments and dentate appendages; variously ornamented capillaries also present. Some taxa with furcate heavy chaetae. Some taxa without chaetae.

Eibye-Jacobsen (1994) demonstrated that the dorvilleid peristomium was structurally similar to the one in the eunicids. A pair of lateral antennae and a median antenna is the plesiomorphic condition according to Kristensen & Eibye-Jacobsen (1995), but either antennae or palps may be small or missing in smaller taxa. Within the family, the notopodia become increasingly reduced and may be represented only by a dorsal cirrus. Gills are present in some taxa, but the plesiomorphic condition is considered to be gills absent. The strongly muscularized ventral eversible pharynx have jaws arranged in two distinct groups, one pair is ventral, called mandibles; the maxillae are situated on lateral muscularized ridges running along the eversible structures (Fauchald 1970). The most pleisomorphic dorvilleids (Eibye-Jacobsen & Kristensen 1994, fig. 9) have ctenognath maxillae with maxillary carriers; other dorvilleids show increasing fusion of jaw pieces and fusion to the carriers, as well as a general reduction in the size of the maxillae. The separate maxillary pieces are often differentiated along an anterio-posterior axis (Fauchald 1970, pl. 26). The mandibles in the more plesiomorphic genera consist of paired basal pieces and several detached denticles; the mandibles are reduced in size and complexity in more apomorphic taxa (*sensu* Eibye-Jacobsen & Kristensen 1994).

EULEPETHIDAE Chamberlin, 1919

Main references: Pettibone 1969*b*, Pettibone 1986.

Evidence for monophyly: Neuropodia wide, distally truncate with distal edges supported by narrow sclerotinized ridges (aciculae terminate in the middle of the neuropodia and are usually called hammer-shaped).

The eulepethids are a morphologically uniform group of scale-worms. As for all other scale-worms, they have periodically been considered members of Aphroditidae. They resemble the polynoids, acoetids and aphroditids in lacking all compound chaetae. All species are solid-bodied and nearly quadrangular in cross-section.

Prostomium frontally truncate. Peristomium limited to lips. Paired lateral antennae and median antenna present. Ventral, tapering palps present; fused basally to ventral, medial side of first parapodia. Nuchal organs present. Organization of longitudinal muscles unknown; segmentation present. First segment curved around prostomium with parapodial bases of first segment fused to prostomium; two pairs of tentacular cirri present. All notopodia shorter than neuropodia; neuropodia truncate. Dorsal cirri only on segments 3 and 6; replaced by marginally lobate elytrae;. Elytrae on alternating segments in first half of the body; posterior half carries pseudoelytrae or lack both elytrae and dorsal cirri; ventral cirri present. Gills absent (see below). One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum an eversible, muscular axial pharynx with two pairs of dorsoventrally arranged jaws; terminal papillae present. Gular membrane absent; gut presumably with diverticula in each segment (based on Darboux 1899). Nephridia presumably metanephridia; relation to coelomoducts unknown. Distribution of segmental organs unknown. Structure of circulatory system and presence of heart body not observed. Aciculae present. Chaetae variously ornamented capillaries and spines.

The structure of the 'gills' reported present in the eulepethids is unknown; they alternate with elytrae in the anterior end and may thus be assumed to be homologues of the dorsal cirri; however, Pettibone (1969b) reported that they corresponded to the dorsal tubercles on non-elytrigerous segments. Documentation of internal structures is largely missing, but is presumably similar to structures reported for other scale-worm families.

EUNICIDAE Berthold, 1827

Main references: Ehlers 1864; Hartman 1944; Fauchald 1992*a*; Orrhage 1995.

Evidence for monophyly: None known.

Fauchald (1992a) reviewed the taxonomic history of the family. The first known species were described in *Nereis*; *Eunice* was named early in the 19th century, and the family is one of the first to be removed from the catch-all *Nereis* commonly used about long-slender polychaetes during the first quarter of the 19th century. The family is usually compared to other taxa with ventrally hypertrophied eversible pharynges with complex jaw structures.

Prostomium anteroventrally continued in paired large upper lips (Orrhage 1995). Peristomium two rings. One pair of lateral and a median antennae present. Slender dorsolateral palps located anterolateral to lateral antennae. Palps or lateral antennae or both absent in some taxa. Nuchal organs under peristomial fold dorsolaterally. Longitudinal muscles grouped in four bundles (Clark 1962, figs 22–23); segmentation present. First segment similar to next following segments; with small parapodia resembling those in other segments. Notopodia dorsal cirri with internal aciculae; neuropodia longer than notopodia. Ventral cirri present. Gills attached to dorsal cirri (i.e. notopodial) when present. Epidermal papillae absent. One pair of long pygidial cirri present; in addition, a pair of very short, peg-like structures present on ventral side of pygidium. Lateral organs not observed. Dorsal cirrus organs present. Stomodaeum with a thickened muscular eversible ventral structure supporting paired mandibles and three or four pairs of maxillae, plus unpaired Mx III. Maxillary apparatus labidognath in construction; Mx III present only on left-hand side; calcification aragonitic. Gular membrane absent; gut a straight tube. Segmental organs mixonephridia present in most segments (Goodrich 1945; Fage 1906). Circulatory system closed; heart body absent. Aciculae present. Appendages of compound chaetae attached by paired ligaments, dentate and protected by paired guards. Capillaries present in all taxa; pectinate chaetae and thick subacicular spines present in most taxa.

Juvenile eunicids have approximately ctenognath maxillae but lack the anterior–posterior differentiation of elements present in ctenognath maxillae of many dorvilleids. The compound falcigers with double ligaments and paired guards are present throughout body. Onuphids and lumbrinerids, the two most similar taxa, have compound (or pseudocompound) chaetae limited to the anterior end. In onuphids, they are pseudocompound or compound protected by paired guards; in the lumbrinerids, these chaetae are compound, but with complete hoods.

EUPHROSINIDAE Williams, 1851

Main references: Gustafson 1930; Kudenov 1987.

Evidence of monophyly: Furcate (ringent) chaetae of characteristic construction present (Gustafson 1930).

Despite the early naming of a separate family for the euphrosinids, they were very nearly always included within the amphinomids until Gustafson's (1930) study of the anatomy and morphology of both groups. Kudenov (1991) described a new genus, *Archinome*, which combines features of both euphrosinids and amphinomids, and named a new family for this genus. A new family is clearly not justified (Kudenov 1994), and the structures of *Archinome* may make it impossible to find apomorphies for the amphinomids. The euphrosinids are morphologically uniform and make up a distinct group; nevertheless, recognition of a separate family may make it difficult to diagnose the amphinomids.

Prostomium a nearly vertically oriented narrow ridge. Peristomium limited to lips. Small paired frontal antennae present; median unpaired antenna located more posteriorly on prostomium. Palps missing externally, but palpal nerves present. Nuchal organ (caruncle) three-lobed with longitudinal ciliated ridges; attached frontally, projecting as free lobes posteriorly. Longitudinal muscles in bundles; segmentation distinct. First segment curved dorso-laterally around prostomium; first parapodia projecting frontally on either side of prostomium. Notopodia transverse ridges nearly meeting medially; neuropodia projecting laterally, tapering to blunt tips. Dorsal and ventral cirri present. Gills divided into small branching bundles behind notopodia. Epidermal papillae absent. One pair of inflated pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum ventrally modified with thick eversible ventral muscle mass covered with thickened cuticle. Gular membrane absent; gut a straight tube. Segmental organs mixonephridia present in most segments. Circulatory system closed; heart body absent. Chaetae calcified. Aciculae present. All chaetae furcate, some slender and capillary; most spine-like with characteristic ornamentation.

The palps are missing externally, but palpal nerves run to ventrolateral lips according to Gustafson (1930); the position of these nerves correspond to the palpal nerves in the amphinomids.

FAUVELIOPSIDAE Hartman, 1971

Main references: Hartman 1971; Riser 1987.

Evidence for monophyly: None known.

The genus *Fauveliopsis* was erected by McIntosh (1922) for what he considered an aberrant flabelligerid. Additional species of *Fauveliopsis* and another genus, *Flabelligella*, were added by Hartman (1965, 1967), who recognized a separate family for the group in 1971 based on a combination of features, including chaetal structures and the interramal papilla. The family is here restricted to the genus *Fauveliopsis* as suggested by Orensanz (1974) and Fauchald (1977).

Prostomium a small square lobe, usually retracted. Peristomium limited to lips. Antennae absent. Paired palps present at corner of mouth. Nuchal organs ciliated grooves. Organization of longitudinal muscles not known; segmentation distinct. First segment similar to other segments with fully developed parapodia. Notopodia and neuropodia short, slightly elevated truncate structures carrying chaetae; interramal papillae present. Interramal papillae closely resembling flabelligerid papillae in structure (Fauchald 1972, pl. 45, fig. c; Riser 1987: 213). Gills absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with eversible ventral buccal organ. Gular membrane present in front of first segment (called a septum by Riser 1987); structure of gut unknown. Structure of segmental organs unknown. Circulatory system present (Riser 1987: 213); probably closed. Presence of heart body not known. Aciculae absent. Chaetae all modified capillaries.

Riser (1987, fig. 8) suggested that a ventral buccal organ is present (see also Purschke & Tzetlin 1996). Riser also mentioned that the oesophagus is looped when the head is retracted; otherwise the structure of the gut is unknown. The larger chaetae might be called spines, but do not differ structurally from the slender capillaries present, and chaetae transitional in size are present.

FLABELLIGERIDAE Saint-Joseph, 1894

Main references: Schlieper 1927; Spies 1973, 1975.

Evidence for monophyly: Gills on expanded peristomial membrane.

After being listed among the terebellids (e.g. Audouin & Milne Edwards 1834), the flabelligerids were recognized as a distinct family by Quatrefages (1849), under the name Chloraemidae. Most flabelligerids are densely covered with papillae of characteristic construction similar to the interramal papillae present in the fauveliopsids. Many are heavily invested with sediment-granules (e.g. *Ilyphagus*, see Hartman 1969: 293) or covered with a mucus-sheath (*Flabelligera*). Recognition of the pelagic, achaetous Poeobiidae may make Flabelligeridae paraphyletic; many features known from the poeobiids match features present in flabelligerids (Heath 1930; Robbins 1965).

Prostomium a narrow ridge. Peristomium limited to lips. Antennae absent. Peristomial paired grooved palps located at corners of mouth. Nuchal organs paired ciliated ridges lateral to prostomium. Longitudinal muscles arranged in bundles. First segment similar to next ones; with biramous parapodia. All notopodia and neuropodia short; distally truncate or tapering. Dorsal and ventral cirri absent. Dorsal segmental gills present (see below). Lateral organs and dorsal cirrus organs not observed. Papillae of characteristic structure present; often especially dense and long around chaetae (Mesnil 1899; Schlieper 1927: 333, 341–342, fig. 13). Stomodaeum with eversible ventral buccal organ. Gular membrane present; gut looped. Segmental organs mixonephridia; anteriormost pair excretory, more posterior ones gonoducts. Circulatory system closed; heart body present. Aciculae absent. Chaetae compound falcigers and variously ornamented capillaries.

Hinge of compound chaetae fold in outer cover of chaetae; appendages distally falcate.

The prostomium was called the prostomial lobe by Spies (1975: 188). None of the epidermal papillae is consistently in position to be either a dorsal or a ventral cirrus. Gills are located on a gill membrane, which appears to be peristomial in position. Spies (1975, pl. 7, fig. 11) demonstrated that blood vessels associated with the gills emerge from the heart posterior to the emergence of the vessel covering the brain, suggesting a morphologically more posterior position. In addition, these vessels emerge in a double row. We conclude that morphologically dorsal segmental gills are present. The relatively thick, distally blunt chaetae in many flabelligerids have been called spines; however, they have exactly the same segmented structure as the capillaries so they are considered here modified capillaries.

GLYCERIDAE Grube, 1850

Main references: Ehlers 1868*a*; Arwidsson 1899.

Evidence for monophyly: Four pharyngeal jaws each with an aileron, arranged in a cross.

The first glycerids were described as nereidids; the genus *Glycera* was recognized by Savigny (in Lamarck 1818). Glycerids and goniadids are similar in that both have tapering ringed prostomia and greatly elongated eversible pharynges tipped with jaws. Each family has well-supported autapomorphies in the structure of the jaws. Potentially, recognition of Goniadidae may make (Glyceridae-Goniadidae) paraphyletic; the best way to test for this, would be to do a study including genera of both families as ingroup taxa.

Prostomium conical, tapering and externally ringed. Peristomium limited to lips. One pair of antennae present. Palps ventral, short and tapering (Hanström 1928). Nuchal organs not observed. Longitudinal muscles in bundles; segmentation present. First segment similar to next segments with similar parapodia. Parapodia biramous with neuropodia slightly longer than notopodia in most taxa (all parapodia uniramous in *Hemipodus*). Pre- and postchaetal lobes and lappets often highly differentiated. Dorsal and ventral cirri present. Gills absent (see below). Epidermal papillae absent. One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum a very large, muscular eversible pharynx tipped with four jaws. Each jaw with an aileron (a support structure). Pharyngeal papillae, scattered more or less evenly, of one or two kinds in any species. Terminal papillae absent. Gular membrane absent; gut a straight tube. Segmental organs protonephromixia present in many segments; ciliophagocytic organs present. Circulatory system and heart body absent. Aciculae present. Compound spinigers with single ligaments joining shaft to appendage; appendages tapering to slender tips. Variously ornamented capillaries also present.

The second, ventral pair of frontal appendages are usually referred to as ventral antennae (Fauvel 1923), but have been shown to be short, tapering ventral palps (Hanström 1928). The structures referred to as gills in the descriptive literature (Fauvel 1923) contain loops of the coelom, since a circulatory system is missing, and are thus not considered gills in this context.

GONIADIDAE Kinberg, 1866

Main references: Fauvel 1923; Hartman 1950.

Evidence for monophyly: Jaws consist of one pair of macrognaths and two arcs of micrognaths in circlet around the mouth.

The study of the goniadids parallel that of the glycerids closely; while the family was first named in 1866, it was not until Støp-Bowitz (1948) and Hartman (1950) explored the differences between the two families that the goniadids became accepted as a distinct family. Generally, goniadids have relatively larger parapodia, and the pharyngeal papillae are much larger than in the glycerids.

Prostomium tapering to blunt, often truncate tips; externally ringed. Peristomium limited to lips. One pair of antennae present. Palps ventral, short and unarticulated. Nuchal organs not observed. Longitudinal muscles in bundles; segmentation distinct. First segment similar to next following ones in size and parapodial development. In first several segments, neuropodia well-developed and notopodia dorsal cirri only; posteriorly notopodia nearly as large as neuropodia. Dorsal and ventral cirri present. Gills absent. Epidermal papillae absent. One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum a very long muscular, eversible pharynx tipped by circlet of jaws consisting of paired lateral macrognaths and several micrognaths forming dorsal and ventral arcs. Pharyngeal papillae relatively large and always present; either differentiated into several different kinds with characteristic distribution along and across pharynx, or only one or two kinds present. Terminal papillae present (Hartman 1950, fig. 1). Gular membrane and structure of gut undocumented. Segmental organs protonephromixia present in most segments; anterior ones presumably excretory function; posterior ones gonoducts (Goodrich 1945). Ciliophagocytic organs absent. Circulatory system and heart body absent. Aciculae present. Chaetae compound spinigers and more rarely falcigers and variously ornamented capillaries. Spine or hook-like, and hooded chaetae present in some taxa. Appendages of compound chaetae joined to shaft by single filaments; tapering to slender tips.

HARTMANIELLIDAE Imajima, 1977

Main reference: Imajima 1977.

Evidence for monophyly: Maxillary carriers paddle-shaped with limited attachment to MxI.

The hartmaniellids are known from a few specimens taken in shelf-depths off Japan and China; they have also been reported from Madagascar (*Pseudoninoe tulearensis* Amoureux 1977) and from the Gulf of Mexico (Gathof 1984), and most recently, they were reported from Triassic fossils (Szaniawski & Imajima 1996). They superficially resemble orbiniids in that both parapodial rami are shifted dorsally in the posterior end of the body; however, the structure of these parapodia closely resembles those present in the euniceans, and the jaw apparatus is characteristically eunicean with a pair of mandibles and several pairs of maxillae. In Orensanz's (1990) study, the hartmaniellids were placed in a separate superfamily, isolated from the ctenognath (i.e. the dorvilleids), the prionognaths (i.e. the oenonids) and the labidognath families (e.g. the eunicids).

Prostomium frontally broadly rounded. Peristomium two rings. Antennae and palps absent. Nuchal organs present. Arrangement of longitudinal muscles undocumented; segmentation distinct. First segment similar in size to next following one; with small parapodia. All notopodia dorsal cirri with internal aciculae; neuropodia well-developed; distally truncate. Dorsal and ventral cirri present. Ventral cirri especially distinct in anterior chaetigers. Gills parapodial. Epidermal papillae absent. Paired pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum a thickened eversible ventral structure supporting heavily sclerotinized jaws. A pair of mandibles and several pairs of maxillae present; poorly sclerotinized, paddle-shaped maxillary carriers (Imajima 1977, plate 1, fig. d) loosely attached to posterior end of Mx I in a prionognath arrangement. Gular membrane not observed; gut a straight tube (pers. obs.). Excretory, reproductive and circulatory systems unstudied. Aciculae present. Compound spinigers and capillaries present. Joints of compound chaetae with double ligaments; appendages with slender tips.

Imajima (1977) reported nuchal organs absent; however, such organs are present as small ciliated pads under a shallow peristomial fold (pers. obs.). Imajima (1977) illustrated the second ring as having surface rugosity similar to that of the body segments, rather than resembling the first ring; thus, it is possible that there is only one peristomial ring and that the second ring represents an achaetous and apodous segment. The differences in surface rugosity is not visible on the specimens at the present time. Imajima (1977) illustrated median notopodia as slightly bifurcated; the lower part of this structure is a gill; they resemble the gills of orbiniids; in the same region, a superior lobe of the neuropodia is also gill-like in structure. The maxillae were characterized as labidognath by Orensanz (1990); however, the maxillae lack the close link to the carriers characteristic of recent labidognaths and resemble reduced prionognath sets such as those present in *Drilonereis* (pers. obs.). Furthermore, the mandibles (Gathof 1984, fig. 57-2j) resemble those present in the oenonids, rather than mandibles present in labidognath taxa (Orensanz 1990, fig. 2).

HESIONIDAE Grube, 1850

Main references: Westheide 1967; Glasby 1993; Pleijel 1993.

Evidence for monophyly: None known.

The first hesionids were described in the genus *Nereis* by Fabricius (1780); the genus *Hesione* was described by Savigny; the family was first recognized as a distinct entity by Grube (1850). Because of the extreme fragility of many species, descriptions of hesionids have been rather inadequate, and the family has remained poorly understood despite Westheide's detailed studies of the subfamily Microphthalminae. Hesionids most closely resemble syllids, pilargids and nereidids. A characteristic feature is the increasing number of cephalized segments in which the dorsal and ventral cirri become elongated and qualify as tentacular cirri, whereas the parapodia proper often retain chaetae or acicula. Glasby (1993) discussed the possible relations between the hesionid pharynx and the pharynges of related taxa. The characterization here is focused on members of the subfamily Hesioninae; members of the subfamily Microphthalminae are often small with reduced anterior appendages in addition to specializations such as copulatory structures (Westheide 1978). According to Glasby (1993: 1556), four to eight pairs of tentacular cirri carried on cephalized segments 2–4 is an autapomorphy of the family; however, the nereidids have three or four pairs of such cirri, and the relationship of these to possible segments in the nereidids is unclear, so this apomorphy appears in need of further documentation.

Prostomium distinct, quadrangular or diamond-shaped. Peristomium limited to lips. One pair of frontal antennae always present; median antenna present in many taxa. Palps ventrally located, slender and usually articulated, rarely absent. Nuchal organs ciliated patches located dorsolaterally behind prostomium. Longitudinal muscles in distinct bundles; segmentation distinct. First segment incomplete dorsally with two pairs of tentacular cirri; up to eight pairs of tentacular cirri present on cephalized segments. Parapodia biramous with well-developed neuropodia and variably, often poorly developed notopodia; notopodia represented by dorsal cirri only in some taxa. Dorsal and ventral cirri present. Gills absent. Epidermal papillae absent. One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum an axial muscular pharynx, jaws missing in most taxa; a pair of lateral jaws when present; terminal papillae often present. Gular membrane absent; gut a straight tube. Segmental organs metanephromixia present in most segments; ciliophagocytic organs present (see below). Circulatory system apparently present in large-bodied taxa, but absent in small-bodied taxa (Smith & Ruppert 1988, table 14); heart body not observed. Aciculae present. Compound chaetae with single ligaments joining shafts and appendages. Appendages tapering to slender tips; bifid or falcate appendages are known in some taxa. Capillaries present.

Terminal papillae surrounding the mouth are absent in several taxa, but their presence can be considered plesiomorphic based on ontogenetic evidence (Fredrik Pleijel, pers. commun.). Protonephridia are present in some taxa (Fage 1906; Westheide 1986). Ciliophagocytic organs, usually considered present in the family, are large structures in *Hesione*, but are very much smaller and may be absent in *Ophiodromus* (Goodrich 1945; the genus *Irma* mentioned by Goodrich is a synonym of *Ophiodromus*).

HISTRIOBDELLIDAE Vaillant, 1890

Main references: Haswell 1900, 1914; Shearer 1910; Mesnil & Caullery 1922; Jamieson *et al.* 1985.

Evidence for monophyly: Posterior end deeply cleft, forming two large 'feet'.

The family consists of two genera, *Histriobdella* and *Stratiodrilus*; both are commensals on crustacean gills, the former on lobsters of the genus *Homarus*, the latter on freshwater crayfish, especially well described from Australia. Histriobdellids are very small-bodied, and the lack of true parapodia and chaetae limits the possibilities for clarifying the relationships between the histriobdellids and other polychaetes; however, the jaw apparatus ties them to the euniceans.

Prostomium frontally rounded. Peristomium a ring; peristomial cirri present (see below). One pair of lateral and a median antenna present. Palps dorsolateral (Shearer 1910, pl. 19, fig. 30; Haswell 1914, pl. 11, figs 1–5). Nuchal organs ciliated pits; present in *Histriobdella*; absent in *Stratiodrilus* (Haswell 1914). Longitudinal muscles in bundles; segmentation distinct. Both genera with five similarly-sized body segments (Shearer 1910, pl. 17, figs 1, 7; Haswell 1914: 199). Parapodia absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with a muscular thickened ventral lining with jaws. Single median anteriorly furcate carrier and three or four pairs of maxillae present; additional sclerotinized plates present (Haswell 1914, pl. 14, fig. 26; Mesnil & Caullery 1922, figs 2–3). Mx 1 loosely articulated against carrier with a few teeth; two outer dentate plates with many slender teeth. Mandibles unusually large, underlying whole maxillary apparatus and linked laterally to maxillae (Mesnil & Caullery 1922) with distinct frontal cutting edges. Gular membrane absent; gut a straight tube. Protonephridia present; coelomoducts and nephridial ducts separated (Goodrich 1945: 214). Segmental organs present in four body segments. Circulatory system absent. All chaetae including aciculae absent.

The suggested evidence for monophyly assumes that the 'feet' of the histriobdellids are structurally different from the 'toes' present in protodrilids and protodrilioids (see below). Positionally, the mouth is located as in euniceans; for that reason, the peristomium must have a ring. The claspers appear to be located on the peristomium and may thus be a pair of peristomial cirri (Shearer 1910). Haswell (1914) called the posterior body-projections 'legs', but structurally, they do not resemble parapodia. Mesnil & Caullery (1922) compared the jaws to the prionognath jaws of the oenonids, and this appears appropriate; Orensanz (1990) did not treat the histrobdellids in his review of the eunicean families.

ICHTHYOTOMIDAE Eisig, 1906

Main references: Eisig 1906.

Evidence for monophyly: Jaws crossed as in a pair of scissors.

The family is known only for a single species parasitic on eels in the Mediterranean Sea, described in great detail by Eisig (1906). The family has usually been considered related to the euniceans (Fauvel 1923). George in George & Hartmann-Schröder (1985) included it in his Nereidoidea. Glasby (1993) in his review of this superfamily excluded the ichthyotomids by referring them to the euniceans. However, the pharyngeal structure is axial rather than ventral, and the chaetal structures resemble those among the nereididoids rather than those present among the euniceans.

Prostomium and peristomium fused, forming a single frontally rounded structure. Paired frontal antennae and a median antenna present. Rudimentary palps present (Eisig 1906, figs 4, 5). Nuchal organs paired ciliated patches. Longitudinal muscles in bundles; segmentation distinct. First segment similar to next following segments with biramous parapodia. Both rami well-developed; neuropodia slightly longer than notopodia. Dorsal and ventral cirri present. Gills not observed. A single pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum a muscular, axial pharynx with paired lateral jaws crossing in a scissor-like arrangement. Terminal papillae absent. Gular membrane absent; gut a straight tube. Segmental organs metanephromixia distributed throughout the body; ciliophagocytic organ not described. Circulatory system and heart body absent (Eisig 1906: 139). Aciculae present. All chaetae neuropodal compound falcigers with single ligaments joining shafts and appendages; appendages either short and distally dentate or tapering.

Eisig's (1906) 'Mundkegel' is the peristomial portion of the fused pro- and peristomium. What Eisig (1906, fig. 8) called a dorsal cirrus is the notopodium; however, his 'stylode' is the dorsal cirrus. Each parapodium has a well-developed lobe ventral to the neuropodium proper. This lobe contains a spinning gland; it may be a homolog of the ventral cirri of other polychaetes or constitute a unique feature. There is, in addition, a 'stylode' near the tip of the neuropodium on the ventral side, which also might qualify as a ventral cirrus (Eisig 1906, fig. 8).

IOSPILIDAE Bergström, 1914

Main references: Bergström 1914; Fauvel 1923; Uschakov 1972.

Evidence for monophyly: Median parapodia abruptly much longer than in first few segments (Fauvel 1923: 194–195; Day 1967: 168, fig. 6.1.f).

The iospilids are small, pelagic worms. They were initially described as phyllodocids, and the family is still often considered a subfamily of the Phyllodocidae (Uschakov 1972: 193). The internal structures are very poorly known.

Prostomium distinct and frontally rounded. Peristomium limited to lips. Antennae absent. Tapering ventral palps present. Nuchal organs present. Arrangement of the longitudinal muscles undocumented; segmentation present. First segment indistinct with two pairs of tentacular cirri. At least first four chaetigers with neuropodia only. In median segments, both rami prominent, but neuropodia longer than notopodia. Dorsal and ventral cirri present. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum in all taxa a muscular eversible axial pharynx; terminal papillae present. In four species, paired bilateral, curved jaws present; other four species without jaws. Gular membrane and structure of digestive tract not observed. Nephridial, reproductive and circulatory systems not studied. Aciculae present. All chaetae compound spinigers with single ligaments joining shafts and appendages.

LACYDONIIDAE Bergström, 1914

Main references: Marion & Bobretzky 1875; Pleijel & Fauchald 1993.

Evidence for monophyly: None known.

The lacydoniids were first described as phyllodocids but were removed from that family by Bergström (1914). Fauvel (1923: 197) treated them as a subfamily of the phyllodocids; Fauchald (1977) suggested that they might be more closely related to the glycerids and goniadids. The lacydoniids are small, benthic worms with biramous parapodia. Internal structures are poorly known. *Paralacydonia* Fauvel (1914) was listed as a lacydoniid by Fauchald (1977); it is treated here as a member of its own family, Paralacydoniidae, as originally recognized by Pettibone (1963).

Prostomium frontally rounded. Peristomium limited to lips. Pair of lateral antennae and a median antenna present. Palps paired, ventral, short, tapering without articulations. Nuchal organs ciliated pits. Arrangement of longitudinal muscles undocumented; segmentation present. First segment narrower than next following segment with two pairs of tentacular cirri (Marion & Bobretzky 1875: 57, pl. 8, fig. 17). Notopodia, while well-developed, consistently shorter than neuropodia. Dorsal and ventral cirri present. Gills absent. Epidermal papillae absent. Two pairs of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with eversible, axial, muscular pharynx; terminal papillae present; jaws absent. Gular membrane absent; gut straight. Nephridial, reproductive and circulatory systems not studied. Aciculae present. Neuropodial chaetae compound spinigers with single ligaments joining shafts and appendages; appendages tapering to fine tips. Notopodial chaetae capillaries.

The median antenna was reported to be present by Pleijel & Fauchald (1993); it may not be present in all species. Marion & Bobretzky (1875) called the muscular part of the pharynx a 'proventricle'; however, the eversible pharynx resembles the one present in the hesionids, rather than in the syllids. A pair of very large glands are attached to the anterior end of the gut (Marion & Bobretzky 1875: 59–60).

LONGOSOMATIDAE Hartman, 1944.

Main references: Ehlers 1875; Hartman 1944, 1957, 1963, 1965; Uebelacker 1984; Borowski 1995.

Evidence for monophyly: Strongly elongated median chaetigers with nearly complete circlets of simple chaetae.

The first longosomatid was described from the north Atlantic by Ehlers (1875) as *Heterospio longissima*; this species was redescribed by Hartman (1965: 163). Hartman (1944) described a genus *Longosoma* from California and placed it in its own family, spelled Longosomidae by Hartman. Hartman (1965) synonymized the two genera and used the family name Heterospionidae as did Fauchald (1977). Borowski (1995) corrected the spelling of the family name to Longosomatidae. Longosomatids are poorly known, since the specimens fragment very readily. Most specimens in collections consist of only the anterior end and the first few median segments, and some records are based on median segments only. The internal structures are unknown.

Prostomium narrowly triangular, widest anteriorly. Peristomium limited to lips. Paired grooved palps present. Nuchal organs narrow grooves along posterior edges of prostomium. Arrangement of longitudinal muscles undocumented; segmentation distinct. First segment similar in length to next ones but without parapodia. All parapodial rami low ridges with weakly-developed postchaetal lobes. Dorsal and ventral cirri absent. Gills slender, cylindrical dorsal filaments present on anterior part of body. Epidermal papillae absent. Pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an eversible ventral buccal organ (?). Gular membrane, digestive tract, nephridia, reproductive and circulatory systems not studied. Aciculae absent. Chaetae capillaries and spines.

LOPADORHYNCHIDAE Claparède, 1868

Main reference: Uschakov 1972.

Evidence for monophyly: None known.

The lopadorhynchids were first described as pelagic phyllodocids and have remained included as a distinct subgroup of the Phyllodocidae in many publications (Fauvel 1923; Uschakov 1972). Uschakov (1972: 113–116, in key) characterized the lopadorhynchids (as a subfamily) as being pelagic, with well-developed, but short parapodia on all segments.

The family consists of two groups of genera. In the first group, which includes *Lopadorhynchus*, the prostomium is a wide, short separate structure with antennae and palps, the first few parapodia are not unusually muscularized and the segments with tentacular cirri have chaetae. The characterization below is based primarily on the type genus. In the other group of genera, the prostomium and peristomium are fused to each other; the anterior parapodia are strongly muscularized, and the segments with tentacular cirri lack chaetae.

Prostomium frontally truncate. Peristomium limited to lips. A pair of lateral antennae present. Palps ventral, tapering without articulations. Nuchal organs ciliated pits. Arrangement of longitudinal muscles not studied; segmentation present. First segment smaller than next following ones with a pair of tentacular cirri. A total of two or three pairs of tentacular cirri present. Notopodia shorter than neuropodia. Dorsal cirri foliose; ventral cirri present. Gills absent. Epidermal papillae absent. One pair of pygidial cirri present, at least in some taxa. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial eversible muscular pharynx; terminal papillae present; jaws absent. Gular membrane undocumented; gut a straight tube. Nephridial, reproductive and circulatory systems not studied. Aciculae present. All chaetae compound with single filaments linking shafts and appendages; appendages oar-shaped and tapering to blunt tips or slender and tapering to fine tips.

LUMBRINERIDAE Schmarda, 1861

Main references: Ehlers 1868a; Hartman 1944.

Suggested apomorphies: Labidognath maxillary apparatus symmetrical with four pairs of maxillae.

The first lumbrinerid was described as *Lumbricus* by O.F. Müller (1776); however, they soon became associated with the eunicids and onuphids because of the similarities of the structure of the jaws (Audouin & Milne Edwards 1834). Members of the Oenonidae were traditionally considered lumbrinerids; the differences between the Lumbrineridae and Oenonidae (as Arabellidae) were clarified by Hartman (1944).

Prostomium frontally rounded, bluntly conical or sharply pointed. Peristomium two rings. Antennae absent in most taxa; a pair of lateral and a median antenna present in some taxa (Day 1967; Fauchald 1970, as nuchal papillae). Palps absent. Nuchal organs paired dorsolateral pits. Longitudinal muscles in bundles; segmentation distinct. First segment including parapodia similar to next following ones. Parapodia biramous; neuropodia well-developed in all taxa; notopodia low, conical knobs with aciculae in most taxa; with large, flattened dorsal cirri in some taxa. Ventral cirri absent; cushion-shaped ventral (glandular?) pads present. Gills, when present, emerging from neuropodial postchaetal lobes. Epidermal papillae absent. Two long and two short pygidial cirri present in many taxa, others with two pairs of similar pygidial cirri. Lateral organs not observed; dorsal cirrus organs present. Stomodaeum with a ventrally muscularized and eversible pharynx; jaws a pair of mandibles and four pairs of maxillae in labidognath arrangement. Calcification of jaws with calcite (Colbath 1987). Gular membrane absent; gut a straight tube. Segmental organs mixonephridia present in most segments. Circulatory system closed; heart body absent. Compound chaetae with double ligaments linking shafts and appendages present in some taxa. Appendages distally dentate and covered with complete hoods. Compound chaetae when present, only in anterior chaetigers; in posterior, chaetae simple and hooded closely resembling compound chaetae. In taxa without compound hooded chaetae, simple hooded chaetae present throughout. Modified capillary (limbate) chaetae present in all taxa.

MAGELONIDAE Cunningham and Ramage, 1888

Main references: Jones 1968, 1977; Orrhage 1966; Wilson 1982.

Evidence for monophyly: Palps with rounded cross-section and a subdistal expanded area covered with papillae. Prostomium shovel-shaped. Chaetiger 9 often modified with unusual postchaetal lobes or different chaetae from those segments in front or behind it or both.

The first description of a magelonid (Müller in Grube 1858) was very brief, and the species, *Magelona papillicornis* became commonly reported in faunistic studies from all over the world. Jones (1977) redescribed the species from the type-locality and limited the concept of the species. The magelonids resemble the spioniform families in parapodial and chaetal structures and have usually been considered related to these families (e.g. Fauvel 1927).

Prostomium flattened and shovel-shaped. Peristomium limited to lips. Palps attached ventrolaterally; round in cross-section with a slightly expanded papillated subdistal region. Nuchal organs absent. Longitudinal muscles grouped in bundles; segmentation present. First segment without parapodia and chaetae in adults (see below). Parapodia biramous; rami low chaetal ridges backed by postchaetal lobes often broken up into several separate lobes. Dorsal and ventral cirri absent. Gills absent. Epidermal papillae absent. One pair of pygidial cirri present (McIntosh 1915: 218). Lateral organs present; dorsal cirrus organs not observed. Stomodaeum a ventral eversible buccal organ. Gular membrane absent; gut a straight tube. Structure and distribution of segmental organs not documented. Circulatory system closed; heart body absent. Aciculae absent. Chaetae capillaries and dentate hooded hooks. Unusual chaetae of chaetiger 9 modified capillaries.

Jones (1968: 273) referred to the whole region between the prostomium and the first adult chaetiger as the peristomium; however, this structure has provisional chaetae in the larvae (Claparède 1864) and must be considered the first segment. Wilson (1982: 395–400, figs 4, 5, table 12) followed the metamorphosis and demonstrated that the adult palps develop directly from the larval tentacles, which in turn are extensions of the prototroch. The dorsal- and ventral-most lobes are here considered part of the postchaetal lobes and not homologous with dorsal and ventral cirri in other polychaetes; thus, dorsal and ventral cirri are absent. Goodrich (1945) suggested similarities between the segmental organs in magelonids and those of the spionids and allies, but did not provide any evidence. A heart body was reported to be present in the larvae (Picton 1899).

MALDANIDAE Malmgren, 1867

Main references: Arwidsson 1906; Pilgrim 1966*a*,*b*, 1977; Rouse 1990.

Evidence for monophyly: Elongated median chaetigers with prominent tori near one end of each chaetiger (bamboo-shaped).

Maldanids were first described as a part of Annelida Serpulea (Savigny 1822); later as part of Limivora (Grube 1850). The family name was put into a nomenclatorally acceptable form by Malmgren (1867), even if the concept of the family was recognized as early as in Savigny's days. Maldanids tend to fragment very readily and as a consequence, many even recent descriptions have been based on fragments. Some members of the family have a fixed number of segments.

Prostomium keel-shaped and fused to peristomium. Cephalic rim, when present, a raised crest on peristomium; region lateral to nuchal organs part of peristomium as well. Antennae and palps absent. Nuchal organs ciliated grooves. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following ones with similar parapodia. Parapodia biramous. Notopodia truncate cylinders or short cones; neuropodia elevated tori. Gills absent (see below). Epidermal papillae absent. Most taxa with many pygidial cirri. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an eversible simple, usually papillose axial sac; a ventral buccal organ present. Gular membrane present; gut a straight tube. Segmental organs apparently mixonephridia; present in four anterior segments, presumably with one anterior excretory pair and remaining three pairs being gonoducts (Pilgrim 1978). Circulatory system closed; heart body absent. Aciculae absent. Chaetae variously ornamented notopodial capillaries and distally dentate neuropodial hooks with distinct protective beards.

In *Branchiomaldane* and *Johnstonia*, posterior segments have multiple vascularized digitiform extensions covering the segments. These extensions are unique to the two genera and are not considered homologous with gills in other polychaetes.

MYZOSTOMIDAE Benham, 1896

Main references: Jägersten 1940; Eeckhaut *et al.* 1994.

Evidence for monophyly: Notopodia represented by cirri only; aciculae with a membranous hood.

The myzostomids are oval or disk-shaped commensals or parasites on asteroid and especially crinoid echinoderms. They are usually treated as a separate class of annelids, but as pointed out by Rouse & Fauchald (1995), this is based more on perceived differences to other articulate groups than on presence of shared similarities. We treat the myzostomids as a single unit at the family level for the purposes of this study; no characters, such as position of the mouth, general body shape and host, used to separate myzostomid taxa (see Prenant 1959) have been included in this study. The first myzostomids were described well before 1850, but nevertheless, Benham (1896) appears to have been the first of the major polychaete reviewers to link them to the annelids as a separate class. A separate literature had developed in the meantime (e.g. see Stummer-Traunfels 1903, 1926) and as a consequence a distinct terminology had developed. Jägersten (1940 and elsewhere) was aware of the similarities between the polychaetes and the myzostomids but preferred to focus attention on the unique features of the myzostomids.

Prostomium fused to peristomium and rest of body; peristomium presumably limited to lips. Antennae and palps absent. Nuchal organs absent. Arrangement of longitudinal muscles not documented; segmentation present. First segment (of a total of five) with chaetae. Neuropodia well-developed; notopodia present as dorsal cirri (Wheeler 1896, but see below). Ventral cirri present. Gills, epidermal papillae and pygidial cirri absent. Lateral organs absent (see below); dorsal cirrus organs not observed. Stomodaeum with eversible, muscular, axial pharynx; terminal papillae present; jaws absent (Eeckhaut *et al.* 1994). Gular membrane absent; gut with segmentally arranged side branches. Nephridia protonephridia completely separated from coelomoducts; segmental organs present in four of five segments (Pietsch & Westheide 1987). Circulatory system and heart body absent. Aciculae present. All chaetae neuropodial; capillaries in larvae and simple falcate hooks in adults.

The whole myzostome body is fused; thus, the head is not a distinct structure. Eeckhaut & Jangoux (1993): 42 described lateral organs as resembling nuchal organs in structure, but none is present in the appropriate position; these lateral organs are totally different from the structures called lateral organs among other polychaetes. An anterior apodous or achaetous segment is absent (Jägersten 1940); we assume that the first chaetae are on the first of a total of five segments present. The marginal cirri were considered homologous with dorsal cirri by Wheeler (1897); however, Jägersten (1940) considered them as *de-novo* sensory structures characteristc of some groups of myzostomes. Myzostomes have five segments, and the most common number of marginal cirri is 10.

NAUTILINIELLIDAE Miura & Laubier, 1990

Main references: Miura & Laubier 1989, 1990; Blake 1990, 1993; Glasby 1993.

Evidence for monophyly: None known.

Members of the family have been found mainly in deep water samples. Morphologically, they resemble simply constructed syllids, pilargids or hesionids. The generic name used by Miura & Laubier (1989), *Nautilinia*, is preoccupied in molluscs; they proposed a replacement name, *Nautiliniella*, thus the correct family name is Nautiliniellidae. The original justification for erecting the family was the presence of a proventricle combined with characteristic chaetae. Blake (1990, 1993) and Glasby (1993) reviewed the family and described or redefined the anterior structures.

Prostomium fused to peristomium; frontally truncate. Peristomial portion limited to lips. One pair of lateral antennae present. Palps ventral, tapering without articulations. Nuchal organs not observed. Arrangement of longitudinal muscles undocumented; segmentation present. First segment similar to the next following segments with similar parapodia. Parapodia biramous; neuropodia well-developed; notopodia dorsal cirri with aciculae. Ventral cirri present in some taxa; both dorsal and ventral cirri absent in some taxa. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae absent; jaws absent. Gular membrane, gut structure unknown. Excretory, reproductive and circulatory systems unknown. Notopodial chaetae absent; neuropodial chaetae simple, distally sharply curved (Miura & Laubier 1989, fig. 1f; 1990, fig. 1e; Blake 1990, fig. 1c; Miura & Ohta 1991, fig. 1j; Miura & Hashimoto 1993, fig. 1g).

The dorsal prostomial appendages are here considered frontal antennae; the ventral appendages [called peristomial cirri by Glasby (1993) and posteroventral antennae by Miura & Laubier (1989)] are palps (Miura & Laubier 1989: 388, Miura & Laubier 1990: 320; Blake 1990: 689; Miura & Hashimoto 1993). The homologies of the anterior appendages are by no means certain and can be resolved only through careful morphological work. The neurochaetae resemble the kinds sometimes referred to as fused compounds (Perkins 1987).

NEPHTYIDAE Grube, 1850

Main references: Fauvel 1923; Paxton 1974; Rainer 1984, 1989; Rainer & Kaly 1988.

Evidence for monophyly: Gill attached to ventral side of notopodium projecting into space between notopodium and neuropodium (interramal in position).

The first species were described in the genus *Nereis*, but were moved to their own genus, *Nephtys* by Cuvier (1817). They have many closely similar segments, and the anterior end is simply structured; nevertheless, they are not easily linked to other families, not least due to modifications in the structure of septa and oblique musculature (Clark R. B. & Clark M. E. 1960, Clark M. E. & Clark R. B. 1960). Recent taxonomic treatments can be found in Rainer (1984, 1989) and Rainer & Kaly (1988).

Prostomium quadrangular or pentagonal. Peristomium limited to lips. One pair of tapering lateral antennae present. Palps ventrolateral, tapering, without articulations. Nuchal organs present; as nuchal papillae in some taxa. Longitudinal muscles grouped in bundles; segmentation distinct. First segment smaller than next following segment with small biramous parapodia. One or two pairs of tentacular cirri present. Both parapodial rami large, neuropodia usually longer than notopodia. Dorsal and ventral cirri present. Gills attached to notopodia, projecting into interramal space. Epidermal papillae absent. Single median pygidial cirrus present. Lateral organs not observed. Dorsal cirrus organs absent. Stomodaeum with axial, muscular eversible pharynx. Terminal papillae present; surface of everted pharynx covered with rows of buccal papillae. One pair of lateral jaws present. Gular membrane absent; gut a straight tube. Segmental organs protonephromixia present in many segments; ciliophagocytic organs present. Circulatory system closed; heart body absent. Aciculae present. All chaetae variously ornamented capillaries.

Nephtyids are often considered as having two pairs of antennae (Ohwada 1985); we consider one pair of antennae to be present. The so-called ventrolateral antennae are ventrally located, simple, tapering palps (illustration in Paxton 1974). The dorsal and ventral cirri of the first segment are relatively larger than those of the next following segments and are here considered tentacular cirri; in some taxa, only the dorsal cirri are larger, whereas in others, both pairs of cirri are larger. Hayashi & Yamane (1994: 769) found organs structurally resembling dorsal cirrus organs scattered over the body in a nephtyid; however, none is in the position of the dorsal cirrus organs present in other families (e.g. eunicids and onuphids, Hayashi & Yamane 1994).

NEREIDIDAE Johnston, 1865

Main references: Ehlers 1868*a*; Fauvel 1923; Fitzhugh 1987; Glasby 1993.

Evidence for monophyly: Notopodia distinct (rarely reduced), usually with one or more flattened lobes, notochaetae compound falcigers and/or spinigers (rarely notochaetae absent) (Glasby 1993: 1558). Another characteristic feature of the nereidid is the inverted T-shaped prostomium; this is present in most taxa, small-bodied species tend to have diamond-shaped prostomia with rounded corners.

The nereidids are probably the most widely recognized group of polychaetes; they were mentioned in pre-Linnean writing, and several species had been described by 1800 (e.g. Linné 1758; Müller 1776). The nereidids most closely resemble syllids and hesionids and more distantly the rest of Phyllodocida (*sensu* Fauchald 1977). Nereidids lack capillary chaetae completely; a feature that they share with the ichthyotomids.

Prostomium with a narrow anterior and a wide posterior part (inverted T-shape) in most taxa; others with triangular or roughly diamond-shaped prostomia. Peristomium limited to lips. Paired frontal antennae present in almost all taxa. Palps ventral, tapering, articulated (but see Harper 1979: 95). Nuchal organs short ciliated grooves. Longitudinal muscles grouped in bundles; segmentation distinct. First segment indistinct with tentacular cirri only; four pairs of tentacular cirri present in most taxa; other taxa with two or three pairs. Both parapodial rami well-developed; notopodia shorter than neuropodia in most taxa. Dorsal and ventral cirri present. Gills and epidermal papillae absent. Paired pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae absent; lateral jaws present. When everted outer surface of pharynx with either papillae or paragnaths or both in characteristic patterns in most taxa. Gular membrane absent; gut a straight tube. Metanephrida completely separated from ciliophagocytic organs; present in most segments. Circulatory system closed; heart body absent. Aciculae present. All chaetae compound; appendages joined to shafts by single ligaments (see below). Appendages slender and tapering to fine tips, or bluntly falcate, sometimes dentate.

Two pairs of tentacular cirri were found to be the plesiomorphic condition by Fitzhugh (1987). The gills present in two genera are modified notopodial ligules rather than gills as here defined in that they lack the interepidermal vascular loops present in gills. At least some chaetae in some taxa may have double ligaments (C. Glasby, pers. commun.).

NERILLIDAE Levinsen, 1883

Main references: Goodrich 1912; Jouin 1967; Purschke 1985*b*; Westheide 1990; Tzetlin *et al.* 1992.

Evidence for monophyly: Unique structure of ventral pharyngeal organ (Purschke 1985b); interramal parapodial cirrus present (Goodrich 1912).

The first nerillids were described in the middle of the 19th century, but, since most species are small-bodied and living in sands, most have been described as a result of the increased interest in the mesopsammon over the last 70+ years. The Nerillidae is one of the five families that used to be considered members of the Archiannelida. They share a number of features with both phyllodociform and eunicean families.

Prostomium fused to peristomium, usually frontally truncate. Peristomial portion limited to lips. A pair of frontal and a median antenna present; either or both absent in some taxa. Palps ventral without articulations. Nuchal organs dorsolateral ciliated grooves. Longitudinal muscles grouped in bundles; segmentation present. First segment resembles next following segments; parapodia absent, uniramous or biramous. Other parapodia biramous, both rami small, tapering or truncate cones. A large interramal cirrus present. Dorsal and ventral cirri absent. Gills and epidermal papillae absent. A pair of pygidial cirri present. Lateral organs absent; dorsal cirrus organs not observed. Stomodaeum with an eversible ventral buccal organ equipped with intracellular skeletal elements (stylets). Gular membrane absent; gut a straight tube.

Nephridia are protonephridia present in most segments in some taxa; for these taxa, relation to coelomoduct unknown. Segmental organs mixonephridia in other taxa. Enteronephridia present in *Trochonerilla* and *Nerillidium* (Jouin 1967; Tzetlin *et al.* 1992: 168, fig. 5). Circulatory system closed; heart body absent. Aciculae absent. Capillaries and distally tapering compound chaetae present. Appendages and shafts linked by single ligaments. Some taxa with capillaries.

Goodrich (1912: 403, fig. 1) mentioned the presence of ciliated lateral patches on each segment; these patches appear to be structurally similar to the lateral organs, but are intersegmental rather than interramal. The presence of metanephridia and compound chaetae have been considered to be the plesiomorphic condition in the family.

OENONIDAE Kinberg, 1865

Main references: Ehlers 1868*a*; Hartman 1944; Colbath 1989; Orensanz 1990.

Evidence for monophyly: Maxillary carriers highly sclerotinized, slender free rods loosely attached to the posterior end of Mx I.

This family includes *Arabella* and related genera formerly included in the family Arabellidae and the genera *Halla*, *Oenone* and *Tainokia*, previously considered lysaretids (Colbath 1989; Orensanz 1990). The genus *Lysarete* has been moved into the Lumbrineridae (Orensanz 1990). The move of *Oenone* into the same family as *Arabella* makes the family name Oenonidae the oldest available family name; up to 1944, *Arabella* and similar genera were considered members of the Lumbrineridae, which they resemble superficially. In contrast to the lumbrinerids, the oenoniids lack hooks of any kind, and the jaw apparatus lacks the click-joint between maxillary carriers and Mx I. They have a flattened, ovate, poorly sclerotinized plate located as an 'apodeme' in the jaw-apparatus; this structure was called the third carrier by Hartman (1944); it is not present in lumbrinerids.

Prostomium usually bluntly conical. Peristomium two rings. A pair of lateral and a median antenna present in some, but not all taxa. When present, antennae located near peristomial fold. Palps absent. Nuchal organs ciliated dorsolateral pits under peristomial fold. Longitudinal muscles grouped in bundles; segmentation present. First segment similar to next following segments with biramous parapodia. Parapodia with neuropodia larger than notopodia in most taxa. Dorsal cirri present; cirriform ventral cirri absent, replaced by cushion-shaped structures in all chaetigers. Gills and epidermal papillae absent. Two pairs of pygidial cirri present. Lateral organs not observed; dorsal cirrus organs present. Stomodaeum heavily muscularized ventrally with paired mandibles and five (sometimes more, often fewer) pairs of maxillae attached to laterally located muscular ridges within the buccal cavity; number of maxillae sometimes asymmetrical. Jaws heavily sclerotinized, black and shiny in most taxa; without calcifications (Colbath 1989). Maxillary carriers long and slender, only loosely attached to Mx I. A flattened, ovate plate located within the muscular part of eversible jaw-apparatus. Maxillary apparatus prionognath. Presence of gular membrane and structure of gut undocumented. Structure of nephridia unknown. Circulatory system closed; heart body not observed. Aciculae present. Most chaetae ornamented capillaries or limbate chaetae; emergent large spines present in some taxa.

When antennae are present, the peristomial fold may be incised to accommodate them. The number of maxillae varies even within individual species (*Arabella mutans*, Colbath 1987) and between genera. The large-bodied genera (*Oenone*, *Halla*, *Arabella*) usually have five or more maxillae on each side; the small-bodied ones (*Drilonereis*) tend to have a smaller number of maxillae, often two per side (pers. obs.).

ONUPHIDAE Kinberg, 1865

Main references: Ehlers 1868*a*; Hartman 1944; Paxton 1986*a*,*b*; Orensanz 1990.

Evidence for monophyly: Palps divided into a frontal and a ventral part. Single peristomial ring.

Paxton (1986*a*, *b*) and Orensanz (1990) comprehensively reviewed the taxonomy. Onuphids and eunicids are very similar; in both groups, the jaw apparatus is labidognath with Mx III present on the left side only. In eunicids, compound hooks are present throughout the body; in the onuphids, compound or pseudocompound chaetae are limited to the first few chaetigers.

Prostomium frontally truncate or rounded. Peristomium a single ring. A median and a pair of lateral antennae present; located posteriorly on prostomium. Each antenna separated into a distinct, often long, ceratophore which may be heavily ringed, and a tapering or digitiform style. Palps located in front of lateral antennae (Orrhage 1995); palps consist of a ringed palpophore and a style; antennae and palps very similar. Dorsal lips usually short, tapering structures without articulations. Nuchal organs paired dorsolateral ciliated pits. Longitudinal muscles grouped in bundles; segmentation distinct. First segment often longer than next following segment, but essentially similar with well-developed parapodia. Neuropodia elongated in first few segments, becoming very low cones in median and posterior chaetigers. Notopodia dorsal cirri with aciculae in all segments. Dorsal and ventral cirri present. Gills present in many, but not all taxa; always associated with notopodia. Epidermal papillae absent. One pair of large and one pair of short peg-like pygidial cirri present in some taxa; others with four similar pygidial cirri or with only a single pair of pygidial cirri. Lateral organs not observed; dorsal cirrus organs present. Stomodaeum with ventral eversible heavily muscularized pharynx with a pair of mandibles and four pairs of maxillae, in addition to an unpaired Mx III. Maxillary carriers short and tightly linked to bases of Mx I (labidognath construction *sensu* Ehlers 1868*a*). Calcification aragonitic (Colbath 1989). Gular membranes absent; gut a straight tube. Segmental organs mixonephridia; distribution poorly documented. Circulatory system probably closed; heart body absent. Aciculae present. Compound chaetae with double ligaments linking shafts and appendages; appendages dentate in all taxa; a few taxa with slender tapering appendages as well. Compound chaetae present in anterior chaetigers only. In most taxa, only few truly compound chaetae present; most anterior chaetae with incomplete hinge (pseudocompound). Other chaetae variously modified capillaries, pectinate chaetae and large subacicular chaetae.

The anteriormost paired 'antennal' structures are two dorsal lips according to Orrhage (1995); they have also been called frontal antennae (Hartman 1944; Fauchald 1982) and more recently the anteriormost part of the palps (Paxton 1986*a*). Juvenile maxillae are ctenognath; they are shed and replaced with adult-shaped jaws at least in one species (Hsieh & Simon 1987). Distribution of segmental organs has been poorly documented; gametes are not present in the anterior most segments, suggesting that anterior chaetigers may have sterile segmental organs, but the distribution of gametes may be size-related (Paxton 1979; Hsieh & Simon 1991), thus complicating the issue. The circulatory system is assumed closed because capillary intraepidermal vessels are present in the branchiae (pers. obs.).

OPHELIIDAE Malmgren, 1867

Main references: Brown 1938; McConnaughey & Fox 1949; Day 1967.

Evidence for monophyly: Body fusiform with tapered cone-shaped prostomium; mouth a transverse slit at the level of chaetiger 1 (Day 1967: 570).

A characteristic, but not unique, feature of the family is the limited and fixed numbers of segments present. Three different body-forms, depending essentially on the presence and relative length of the ventral groove, are represented; all three are well-illustrated in Day (1967). Opheliids were first described by Savigny (1822) and grouped among the sedentaries, despite the lack of tubes and distinct body regions in some (e.g. *Ophelina*). The family was recognized by Grube (1850) and the family name given the correct form by Malmgren (1867). The opheliids are usually compared to the scalibregmatids, which especially the *Travisia*-like taxa resemble in the simple parapodia with capillary chaetae and the distinct epidermal rugosity (Ashworth 1902).

Prostomium usually conical; a distal palpode present in some taxa. Peristomium limited to lips. Antennae and palps absent. Nuchal organs paired, eversible structures. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following ones with similar parapodia. Both parapodial rami small, with notopodia slightly smaller than neuropodia in most taxa (Brown 1938, figs 4,5); in *Travisia* both rami similar in size, well-developed and large. Gills single filaments closely associated with upper end of parapodia. Dorsal and ventral cirri absent. Epidermal papillae absent. Pygidium hood-shaped with internal and marginal cirri or hoods absent and multiple cirri present. Lateral organs present; dorsal cirrus organs not observed. Stomodaeum with axial, simple, sac-like eversible pharynx. Gular membrane present; gut a straight tube. Both proto- and metanephridia reported present; distribution poorly understood (see below). Circulatory system closed; heart body present. Aciculae absent. All chaetae are variously ornamented capillaries.

Both metanephrida and protonephridia have been reported present in different genera. Goodrich (1945: 189) called the segmental organs mixonephridia. The distribution is also uncertain. Brown (1938: 154–155) found nephridia limited to three segments in *Ophelia*; other genera have many pairs of nephridia.

ORBINIIDAE Hartman, 1942

Main references: Eisig 1914; Hartman 1957; Mackie 1987.

Evidence for monophyly: Both noto- and neuropodia shifted dorsally in posterior part of the body.

The first orbiniids were described by Audouin & Milne Edwards (1833c) as *Aricia*; for many years, they were considered related to the errant, rather than sedentary groups (Grube 1850; Levinsen 1883; Benham 1896); they have more recently been considered sedentaries (Fauvel 1927; Hartman 1969). Hartman (1942) pointed out that the generic name *Aricia* was invalid and had to be replaced with *Orbinia* and changed the family name to Orbiniidae.

The larger orbiniids are multi-segmented and slender, with a short thorax and a long abdomen in which both parapodial rami project dorsally. The family consists of two subfamilies, Orbiniinae and Protoariciinae, separated on the presence of one or two achaetigerous rings between the prostomium and the first chaetiger (Hartman 1957). The first ring is here considered peristomial; the second ring in the protoariciins is an achaetigerous segment (Eisig 1914).

Prostomium conical, rounded or truncate. Peristomium a complete ring. Antennae and palps absent. Nuchal organs dorsolateral ciliated pits. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following segments with similar parapodia. Anterior parapodia low ridges, similar in both rami; posterior parapodia with both rami projecting dorsally, long and slender. Dorsal and ventral cirri absent. Gills paired, dorsal and flattened. Epidermal papillae absent (see below). Two to many pygidial cirri present. Lateral organs present; dorsal cirrus organs not observed. Stomodaeum with a ventral eversible buccal bulb; axial pharynges present in some taxa derived from buccal bulb (Dales 1962: 419–420). Gular membrane absent; gut straight; anterior diverticulae present in some taxa (Eisig 1914). Segmental organs mixonephridia or possibly metanephromixia; present in many segments. Circulatory system closed; presence of a heart body not documented. Aciculae present in posterior notopodia. Chaetae variously ornamented capillaries and spines.

The protoariciins have two anterior achaetous rings; thus, in this subfamily, the first segment lacks parapodia and chaetae. The podial and subpodial lobes are parts of the subdivided neuropodial lobes proper and are not ventral cirri. In some taxa, the ventral surface of the body becomes studded with papillae starting in late thoracic segments and continuing through at least the first few segments of the abdomen (see Hartman 1957 for illustrations). These papillae, which are short, conical structures, differ morphologically from those present in the flabelligerids. The structure of the segmental organ appears to be variable in the family.

OWENIIDAE Rioja, 1917

Main references: Wilson 1932; Dales 1957; Hartman 1969; Gardiner 1978; Nilsen & Holthe 1985.

Evidence for monophyly: Neuropodia with dense fields of very small hooks.

The family used to be known as Ammocharidae, a name based on an invalid generic name, *Ammochares*, a synonym of *Owenia*. *Owenia fusiformis* delle Chiaje (1828), the best known oweniid, is completely encased, as are all oweniids, in a close-fitting and extremely tough tube. The oweniids lack a cuticle, and the structure of the body-wall is different from all other polychaetes (Gardiner 1978; Gardiner & Rieger 1980). Bubko (1973) and others have related the oweniids to the archiannelidan families using the unusual morphological structure as evidence. The presence of small hooks in the neuropodia is usually the reason used to ally the oweniids with a variety of the families, from spionids to sabellids.

Prostomium fused to peristomium; in *Owenia* as a low, lobed terminal structure surrounding head; in other taxa prostomium frontally rounded, sometimes inflated and bilobed (Hartman 1969). Peristomium a complete ring. Antennae absent. Prostomial palps form the lobed structure in *Owenia*, or are present as a pair of grooved dorsally emerging palps or are missing (illustrated in Hartman 1969). Nuchal organs not observed. Longitudinal muscles grouped in bundles; segmentation present. First segment similar to next following segment with similar parapodia (notopodia only present). All notopodia short, truncate cylinders; neuropodia wide, flattened tori. Dorsal and ventral cirri absent. Gills absent. Epidermal papillae absent. Pygidial cirri usually absent; multiple pygidial cirri present in some species. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an eversible ventral buccal organ (Wilson 1932; Dales 1957). Gular membranes absent; gut a straight tube. Segmental organs called mixonephridia by Goodrich (1945); opening individually; limited to one or a few anterior segments. Circulatory system closed; heart body absent (S. Gardiner, pers. commun.). Aciculae absent. Chaetae variously ornamented notopodial capillaries and very small, unprotected neuropodial dentate hooks.

Gilson (1895) claimed that the segmental organs were used for release of gametes; however, Watson (1901) described spawning from anal pores.

PARALACYDONIIDAE Pettibone, 1963

Main references: Fauvel 1914; Pettibone 1963.

Evidence for monophyly: None known.

Named for the genus *Paralacydonia* Fauvel, 1914, previously considered a member of the Lacydoniidae, Pettibone (1963: 184) pointed out that this genus has little in common with *Lacydonia*, which appear more similar to the phyllodocids than does *Paralacydonia*. Fauchald (1977) suggested a relationship to the glycerids; Pettibone (1963) compared them to the nephtyids. The anatomy has not been studied.

Prostomium a tapering, blunt-tipped cone. Peristomium limited to lips. One pair of antennae present. One pair of ventral tapering palps present. Nuchal organs lateral depressions (F. Pleijel, pers. commun.). Arrangement of longitudinal muscles not documented; segmentation distinct. First segment small relative to next following segments; without parapodia according to Pettibone (1963); with neuropodia according to Fauvel (1914). Parapodia biramous with both rami well-developed; neuropodia longer than notopodia. Dorsal and ventral cirri tapering. Gills absent. Epidermal papillae absent. Pygidial cirri not observed; possibly absent (Pettibone 1963). Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an eversible, axial, muscular pharynx; presence of terminal papillae not documented; jaws absent (Pettibone 1963). Presence of gular membrane and structure of gut not known. Nephridial, reproductive and circulatory systems not studied. Aciculae present. Notopodial chaetae slender, marginally spinous capillaries; neuropodial chaetae compound spinigers with single ligaments tying appendages to shafts; a few neuropodial capillaries also present.

The ventral pair of anterior appendages is here considered a pair of ventral palps (as in glycerids, nephtyids and phyllodocids).

PARAONIDAE Cerruti 1909

Main references: Cerruti 1909; Strelzov 1973.

Evidence of monophyly: Nuchal organs dorsolateral paired slits on head.

The paraonids are small, slender worms with overall simple construction; the first species were described as orbiniids or spionids. The family concept was recognized by Mesnil & Caullery (1898); the currently used family name was coined by Cerruti (1909).

Prostomium and peristomium fused into distinct, more or less bluntly conical structure. Peristomium limited to lips (Strelzov 1973). Single median antenna present in some taxa. Palps absent externally, but palpal nerves present (Orrhage 1966). Nuchal organs gently curved or comma-shaped ciliated structures located dorsally on head. Longitudinal muscles in bundles; segmentation distinct. First segment similar to next following segments with biramous parapodia. Parapodia biramous; both rami papillar or short ridges. Tentacular, dorsal and ventral cirri absent. Slender, postchaetal notopodial lobes present (Strelzov 1973: 44). Dorsal flattened gills present, usually on a limited number of anterior segments. Epidermal papillae absent. Three, sometimes more, pygidial cirri present. Lateral organs present; dorsal cirrus organs absent. Stomodaeum with ventral buccal organ (illustrated in Strelzov 1973); terminal papillae absent; jaws absent. Gut a straight tube; gular membrane absent. Segmental organs metanephridia of unknown distribution. Circulatory system closed; heart body absent. Aciculae absent. All chaetae limbate or capillaries. Most, but not all with 'modified' chaetae in one or both rami; most modified chaetae slightly thicker than limbate chaetae, but variously ornamented distally.

Dales (1963) considered the eversible stomodaeal structure to be a simple, axial proboscis rather than a ventral buccal organ.

PARERGODRILIDAE Reisinger, 1925

Main references: Karling 1958; Reisinger 1960; Purschke 1986, 1987*a*.

Evidence for monophyly: Arrangement of muscle and glandular cells of ventral pharyngeal organs (Purschke 1987*a*).

Parergodrilus was described from damp soil in Austria by Reisinger (1925); *Stygocapitella* was described from the Kieler Canal by Knöllner (1934; presumably through a lapsus, the generic name is spelled *Stypocapitella* in the title of Knöllner's paper. In the rest of the paper, including the formal proposal of the generic name, it is spelled *Stygocapitella*). Karling (1958) compared the two and, emphasizing the differences between them, placed each in a separate family. Reisinger (1960) emphasized the similarities and concluded that they belong to the same family, for which the name Parergodrilidae is the valid name.

Prostomium bluntly rounded. Peristomium a complete ring. Antennae and palps absent. Nuchal organs present in *Stygocapitella*; absent in *Parergodrilus* (Purschke 1986: 13). Longitudinal muscles grouped in bundles; segmentation present. First segment similar to other segments. All parapodial structures absent. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an eversible ventral buccal organ. Gular membrane absent; gut a straight tube. Nephridia metanephridia; relation to coelomoducts unknown; distribution of segmental organs poorly known. Circulatory system of *Parergodrilus* closed; heart body absent. Aciculae absent. All chaetae capillary in *Stygocapitella*; distally furcate in *Parergodrilus*.

One septum at the posterior edge of the head is better developed than the other, largely incomplete septa according to Karling (1958) and Reisinger (1960); it is, however, not muscularized as are the gular membranes of other polychaetes; in *Stygocapitella*, nephridia are present along the body, but gonoducts are restricted in distribution; in *Parergodrilus*, the nephridia have a restricted distribution; the issue requires further study.

PECTINARIIDAE Quatrefages, 1866

Main references: Nilsson 1928; Fauvel 1927; Holthe 1986.

Evidence for monophyly: Cone-shaped tubes of unique shape and construction. Cephalic veil present. Posterior end a flattened scaphe with spine-like chaetae.

Pectinariids were among the first polychaetes described; the history of the early studies was detailed by Lucas & Holthuis (1975). Pectinariids have always been considered to be related to the terebellids (Savigny 1822; Grube 1850; Levinsen 1883; Fauvel 1927). The two families do not share many external features, except the presence of tori with uncini, but the internal structures are rather similar.

Prostomium completely fused to peristomium and reduced. Peristomium represented by lips. Antennae absent. Peristomial palps (buccal antennae) grooved, located on or around lips; cannot be retracted into buccal cavity. Nuchal organs presumably represented by dorsal ciliated crests (Nilsson 1912; Söderström 1930). Longitudinal muscles grouped in bundles; segmentation present. First segment wholly fused to head; with notopodial paleae. Other notopodia short truncate cylinders; neuropodia tori. Dorsal and ventral cirri absent. Gills dorsal and branching, limited to two pairs anteriorly. Epidermal papillae and pygidial cirri absent. Lateral organs present; dorsal cirrus organs not observed. Stomodaeum with ventral buccal organ. Gular membrane present between two anterior segments; gut looped. Segmental organs mixonephridia by implication (Goodrich 1945: 192); limited to a few pairs of anterior nephridia and posterior gonoducts. Circulatory system closed; heart body present. Aciculae absent. Chaetae notopodial capillaries, spines (anterior paleae) and neuropodial uncini.

Nuchal organs have been assumed to be represented by dorsal ciliated crests similar to the dorsal organs in spionids (Nilsson 1912; Söderström 1930). In view of Schlötzer-Schrehardt's (1991) study of *Pygospio*, the dorsal organs should be re-examined to determine whether they have the appropriate innervation to be homologs of the nuchal organs. Segments 2 and 3 carry pairs of cirri (Holthe 1986: 19), but the first segment, the paleal segment, carries no such structures. The cirri present on segments 2 and 3 have unknown relationships to other kinds of cirri reported and may be *de-novo* structures present in the pectinariids; they are not considered homologous to tentacular cirri. Goodrich (1945) generalized for segmental organs of all terebellomorphs and did not specifically mention the pectinariids.

PHOLOIDAE Kinberg, 1858

Main reference: Pettibone 1992.

Evidence for monophyly: None known.

Kinberg (1858) based this family on the genus *Pholoe* Johnston 1839. Hartman & Fauchald (1971) recognized a related family, Peisidicidae, based on the genus *Peisidice* Johnson 1897. *Peisidice* is a subjective synonym of *Pholoides* Pruvot 1895; accordingly Fauchald (1977) changed the name of the family Peisidicidae to Pholoididae. Pettibone (1992) synonymized Pholoididae with Pholoidae, retaining the older name Pholoidae. The two 'families' differ in some characters currently used to recognize scale-worm families, e.g. the distribution of elytrae on posterior chaetigers. These are present on all posterior chaetigers in *Pholoe* and on alternate chaetigers in *Pholoides*. The issue may be moot, in that recognition of either one or two families with elytrae and compound chaetae in addition to the Sigalionidae may make the latter paraphyletic.

Prostomium truncate. Peristomium limited to lips. A pair of lateral and a median antenna usually present. Ventral palps fused to ventral side of first segment; tapering; without articulations. Nuchal organs not observed. Arrangement of longitudinal muscles not documented; segmentation distinct. First segment curved around prostomium with fully developed parapodia; neuropodia fused to lower side of head; chaetae present in some, but not all, taxa; two pairs of tentacular cirri present. In other segments, neuropodia better developed than notopodia but both rami well-developed. Dorsal cirri in part elytrae alternating with dorsal cirri in all segments in *Pholoides*. In *Pholoe*, cirriform dorsal cirri absent;

elytrae present on every second segment anteriorly and present on all posterior segments. Ventral cirri present. Gills and epidermal papillae absent (see below). A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular, eversible pharynx; frontal edge with terminal papillae; two pairs of dorsoventrally arranged jaws present. Gular membrane absent; gut a straight tube (Heffernan 1988). Nephridia metanephridia in *Pholoe minuta* (Bartolomaeus & Ax 1992);. Reproductive and circulatory systems not studied. Aciculae present. Compound chaetae with single ligaments; appendages distally falcate, resembling those present in certain sigalionids (e.g. *Sthenelanella*). Other chaetae variously ornamented capillaries.

Epidermal papillae similar to those present in the aphroditids may be present; no papillae resembling those present in the flabelligerids are present. Nephridia were reported to be metanephridia without any mesodermal involvement in juvenile *Pholoe minuta* (Bartolomaeus & Ax 1992); however, the condition in mature individuals is unknown; the issue must be further studied and the relationship to the reproductive organs clarified.

PHYLLODOCIDAE Örsted, 1843

Main references: Bergström 1914; Uschakov 1972; Pleijel 1991.

Evidence for monophyly: Foliose dorsal cirri on reduced notopodia. All chaetae compound spinigers with distally inflated shafts.

The relationships and monophyly of the phyllodociform families while under active study, have yet to be settled, including the relationship between the phyllodocids and the various groups of pelagic polychaetes. Uschakov (1972) listed the following subfamilies within the Phyllodocidae: Phyllodocinae, Lopadorhynchinae, Pontodorinae and Iospilinae. He gave the Alciopidae, Tomopteridae, Typhloscolecidae and Lacydoniidae status as families. Day (1967) separated the Pontodoridae and Iospilidae as separate families, leaving only the Phyllodocinae and Lopadorhynchinae within the Phyllodocidae. Pleijel (1991) separated the Phyllodocidae into three subfamilies, Notophyllinae, Phyllodocinae and Eteoninae; he thus separated what Uschakov and Day had considered a single subfamily of benthic phyllodocids, into three subfamilies. We accept the family as diagnosed by Pleijel (1991) and all the other groups mentioned above as distinct families subject to further analysis.

Prostomium pentagonal or quadrangular. Peristomium limited to lips. A pair of frontal antennae always present; median antenna present in pleisomorphic taxa (Pleijel 1991: 226). Palps ventral; tapering and without articulations similar in shape to antennae (Pleijel 1991: 226–227). Eyes when present, a single pair. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation distinct. First segment reduced with a pair of tentacular cirri (two pairs in *Eteone*); maximum four pairs of tentacular cirri present. Neuropodia well-developed; notopodia represented by dorsal cirri in most taxa. Taxa with notopodial chaetae plesiomorphic (Pleijel 1991: 228). Dorsal cirri foliose, attached to cirrophores along edge; ventral cirri present, often also flattened. Gills absent. Epidermal papillae absent. A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an axial, muscular eversible pharynx without jaws; terminal papillae are present; in many taxa, pharyngeal surface covered with buccal papillae. Gular membrane absent; gut a straight tube. Segmental organs protonephromixia present in many segments; ciliophagocytic organ absent. Circulatory system reduced to main branches only (Smith & Ruppert 1988); heart body absent. Aciculae present. Appendages of compound chaetae joined to shafts by single ligaments; appendages tapering to slender tips. Notopodial capillaries present in some taxa.

The ventral pair of the frontal appendages are palps; they are often considered to be a second pair of frontal antennae (e.g. Fauvel 1923).

PILARGIDAE Saint-Joseph, 1899

Main references: Pettibone 1966; Katzmann *et al.* 1974; Licher & Westheide 1994.

Evidence for monophyly: None known.

The pilargids were originally described as members of Hesionidae; Pettibone (1966) tracked the history of the family and reviewed the genera known at that time. The family was synonymized with the Hesionidae by Licher & Westheide (1994); this action warrants further study. The two families are here considered distinct. Licher & Westheide pointed out that spelling the family name with 'ii' is incorrect.

Prostomium distinct; either small and located behind a pair of large palps or larger and frontally truncated. Peristomium limited to lips. A pair of frontal antennae present; median antenna present in some, but not all, taxa. Palps ventral; articulated in species considered plesiomorphic by Licher & Westheide (1994). Nuchal organs present. Arrangement of longitudinal muscles not documented; segmentation distinct. First segment indistinct with two pairs of tentacular cirri in plesiomorphic condition (Fitzhugh & Wolf 1990; Licher & Westheide 1994). Neuropodia large; notopodia smaller than neuropodia. Dorsal cirri present in most taxa; ventral cirri present in all taxa. Gills absent. Complex (flabelligerid-style) epidermal papillae absent; simple papillae present in some taxa. A pair of pygidial cirri present in many taxa. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular, eversible pharynx without jaws; terminal papillae present. Gular membrane not observed; structure of gut undocumented. Nephridial, reproductive and circulatory systems not studied. Aciculae present. Most neuropodial chaetae distally slightly hooked, but slender tapering capillaries are present. Notopodial chaetae, when present, often thick spines; spines may be distally straight or curved into a shepherd's crook.

The two pairs of tentacular cirri were considered peristomial cirri by Glasby (1993).

PISIONIDAE Southern, 1914

Main references: Åkesson 1961; Stecher 1968.

Evidence of monophyly: None known.

Pisionids are small and slender; the cuticle is often relatively thick. Most taxa are associated with shallow-water sandy areas and have been studied as part of the interstitial fauna for the last 80 years. They appear to be members of the Phyllodocida (*sensu* Fauchald 1977); other relationships have been debated not least since the family includes taxa with very different head structures. The two pairs of dorsoventral jaws resemble the jaws present in scale-worms (Åkesson 1961; Stecher 1968).

Prostomium small, located between large, anteriorly directly first parapodia in *Pisione*. Prostomium conical in *Pisionidens*. Peristomium limited to lips. Frontal antennae present in *Pisionidens*; other taxa without antennae. Palps fused to ventral side of first parapodium in *Pisione*; emerging ventrally on conical head in *Pisionidens*. Nuchal organs absent (pers. obs.). Longitudinal muscles grouped in bundles; segmentation present. First segment folded around prostomium with neuropodia present in *Pisione*; first segment indistinct with two pairs of tentacular cirri in *Pisionidens*. Neuropodia well-developed; notopodia represented by short cirri with internal acicula. Dorsal and ventral cirri present. Gills and epidermal papillae absent. A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae present; two pairs of dorsoventral jaws present. Gular membrane absent; gut a straight tube. Segmental organs protonephromixia present in many segments. Eggs are present in up to 40 segments in *Pisione*; gonads are limited to a few segments in *Pisionidens*. Circulatory system and heart body absent. Aciculae present. All chaetae neuropodial. Compound chaetae with distally falcate appendages attached to shafts by single ligaments. Capillary chaetae present. Other chaetae spine-like, but no thicker than capillaries. *Pisionidens* with aciculae; without any other chaetae.

POECILOCHAETIDAE Hannerz, 1956

Main references: Allen 1905; Orrhage 1964; Mackie 1990.

Evidence of monophyly: Parapodial lobes flask-shaped or tapering; chaetae feathered (Orrhage 1964, fig. 10).

Poecilochaetus was originally included in the Trochochaetidae (=Disomidae) before Hannerz (1956) in a study of the spioniform larvae separated them into a distinct family. Mackie (1990: 360) demonstrated that the only other genus in the family, *Elicodasia* Laubier & Ramos 1973, was based on a posterior end. The family is by far best represented in shallow marine warm waters. Many species have been described on anterior fragments only.

Prostomium triangular or frontally blunt in dorsal view. Peristomium limited to lips. A median ventrally attached, papillose 'antenna' present (Allen 1905). Paired peristomial grooved palps present. Nuchal organs usually divided into three separated, digitiform processes detached along most of their length (Allen 1905: 87, 111–114, pl. 8, fig. 7). Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next segments; with biramous parapodia. Parapodia low ridges with distinct, usually flask-shaped or tapering postchaetal lobes. Dorsal and ventral cirri absent. Gills parapodial, flattened structures. Epidermal papillae absent (see below). Multiple pygidial cirri present. Lateral organs present; dorsal cirrus organs not observed. Stomodaeum with eversible ventral buccal organ. Gular membrane absent; gut a straight tube; Segmental organs metanephromixia (Allen 1905); mixonephridia (Goodrich 1945). Anterior ones strictly excretory, posterior ones gonoducts. Circulatory system closed; heart body absent. Aciculae absent. Chaetae variously ornamented capillaries and, in anterior chaetigers, thick spines.

The ventral median antenna appears to be unique to the poecilochaetids (Allen 1905). The epidermal papillae present in poecilochaetids are small, tapering structures, very different from the long, complex papillae present in flabelligerids. Allen (1905: 139, pl. 7, fig. 1) mentioned 'large intestinal pouches' in the middle body region. These pouches are of the kind associated with passage of the gut through segmental septa. Mackie (1990) recognized 14 different kinds of simple chaetae including a variety of feathered chaetae.

POEOBIIDAE Heath, 1930

Main references: Heath 1930; Robbins 1965.

Evidence for monophyly: Two septa in an otherwise unsegmented body without parapodia or chaetae.

Originally, the pelagic poeobiids were described as "a connecting link between the Annelida and the Echiuroidea (Gephyrea armata)" to quote the title of the original description (Heath 1930). This statement is inaccurate as demonstrated by Robbins (1965), the poeobiids are clearly polychaetes. Most features present point to a close relationship to the Flabelligeridae (Robbins 1965).

Prostomium truncate and retractable. Peristomium limited to lips. Antennae absent. Peristomial paired grooved palps located dorsolateral to the mouth. Nuchal organs present. Arrangement of longitudinal muscles unknown; segmentation indistinct; two septa dividing body into three coelomic pockets present (Robbins 1965); the anteriormost of these structures do not differ from others. All parapodial structures absent. Five pairs of gills eversible as part of anterior end; apparently similar to those present in flabelligerids (Robbins 1965). Epidermal papillae of flabelligerid type present. Stomodaeum with ventral, eversible buccal organ. Gular membrane apparently present; gut folded. Lateral organs and dorsal cirrus organs not observed. Nephridia metanephridia, segmental organs possibly mixonephridia. Single pair of nephridia present anteriorly; opening in front of the gills (Robbins 1965). A pair of gonoducts present. Circulatory system closed, heart body present. All chaetae, including aciculae, absent.

Robbins (1965): 203 found no gametes in the nephridia; she reported that at maturation, the septa broke down so the gametes are spread throughout the body. A single pair of nephridia are present anteriorly, opening anteriorly in front of the gills (Robbins 1965). Robbins (1965, fig. 2b) showed the gonadal openings as well, as a pair of small dots in front of the gills. In fig. 1a, she showed a pair of coelomic funnels extending laterally from the middle coelomic cavity; i.e. the cavity in which the gonads are found.

POLYGORDIIDAE Czerniavsky, 1881*a*

Main references: Hatschek 1878, 1885; Westheide 1990.

Evidence for monophyly: Solid antennae; pygidium inflated (Schmidt & Westheide 1977, figs 2a–c, 3a–b).

The larva and metamorphosis of *Polygordius* was the subject of a major study by Hatschek (1878). The family is extremely uniform in structure. While it was considered a member of the Archiannelida, some species of *Polygordius* can be as much as 10 cm in length, so the polygordiids do not belong among the interstitial taxa, even if they traditionally have been treated in studies of interstitial polychaetes. The reason for including them among the archiannelids was that morphologically they resemble *Protodrilus* and *Saccocirrus* (see below) in having paired frontal antennae and lack many of the polychaete features, such as segmentation and parapodia.

Prostomium and peristomium fused; conical or rounded. Peristomial portion a complete ring. One pair of anterior grooved palps similar to prostomial palps in other polychaetes present. Other anterior appendages absent. Nuchal organs paired dorsolateral slits. Longitudinal muscles grouped in bundles. First segment similar to other segments. All parapodial structures and gills absent. Epidermal papillae absent. Pygidium expanded with flattened lobes; a pair of pygidial cirri sometimes present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with a variously folded, partially protrusible atrium; ventral buccal organ absent. Gular membrane absent; gut straight. Metanephridia present in adults in most segments; separate genital ducts not observed (Westheide 1990). Circulatory system closed; heart body absent. All chaetae absent.

POLYNOIDAE Malmgren, 1867

Main references: Fauvel 1923; Pettibone 1963.

Evidence of monophyly: None known.

The first polynoids were described in the genus *Aphrodita*. The genera *Polynoe*, *Harmothoe* and *Lepidonotus* were also known by 1830 (Audouin & Milne Edwards 1834). All scale-worms were originally included in the family Aphroditidae. Over the years, one uniform group after another has been segregated into its own family (or subfamily), whereas the remnant taxa were retained in the Polynoidae. The recognition of Acoetidae, Aphroditidae and Eulepethidae has left the Polynoidae without a unique feature uniting the whole family. A major revision of the scale-worms is clearly needed.

Prostomium bilobed or rounded. Peristomium limited to lips. Paired antennae present in most taxa; median antenna present in many taxa. Ventral palps fused to first segment; tapering without articulations. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation distinct. First segment curved around prostomium; usually with very small biramous parapodia with neuropodia fused to lower side of head; two pairs of tentacular cirri present. Neuropodia longer than notopodia in all segments; both rami are distinct; notopodia sometimes short with few chaetae. Dorsal cirri and elytrae alternate at least in anterior end; posterior end may be covered by elytrae, or elytrae may be absent on posterior end. Ventral cirri present. Gills absent (see below). Epidermal papillae absent. A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae present; two pairs of dorsoventral jaws present. Gular membrane absent; gut with segmentally arranged side-branches. Segmental organs mixonephridia present in many segments. Circulatory system closed; heart body absent. Aciculae present. Chaetae variously ornamented capillaries and spines.

Epidermal extensions may be present on the elytrophores and on the body wall under the elytrae; these are assumed to have a respiratory function, but do not correspond to gills as defined here.

PONTODORIDAE Bergström, 1914

Main references: Bergström 1914; Uschakov 1972.

Evidence of monophyly: Surface of eversible pharynx with long, slender, tapering papillae forming no distinct pattern. Parapodia with an elongate distal finger-shaped cirrus.

Pontodorids are small, pelagic, and similar to the phyllodocids in many features. They were first described in the second half of the 19th century and considered members of the Phyllodocidae of which they are still often considered a subfamily (Uschakov 1972). They differ from the phyllodocids in having taeniform rather than foliose dorsal cirri. The everted pharynx resembles the one present in nephtyids, but in the latter, the tapering pharyngeal papillae are arranged in rows and decrease in size towards the base of the pharynx. In the pontodorids, the papillae are scattered and are similar in size throughout as they are in many phyllodocids.

Prostomium truncate. Peristomium assumed limited to lips. A pair of frontal antennae present. Ventral palps tapering; without articulations. Nuchal organs present. Arrangement of longitudinal muscles unknown; segmentation distinct. First segment indistinct with two pairs of tentacular cirri. Parapodia biramous; notopodia represented by long dorsal cirri only. Neuropodia longer than notopodia; with long, terminal cirri (Uschakov 1972). Dorsal and ventral cirri present. Epidermal papillae absent. Pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae present; surface of everted pharynx covered with long papillae; jaws absent; proventricle present. Gular membrane absent; gut straight. Nephridial, reproductive and the circulatory systems not studied. Aciculae present. All chaetae compound; appendages tapering to slender tips; attached to shafts by single ligaments.

Day (1967: 167) reported that the papillose unarmed muscular pharynx was followed by a barrel-shaped muscular gizzard, similar to the proventricle of the syllids.

POTAMODRILIDAE Bunke, 1967

Main reference: Bunke 1967.

Evidence for monophyly: None known.

The potamodrilids are very similar to the aeolosomatids. The family consists of a single genus removed from the aeolosomatids, which may have been left paraphyletic by recognition of the family.

Prostomium fused to peristomium, flattened, frontally blunt. Peristomial part limited to lips. Antennae and palps absent. Nuchal organs present (as paired sensory papillae in Bunke 1967: 339, fig. 81b). Longitudinal muscles apparently grouped in bundles (Bunke 1967, figs 87–90); segmentation present. All segments similar with similar equipment. All parapodial structures, including tentacular, dorsal and ventral cirri absent. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with structure resembling a ventral buccal organ. Gular membrane absent; gut a straight tube. Nephridia metanephridia; connection to coelomoducts not documented. Nephridia present in segments 1 and 2; female gonads in segment 5 and male gonads in segment 6. Circulatory system closed; heart body absent. Aciculae absent. All chaetae capillaries.

The distribution of segmental organs resembles the restricted gonadal pattern present in other polychaetes.

PROTODRILIDAE Czerniavsky, 1881*a*

Main references: Hatschek 1880; Purschke & Jouin 1988; Purschke 1993; Westheide 1990.

Evidence for monophyly: Paired palps with internal cavities connected behind brain (Purschke & Jouin 1988).

Protodrilids were among the taxa included in Archiannelida by Hatschek (1893). The relationship between the saccocirrids, protodrilids and protodriloidids were explored in detail by Purschke & Jouin (1988), who also demonstrated the relationship between these three families and the spiomorph families. Purschke (1993) demonstrated through a study of the innervation that the 'tentacles' of the protodrilids, protodriloidids and saccocirrids were palps. He concluded that the three families form a distinct order, Protodrilida, as a sister-group to Spionida.

Prostomium fused to peristomium as a triangular structure with peristomium forming a complete ring. Antennae absent. Paired grooved palps with distinct internal canals connected to each other within prostomium. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation present. First segment similar to other segments. All parapodial structures, including dorsal and ventral cirri, absent. Gills and epidermal papillae absent. Pygidium posteriorly furcate (pygidial cirri present). Lateral organs absent; dorsal cirrus organs not observed. Stomodaeum with distinct ventral pharyngeal organ. Gular membrane absent; gut a straight tube. Protonephridia present; separate from coelomoducts at least in some taxa (see below and Rouse and Fauchald, 1997); anterior and posterior segmental organs entirely excretory; a few anterior segments fertile. Circulatory system present; heart body absent (however, see Smith & Ruppert 1988). All chaetae absent.

The structures called lateral organs in the protodrilids are associated with sexual maturity and do not correspond structurally to the similarly named organs in other polychaetes (Westheide 1990). Both metanephridia and protonephridia have been reported to be present; the issue is explored in greater detail in Rouse & Fauchald (1997); we consider the presence of protonephridia as having been convincingly demonstrated.

PROTODRILOIDIDAE Purschke & Jouin, 1988

Main references: Jouin 1966; Purschke & Jouin 1988; Westheide 1990; Purschke 1993.

Evidence for monophyly: None known.

The protodriloidids were separated from the protodrilids on the structure of the palps. The spelling of the family name is corrected here; the stem of the generic name is Protodriloid-, to which is added the ending -idae.

Prostomium and peristomium fused to triangular structure with peristomium forming complete ring. Antennae absent. Prostomial paired grooved palps; palps without a central cavity. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation present. First segment similar to all other segments. All parapodial features absent. Gills and epidermal papillae absent. Pygidium posteriorly furcate (pygidial cirri present). Lateral organs and dorsal cirrus organs not observed. Stomodaeum with a well-developed, probably eversible, ventral buccal organ. Gular membrane absent; gut a simple tube. Metanephridia present; relationship between coelomoducts and nephridia unknown. Anterior nephridia excretory; gametes present from about segment 20. Circulatory system closed; heart body absent. Aciculae absent. Chaetae present in some taxa as distally dentate hooks; other taxa without chaetae.

Note that the polygordiids also have solid palps; polygordiids lack the posterior furcation present in the protodriloidids.

PSAMMODRILIDAE Swedmark, 1952

Main references: Swedmark 1952, 1955, 1958; Kristensen & Nørrevang 1982.

Evidence for monophyly: Multidentate, unprotected hooks with slender shafts in posterior neuropodial tori.

Swedmark first found the psammodrilids in mesopsammic environments off France; later Kristensen & Nørrevang (1982) reported another species from Greenland. Psammodrilids resemble apistobranchids in having a series of slender anterior notopodia supported by aciculae. The apistobranchids lack hooks; the psammodrilids have one or more strongly bent hooks in neuropodia in a posterior body region.

Prostomium frontally bluntly rounded. Peristomium forming two rings (Swedmark 1955). Antennae and palps absent. Nuchal organs present in one species, absent in two other species. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following segment. In 'thorax', long slender notopodia with aciculae; in the 'abdomen', barely distinguishable low neuropodial tori with uncini (Swedmark 1955,1958; Kristensen & Nørrevang 1982). Tentacular cirri absent. Dorsal cirri and ventral cirri absent. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum a simple tube with a complex muscular structure in second peristomial ring (see below). Gular membrane absent; gut a straight tube.

Nephridia metanephridia of unknown relation to coelomoducts. A single pair of nephridia present anteriorly; gametes present in the abdomen; no gonoducts observed. Circulatory system and heart body absent. Aciculae present; chaetae presumably composed of chitin impregnated with scleroprotein; however, scleroprotein cover absent in the notopodial acicula (Kristensen & Nørrevang 1982: 276–277). Only other chaetae present slender-shafted, dentate hooks without hoods or other protection.

Kristensen & Nørrevang (1982: 270, 276–277, fig. 17) pointed out that the structure of the notopodial aciculae was unusual in that they lack the covering matter usually present in polychaete chaetae and that the position of the chaetoblast is unusual.

Stomodaeum has an unusual structure not resembling any of the patterns present among other polychaetes. The buccal cavity is simple; but the second peristomial ring has massive musculature forming a pair of diaphragms at each end (Swedmark 1955, fig. 12). These diaphragms are continued as a short muscular sleeve covering the gut at each diaphragm, and the two diaphragms are linked by two large muscles, one above and one below the digestive tract. The whole structure appears to be a strongly muscular pump.

QUESTIDAE Hartman, 1966

Main references: Giere & Riser 1981; Jamieson & Webb 1984.

Evidence for monophyly: None known (see below).

The first questids were described from southern California by Hartman (1966) and from the New England region by Hobson (1971). They have also been reported from the Galapagos Islands (Westheide 1981) and the Great Barrier Reef (Jamieson & Webb 1984). The questids resemble the clitellates in the presence of clitellar material and, in having the gonads limited to a few segments. The bifid hooks resemble hooks present in certain clitellates. Giere & Riser (1981) and Jamieson & Webb (1984) demonstrated that they are gonochoristic; all clitellates are hermaphrodites. Jamieson & Webb (1984: 32–33) also found that the sperm lack the unique clitellate structures. Jamieson (1983) introduced the term Euclitellata for the taxa ordinarily grouped within the Clitellata anticipating that the latter term might have to be expanded to groups ordinarily considered in the Polychaeta since clitellar structures apparently had evolved repeatedly within the Annelida (Jamieson & Webb 1984).

Prostomium bluntly conical. Peristomium forming a ring. Antennae and palps absent. Nuchal organs present (dorso-lateral, apparently ciliated grooves in Jamieson & Webb 1984: 22). Arrangement of longitudinal muscles not documented; segmentation distinct. First segment similar to next following segment, but without parapodia and chaetae. Parapodia biramous with short, papilliform chaetal lobes. Tentacular, dorsal and ventral cirri absent. Dorsal simple paired gills present posteriorly. Epidermal papillae absent. Multiple pygidial cirri present in at least one species (Jamieson & Webb 1984, fig. 21). Lateral organs ciliated pits below notopodial chaetal bundles in posterior chaetigers (Jamieson & Webb 1984: 26, fig. 4); dorsal cirrus organs not observed. Stomodaeum eversible with a ventral buccal organ. Gular membrane absent; gut straight. Nephridia are present; structure and distribution unknown. Circulatory system closed; heart body absent. Aciculae absent. Chaetae variously ornamented capillaries and distally bidentate hooks. Hooks with short hoods (Giere & Riser 1981); a thin hood-like structure covering base of secondary tooth; but leaving distal tooth free present in *Questa ersei* Jamieson & Webb (1984, fig. 7).

Jamieson & Webb (1984: 32) discussed a series of possible autapomorphies for the family based on ultrastructure of the sperm. The peristomium is the first part of what Hobson (1971) called a biannulate first segment.

SABELLARIIDAE Johnston, 1865

Main references: Dales 1952; Wilson 1970*a*,*b*; Eckelbarger 1978; Kirtley 1994.

Evidence for monophyly: Chaetae of the first two chaetigers form opercular structure.

Sabellariids were first described as sabellids, and moved to the terebellids by Savigny (1822). Grube (1850) put them into a separate family among the limivores (sedentaries), and Levinsen (1883) gave them status as a separate suborder on line with the sabellids. More recently, the sabellariids have been considered related to the sabellids and serpulids based on the shared presence of chaetal inversion (Fitzhugh 1989). However, Dales (1963) listed them in the order Spionida and Fauchald (1977) assigned them to the Terebellida. Most sabellariids live in colonies formed by mass settlement (Wilson 1970*a*,*b*; Eckelbarger 1978).

Prostomium fused to peristomium, largely indistinct, but at least forming a median keel. Peristomium visible only as lips; mostly covered by first two chaetigers from which operculum originates. Antennae absent. Paired palps located lateral to central ridge of prostomium. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation distinct. First segment completely fused to head; notochaetae of this and next segment forming operculum. Notopodia short cylinders; neuropodia tori. Dorsal and ventral cirri absent. Gills dorsal and flattened. Epidermal papillae and pygidial cirri absent. Stomodaeum without ventral buccal organ. Gular membrane not observed; gut a straight tube. Segmental organs mixonephridia; a single anterior pair excretory, posterior ones gonoducts. Circulatory system closed; heart body absent. Aciculae absent. Chaetal inversion present: uncini notopodial rather than neuropodial; chaetae variously decorated capillaries, spines and uncini.

Dales (1952) traced the ontogenesis of the chaetae and thus demonstrated the chaetal inversion.

SABELLIDAE Malmgren, 1867

Main references: Orrhage 1980; Fitzhugh 1989; Rouse & Fitzhugh 1994.

Evidence for monophyly: Long-handled thoracic hooks; thoracic uncini with main tooth surmounted by small teeth.

Sabellids and serpulids, the two families with tentacular crowns, have been known since pre-Linnean times. The history of exploration of the family was detailed by

Fitzhugh (1989). The sabellids were originally grouped with the serpulids until Malmgren (1867) removed them; Malmgren also recognized a separate family, Eriographidae, for *Myxicola*. Later, the fabriciins and small sabellins were moved to a separate family, Amphicorinidae (e.g. Benham 1896). Finally, in this century, Hartman (1969) erected a new family, Sabellongidae for a single genus and Jones (1974) moved the morphologically highly distinct *Caobangia* into a separate family. Fitzhugh's (1989) analysis demonstrated that all these families, with the exception of the serpulids, belong to a single monophyletic group, Sabellidae.

Prostomium fused to peristomium and forming a prostomial branchial crown. Peristomium ring shaped; usually with an anterior collar and an anteriorly projecting section around terminal mouth. Anterior appendages branchial crown and extensions of dorsal lips (see below). Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following segment; but with notopodial chaetae only. Parapodia biramous; anterior notopodia cylindrical or tapering and anterior neuropodia tori; posterior notopodia tori and posterior neuropodia short cylinders. Dorsal and ventral cirri absent. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum without buccal organ. Gular membrane absent; gut a straight tube. Segmental organs mixonephridia; first pair excretory, posterior ones gonoducts. Circulatory system closed; heart body absent. Aciculae absent; chaetal inversion present. Chaetae variously modified capillaries (Fitzhugh 1989), dentate hooks without hoods and uncini.

The crown is innervated by what in other polychaetes would be the palpal nerves; the dorsal lips are more complexly innervated, but do not correspond to either antennae or palps (Orrhage 1980); thus, the branchial crown is homologous to the palps rather than to the gills of other polychaetes.

SACCOCIRRIDAE Czerniavsky, 1881*b*

Main references: Hatschek 1878, 1888 (see 1888–1891), 1893; Brown 1981; Purschke & Jouin 1988; Westheide 1990.

Evidence for monophyly: Palpal cavities joined posteriorly and caudally with ampullae (Purschke & Jouin 1988).

Hatschek (1878, 1888) proposed an evolutionary scheme for the annelids which implied that the small, achaetigerous archiannelids were the most primitive annelids currently present. He then placed *Saccocirrus* in a taxon that he called Protochaeta, as an intermediary between the archiannelids and the polychaetes. Hatschek considered the spionids to be the most primitive of the polychaetes. Hatschek's Archiannelida was accepted, but the intermediate position of *Saccocirrus* was not; it was quickly considered part of Archiannelida (Benham 1896). The saccocirrids resemble the protodrilids and protodriloidids in having frontal, prostomial palps of a rather unusual construction (Purschke & Jouin 1988). The family is widely dispersed in sandy, intertidal areas; the different species resemble each other closely.

Prostomium triangular. Peristomium a complete ring. Antennae absent. Paired ventrolaterally attached prostomial palps present; palps with internal canals connected to each other through central canal equipped with large ampullae. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation present. First segment similar to those following with similar appendages. Parapodia are uniramous, short and stubby. Dorsal and ventral cirri absent. Gills and epidermal papillae absent. Pygidium distally furcate. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with large ventral bulb at least in some taxa; anterior pharynx eversible in some taxa (Purschke & Tzetlin 1996). Gular membrane absent; gut a simple tube. Segmental organs, possibly metanephromixia, present in most segments (Goodrich 1901; Westheide 1990). Circulatory system closed; heart body absent. Aciculae absent. Chaetae all simple; distally forked, trifid or truncate. Variable number of achaetous segments present.

SCALIBREGMATIDAE Malmgren, 1867

Main references: Ashworth 1902; Kudenov & Blake 1978.

Evidence for monophyly: None known.

The scalibregmatids were first described from Scandinavia (Rathke 1843; Örsted 1843) and were originally associated with the opheliids. Ashworth (1902) explored the anatomy of *Scalibregma*; the morphology of other genera has not been studied in detail. The scalibregmatids have strongly rugose epidermis, and furcate chaetae are present in many taxa. Members of the family have two distinct body forms. They may be relatively long-bodied and only moderately inflated anteriorly (*Scalibregma*) or they may be thick and sausage-shaped (*Polyphysia*). Scalibregmatids resemble the opheliids in having each segment subdivided into two or three rings.

Prostomium truncate or T-shaped. Peristomium a ring partially subdivided into two dorsally and laterally (Ashworth 1902). Antennae absent. External palps absent, although Orrhage (1966, 1993) found palpal nerves. Nuchal organs ciliated short grooves. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following segment; with fully developed, but small, parapodia. Parapodia biramous; both rami short, conical or truncate. Tentacular, dorsal and ventral cirri absent. Gills, present in many but not all taxa, branching, associated with parapodia. Epidermal papillae absent. Multiple pygidial papillae present. Lateral organs present; dorsal cirrus organs not observed. Stomodaeum with eversible, simple axial sac. Gular membrane absent; gut a simple tube. Segmental organs mixonephridia present in many segments. Circulatory system closed; heart body absent. Aciculae absent. Chaetae variously ornamented capillaries, furcate chaetae in many taxa and, in some taxa, spines in first few chaetigers.

Ashworth (1902) described 'tentacular processes'; these are slightly extended fronto-lateral corners of the prostomium, but are not considered homologous with the antennae. Similar structures are also present in some spionids (Fauvel 1927: 26 and illustrations).

Ashworth (1902) did not believe that the posterior nephridial ducts were large enough to function as oviducts, and quoted an observation by Danielssen (1859) who reported eggs to be squeezed out intersegmentally through strong muscular contractions; this observation needs to be verified.

SERPULIDAE Johnston, 1865

Main references: Meyer 1887, 1888; Johansson 1927; Orrhage 1980.

Evidence for monophyly: Tube calcareous, formed from tube glands. Thoracic membrane present.

Serpulid tubes were in part considered molluscs and described in the mollusc literature for nearly 100 years (Mörch 1863) in addition to being described as annelids; consequently, the taxonomy is unusually tangled. Pillai (1970) segregated the spirorbins into a separate family (see also Fauchald 1977); this cannot be justified, and the spirorbins are here considered part of the Serpulidae.

Prostomium fused to peristomium; forming a branchial crown anteriorly. Peristomium forming a ring with a partial anterior collar. Antennae absent. Branchial crown homologous to palps of other polychaetes; emerging in juveniles from prostomial region. Nuchal organs present (see below). Longitudinal muscles grouped in bundles; segmentation present. First segment similar to next following segments; but with notopodial chaetae only. Variably developed thoracic membrane present. Thoracic notopodia short, truncate cylinders and thoracic neuropodia tori; in abdomen notopodia tori and neuropodia short cylinders. Dorsal and ventral cirri, gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum without ventral buccal organ. Gular membrane absent; gut a straight tube. Segmental organs mixonephridia; first pair excretory, posterior ones gonoducts. Circulatory system closed; heart body absent. Aciculae absent; chaetal inversion present. Chaetae variously ornamented capillaries and uncini.

Orrhage (1980: 123–124) reported that the mid-dorsal part of the dorsal pit had epithelium and innervation characteristics of nuchal organs. Dales (1962, fig. 17) listed the serpulids among those polychaetes in which the ventral buccal organ had been secondarily lost.

SIGALIONIDAE Malmgren, 1867

Main references: Ehlers 1864; Pettibone 1969*a*, 1970*a*,*b*,*c*, 1971; Mackie & Chambers 1990.

Evidence for monophyly: None known.

The first sigalionids were described by Audouin & Milne Edwards (1832). Sigalionidae and Pholoidae are the only two families of scale-worms with compound chaetae. Sigalionids have been recognized as a distinct group of scale-worms since they were first described; the family was reviewed in part in the series of papers by Pettibone cited above. Internal structures were explored by Ehlers (1864).

Prostomium frontally blunt or rounded. Peristomium limited to lips. Paired lateral and a median antenna present in most taxa; median antenna may be missing (Mackie & Chambers 1990). Lateral antennae either located on prostomium or fused to first parapodia. Palps ventral, tapering; without articulations; fused basally to parapodia of first segment. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation distinct. First segment curving around head; fused basally to prostomium; with biramous parapodia; two pairs of tentacular cirri present. Parapodia biramous with neuropodia longer than notopodia. Dorsal and ventral cirri present. Dorsal cirri alternate with elytrae in anterior end. Some taxa with tapering dorsal cirrus in segment 3; others with neither elytrae nor dorsal cirri in segment 3. Elytrae present on every segment in posterior end. Gills absent. Epidermal papillae absent. One pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae present; two pairs of dorsoventrally oriented jaws present. Gular membrane absent; gut with segmentally arranged side branches. Segmental organs mixonephridia present in most segments. Circulatory system closed; heart body absent. Aciculae present. Appendages of compound chaetae distally tapering to fine tips, distally dentate or falcate; shafts and appendages joined by single ligaments. Other chaetae variously ornamented capillaries.

Slender, digitiform extensions from the body wall projecting under the elytrae are present in many taxa; these have presumably a respiratory function.

SPHAERODORIDAE Malmgren, 1867

Main references: Ruderman 1911; Reimers 1933; Fauchald 1974*b*.

Evidence of monophyly: Inflated capsules (dorsal cirri) and tubercles present in two or more rows on dorsum.

The first species described were among the long-bodied species (Örsted 1843). However, most sphaerodorids are short-bodied, maggot-like, inflated and densely covered with papillae of varying sizes, making them resemble syllids of the genus *Sphaerosyllis*. Lützen (1961) pointed out a confusion in the use of one of the generic names and corrected the error. Hartman & Fauchald (1971) and Fauchald (1974b) described several new taxa. The systematic history was reviewed by Fauchald (1974*b*).

Prostomium distinct in the long-bodied taxa; fused to peristomium in many short-bodied taxa. Peristomium limited to lips. Paired lateral and a median antenna present. Ventral pair of frontal appendages unarticulated ventral palps. Nuchal organs present. Longitudinal muscles grouped in bundles; segmentation present. First segment indistinct; with tentacular cirri only. Parapodia with well-developed neuropodia; notopodia possibly represented by large capsules (see below). Ventral cirri present. Gills absent. Most sphaeodorids densely studded with papillae; papillae inflated; usually with retractable distal end, and distinctly different from flabelligerid papillae. A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with axial, muscular eversible pharynx; terminal papillae present; jaws absent; muscular proventricle present. Gular membrane absent; gut spiralled, but essentially a straight tube. Nephridia metanephridia; possibly mixonephridia (Goodrich 1945). Segmental organs including either one or three pairs (see below). Circulatory system absent or reduced; heart body absent. Aciculae present. Chaetae compound falcigers and variously ornamented capillaries and, in some taxa anterior, curved spines. Appendages of compound chaetae falcate; single ligaments join shafts and appendages.

The large capsules were called 'macrotubercles' by Fauchald (1974b). Both Ruderman (1911) and Reimers (1933) called these structures dorsal cirri; however, morphological similarities and differences must be explored to verify this homology statement. The structure of the nephridia is poorly known and has been studied only in two species (Ruderman 1911; Reimers 1933). Better documentation is needed to show the relationship between nephridia and coelomoducts.

SPINTHERIDAE Johnston, 1865

Main references: Hartman 1948; Manton 1967.

Evidence for monophyly: Notopodia forming long transverse ridges; prostomium a small rounded structure located well behind the frontal margin (Fauchald 1977, fig. 28e).

The spintherids are flattened, ovate ectoparasites on sponges. They are often considered related the amphinomids and euphrosinids (Fauvel 1923; Hartmann-Schröder 1971) or as a distinct order (Dales 1963; Fauchald 1977). In dorsal view, the notopodial ridges with their dense mass of short spines and the small, rounded prostomium located well behind the front margin of the worm are highly characteristic. The mouth is located well behind the front margin as well. Sharov (1966) considered them ancestral to the arthropods, provoking Manton (1967) to review their external and internal features in what remains the most detailed study of the morphology of the family.

Prostomium partially emerging dorsally as a distinct, rounded papilla. Peristomium limited to lips. Median antenna present; other antennae and palps absent. Nuchal organs absent (Racovitza 1896). Arrangement of longitudinal muscles not documented; segmentation present. First segment completely fused in front of prostomium, similar to those present in amphinomids and, especially in euphrosinids. All parapodia biramous, notopodia long ridges crossing dorsum; neuropodia short and truncate. Tentacular and dorsal cirri absent; ventral cirri present in some taxa. Gills and epidermal papillae absent A single pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with a ventral pharynx; without heavy ventral musculature present in amphinomids (Manton 1967); retractable rather than inverted. Gular membrane absent; gut branching throughout body. Nephridial, reproductive and circulatory systems unknown. Slender, tapering multiple aciculae present. Appendages and shafts of compound chaetae joined by folds; appendages distally falcate. Capillary chaetae absent; notopodial chaetae all spines.

SPIONIDAE Grube, 1850

Main references: Foster 1971; Blake & Kudenov 1978; Sigvaldadóttir *et al.* 1997.

Evidence of monophyly: Noto- and neuropodia with foliose postchaetal lobes; prostomium with posterior prolongation with first segment folded around the prostomium.

Additional evidence of monophyly will undoubtedly emerge as the family is further studied; reviews (Foster 1971; Blake & Kudenov 1978) have removed a number of old problems, and a recent cladistic analysis (Sigvaldadóttir *et al.* 1997) has started to clarify relations among the genera. Spionids are among the most familiar of polychaetes; they are present in all environments and are often both species-rich and abundant.

Prostomium frontally truncate (sometimes with lateral 'horns'), rounded or pointed. Peristomium more or less limited to lips; partially folded up around prostomium. A median antenna present in some taxa. Paired dorsal grooved peristomially inserted palps present. Nuchal organs ciliated crests on either side of posterior prolongation of prostomium. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following one; anteriorly folded around posterior prolongation of prostomium; with biramous parapodia in most taxa; first notopodia missing in some taxa. Parapodia biramous; both notopodial and neuropodial chaetal lobes low, transverse ridges or low mounds, backed by flattened, postchaetal lobes at least anteriorly. Dorsal and ventral cirri absent. Gills, when present, flattened and dorsal, sometimes fused laterally to notopodial postchaetal lobes. Epidermal papillae absent. Pygidium variously ornamented including flattened lobes or many cirri; plesiomorphic condition apparently one median ventral cirrus and a varying number of lateral pairs (Foster 1971). Lateral organs present; dorsal cirrus organs not observed. Stomodaeum a ventral buccal organ or an axial sac-like pharynx (see below). Gular membrane absent; gut a straight tube. Nephridia metanephridia; relation to coelomoducts unresolved. Anterior segmental organs excretory, posterior ones gonoducts. Circulatory system closed; heart body absent. Aciculae absent. Chaetae variously ornamented capillaries and distally dentate, protected or unprotected hooks.

The nuchal organs have been assumed to continue as dorsal organs in some taxa (Söderström 1920,1930); however, Schlötzer-Schrehardt (1991) demonstrated that at least in one species, *Pygospio elegans*, the dorsal organs are structurally completely different and lack the innervation associated with nuchal organs; since they were present only in males, she suggested that they functioned in transportation of spermatophores. The plesiomorphic structure for the pharynx is uncertain; it may be a ventral buccal organ or an axial sac-like pharynx (Dales 1962,1963,1977; Orrhage 1973).

STERNASPIDAE Carus, 1863

Main references: Vejdovsky 1882; Goodrich 1898.

Evidence for monophyly: Posterior end covered ventrally by a cuticularized shield.

The sternaspids were initially considered related to the echiurids (Blainville 1828) and were included in the Gephyrea armata (Quatrefages 1866, see Appendix B). The sternaspids have been considered difficult to relate to other polychaetes; some scientists have considered them as an 'isolated group', but most often they have been compared tentatively to other polychaetes with minimal anterior appendages and simple, capillary chaetae and spines. Levinsen (1883) considered them a separate order. Hatschek (1893) listed them as an appendix to the drilomorph families, and Benham (1896) treated them as one of the scolecimorph families. More recently, they have been considered a member of the Drilomorpha (Uschakov 1955) and as a separate order (Dales 1963; Fauchald 1977; George in George & Hartmann-Schröder 1985).

Prostomium distinct and frontally truncate; peristomium limited to lips. Antennae and palps absent. Nuchal organs absent (but see Dahl 1955). Longitudinal muscles grouped in many bands; segmentation present. First segment similar to next following ones; with similar chaetae. Whole anterior body retractable. Posterior ventrum covered with a sclerotinized shield covering several segments. Parapodia biramous except in posterior end; only notopodia present in region covered by shield. All biramous parapodia with both rami short, barely raised papillae; notopodia associated with ventral posterior shield very short, truncate cylinders. Dorsal and ventral cirri absent. Gills posterior, dorsal and simple. Epidermal papillae similar to flabelligerid papillae present. Pygidial cirri absent. Stomodaeum with eversible axial sac-like proboscis. Gular membrane absent; gut folded. Segmental organs mixonephridia; anteriormost pair is excretory; posterior pair gonoducts (Goodrich 1945). Circulatory system closed; heart body absent. Aciculae absent. Chaetae capillaries and heavy spines.

SYLLIDAE Grube, 1850

Main references: Malaquin 1893; Fauvel 1923; Garwood 1991.

Evidence of monophyly: Proventricle with radiating muscle fibers present.

The proventricle consisting of a muscular section of the anterior digestive tract with radiating muscle fibers preceded by an eversible buccal tube is usually considered an autapomorphy for this family (Glasby 1993: 1559); as mentioned above, the pontodorids and sphaerodorids also have a proventricle, but without the characteristic muscle arrangement.

Syllids were first included among the nereidids and have always been considered related to the nereidids and hesionids (e.g. Fauvel 1923; Fauchald 1977; Pettibone 1982). Sexually immature individuals have uniramous parapodia; notopodia develop in many but not all members of the family at maturity.

Prostomium usually frontally truncate. Peristomium limited to lips. A pair of lateral and a median antenna present. Palps ventral, tapering and unarticulated; often more or less fused to each other medially. Nuchal organs present, most usually as short ciliated grooves; as nuchal epaulettes in some taxa. Longitudinal muscles grouped in bundles; segmentation distinct. First segment similar to next following one; with two pairs of tentacular cirri only (see below). Parapodia biramous; in atokous forms notopodia represented by dorsal cirri only; in some epitokes, notopodia large and chaetiferous. Neuropodia always better developed than notopodia; distally triangular or truncate. Dorsal and ventral cirri present in most taxa; ventral cirri absent in one subfamily (Autolytinae). Gills absent. Epidermal papillae of flabelligerid construction absent. A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum an axial eversible muscular structure; terminal papillae present; a median dorsal tooth present in many taxa; muscular proventricle present. Front edge of eversible pharynx with a sclerotinized, dentate crown (trepan) in some taxa. Gular membrane absent; gut tubular. Segmental organs metanephromixia present in most segments. Circulatory system closed; heart body absent. Aciculae present. Appendages of compound chaetae distally dentate or tapering to slender tips; joined to shafts by single filaments. Other chaetae variously ornamented capillaries.

The tentacular cirri were considered peristomial cirri by Glasby (1993).

TEREBELLIDAE Malmgren, 1867

Main references: Hessle 1917; Heimler 1983; Holthe 1986.

Evidence for monophyly: Multiple grooved palps of prostomial origin (Heimler 1983).

Terebellidae is a species-rich family divided into four subfamilies, Amphitritinae, Thelepodinae, Polycirrinae and Artacaminae; a fifth taxon, Trichobranchidae was originally also considered a terebellid subfamily but is now usually considered a separate family. This may create problems in making Teebellidae paraphyletic. The first terebellids were described by Müller (1776); the family was recognized early, with family names based on the generic name *Amphitrite*; the ampharetids and pectinariids were originally named in the family, but were removed by Malmgren (1867). While most terebellids have uncini, members of two genera, *Biremis* and *Hauchiella* lack chaetae, but other features connect them to the terebellids.

Prostomium reduced and fused along frontal edge with peristomium. Peristomium also fused to anterior segments; projecting forwards underneath prostomium as an extended upper lip. Antennae absent. Palps emerging at edge of prostomium where it fuses to peristomium, usually present as numerous tentacles. Nuchal organs present in some, but not all taxa. Longitudinal muscles grouped in bands; segmentation distinct. First segment fused to head; without parapodia and chaetae. Parapodia biramous; notopodia slender, truncate or tapering cylinders, usually present only in first half of body; neuropodia tori. Tentacular, dorsal and ventral cirri absent. Gills dorsal; present only on a few anterior chaetigers; most frequently stalked and branching; sessile filaments in Thelepodinae; absent in Polycirrinae. Epidermal papillae absent. Pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with a non-eversible ventral buccal organ (Sutton 1957). Gular membrane present; gut a straight tube in some taxa, looped in others. Segmental organs mixonephridia; anterior ones excretory; posterior ones gonoducts (but see Smith 1988 for another opinion; see also Rouse and Fauchald 1997, for further discussion). Circulatory system closed; heart body present. Aciculae absent. Chaetae variously ornamented capillaries and uncini rarely absent.

TOMOPTERIDAE Johnston, 1865

Main references: Fauvel 1923; Åkesson 1962.

Evidence for monophyly: Only chaetae are aciculae in the first and second segment (of which only the second segment is present in adults).

Grube (1850) erected a separate class, Gymnocopa, for the tomopterids. The absence of chaetae other than the aciculae of the first and second segment and the elongated parapodia with paired distal flattened parapodial rami makes the tomopterids easily recognizable, but not easily compared to other polychaetes. They are usually placed in the vicinity of the phyllodocids (Uschakov 1955). George in George & Hartmann-Schröder (1985) named a superfamily, Tomopteroidea, within the Phyllodocida for the tomopterids. Fauchald (1977) listed the family as a member of the Phyllodocida, but declined to place them closer in relation to the other families in the order.

Prostomium fused to peristomium. Peristomium limited to lips. Antennae absent. Palps ventral; without articulations. Nuchal organs a pair of dorsal crests. Arrangement of longitudinal muscles undocumented; segmentation distinct. Second segment and its cirri first visible parapodial structures of adults. Noto- and neuropodia oar-shaped pinnae. Dorsal and ventral cirri absent. Gills, epidermal papillae and pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an axial, strongly muscularized eversible proboscis; without terminal papillae or jaws. Gular membrane absent; gut a straight tube. Segmental organs protonephromixia present in most segments. Circulatory system and heart body absent. Only chaetal structures present aciculae of second segment; all other chaetae absent.

The palps were called prostomial tentacles by Uschakov (1955) and divergent antennae by Day (1967). Åkesson (1962) demonstrated that the 'tentacular cirri' of the tomopterids are parapodial rudiments of the two first segments; during larval development, the first segment is no smaller than the other segments, but is subsequently reduced and finally incorporated into the head.

TRICHOBRANCHIDAE Malmgren, 1866

Main references: Hessle 1917; Holthe 1986.

Evidence for monophyly: First neurochaetae curved or bent spines.

Members of the genus *Terebellides* are present in shallow water soft benthos in all environments; a series of species has been described, but has been synonymized, based on descriptions only, with one of the earliest described species, e.g. *T. stroemi* Sars 1835; when careful examinations are made, many species have become reinstated, and others have been newly recognized (Williams 1984; Solis-Weiss *et al.* 1991). The trichobranchids have been segregated as a subfamily (often under the name Canephorinae, based on an invalid generic name) or a family closely related to the terebellids. The trichobranchids is a uniform, probably monophyletic group; recognition of the family may create problems in keeping Terebellidae monophyletic.

Prostomium and peristomium fused along anterior edge. Peristomium forming extended lips, upper lip similar to terebellid structure. Antennae absent. Palps represented by multiple buccal tentacles, i.e. multiple grooved prostomial palps emerging from prostomial edge. Nuchal organs present in *Trichobranchus*; absent in *Terebellides*; unknown for other genera. Arrangement of longitudinal muscles undocumented; segmentation distinct. First segment fused to head; without parapodia and chaetae. Parapodia biramous; notopodia, present only in anterior chaetigers, tapering or truncate cylinders; neuropodia tori. Dorsal and ventral cirri absent. Gills dorsal; as two to three groups of single filaments on anterior segments (segments 2, 3 and 4); or a single large gill bearing four lamellate lobes. Epidermal papillae absent. Pygidial cirri absent. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with a non-eversible ventral buccal organ. Gular membrane present; gut looped. Nephridia metanephridia; relation to coelomoducts not documented. Anterior most pair of segmental organs excretory; posterior ones presumably gonoducts. Circulatory system closed; heart body apparently present (Wirén 1885). Aciculae absent. Other chaetae variously ornamented capillaries and uncini. Neuropodial bent spines present in one anterior segment.

TROCHOCHAETIDAE Pettibone, 1963

Main references: Pettibone 1963, 1976; Mackie 1990, 1996.

Evidence for monophyly: Uniramous parapodia (notopodia missing) in a series of segments in midbody (Orrhage 1964).

Mackie (1996) reviewed the history of description of the trochochaetids. The current family name replaces Disomidae Mesnil 1897, based on *Disoma* Örsted 1843; the name *Disoma* had already been used for a protozoan. Levinsen (1883) proposed the generic name *Trochochaeta*. The family contains a single genus; all trochochaetids live in soft substrates in tubes.

Prostomium frontally rounded or blunt. Peristomium limited to lips. Median antenna present in some taxa, absent in others. Paired grooved peristomial palps present. Nuchal organs ciliated grooves on both sides of the posterior prolongation. Longitudinal muscles grouped in bundles; segmentation present. First segment similar to next segment with biramous parapodia projecting anteriorly. Parapodia biramous; notopodia and neuropodia low, transverse ridges or mounds backed by postchaetal lobes of various shapes, but including finger-shaped or flask-shaped kinds and in part flattened structures. Tentacular, dorsal and ventral cirri absent. Gills absent. Pygidial cirri reported absent (but see Pettibone 1963: 314). Lateral organs present; dorsal cirrus organs not observed. Stomodaeum a simple axial sac (Purschke & Tzetlin 1996); without a ventral buccal organ (Orrhage 1966). Presence of gular membrane and structure of gut undocumented. Nephridia metanephridia; relation between nephridia and coelomoducts undocumented. Anterior segmental organs presumably excretory; posterior ones gonoducts (see below). Circulatory system and heart body undocumented. Aciculae absent. Chaetae variously ornamented capillaries, aristate chaetae and spines.

The discussion in Orrhage (1964) implies that the distribution of segmental organs is similar to that in other spiomorphs with excretory function in anterior chaetigers and gonoducts in more posterior chaetigers.

TYPHLOSCOLECIDAE Uljanin, 1878

Main references: Greeff 1879; Uschakov 1972.

Evidence for monophyly: Forwardly directed foliose tentacular cirri wrapped around prostomium laterally. Dorsally located retort organ present in the eversible pharynx.

Typhloscolecids were first described in the second half of last century. They are usually considered a distinct family within Phyllodocida (Uschakov 1955; Dales 1963). Fauchald (1977) listed the family as a member of the Phyllodocida, but was unable to relate them to any of the super-families of his order Phyllodocida. George in George & Hartmann-Schröder (1985) placed the family in a separate superfamily, Typhloscolecoidea within Phyllodocida. The typhloscolecids are spindle-shaped and pelagic with foliose, easily dehiscent parapodial lobes.

Prostomium frontally usually sharply pointed. Peristomium limited to lips. Two of three genera with a median antenna (called a dorsal caruncle by Day 1967). Palps absent. Nuchal organs dorsal crests. Arrangement of longitudinal muscles undocumented; segmentation present. First segment indistinct; with two pairs of foliaceous tentacular cirri. A total of four pairs of tentacular cirri present. Parapodia biramous; neuropodia better developed than notopodia. Dorsal and ventral cirri present. Gills and epidermal papillae absent. A pair of pygidial cirri present. Lateral organs and dorsal cirrus organs not observed. Stomodaeum with an axial muscular eversible proboscis; terminal papillae not observed; jaws absent. Retort organ present in dorsal wall of pharynx (Greeff 1879). Presence of gular membrane and structure of gut undocumented. Nephridia protonephridia; relation between nephridia and coelomoducts and distribution of segmental organs unknown. Circulatory system reduced; heart body not documented. Aciculae present. All chaetae variously ornamented capillaries and spines.

UNCISPIONIDAE Green, 1982

Main reference: Green 1982

Evidence for monophyly: Very large, strongly curved hooks in some chaetigers (illustration in Green 1982).

The family was described from southern California by Green (1982). Previously Fauchald & Hancock (1981) described another taxon, *Uncopherusa bifida*, from deep water off Oregon with similar hooks; Green moved this taxon into her new family.

The uncispionids resemble the spioniform taxa in many features. Sigvaldadóttir *et al.* (in press) in an analysis of spionid genera, found that recognition of the uncispionids might make Spionidae paraphyletic; they, however, did not suggest synonymizing the two families due to the generally weak support for clades in their analysis.

Prostomium anteriorly truncate. Peristomium limited to lips. A median antenna present. Peristomial palps paired, grooved and emerging dorsally. Nuchal organs not observed. Arrangement of longitudinal muscles undocumented; segmentation distinct. First segment similar to next following segment; with biramous parapodia. Parapodia biramous, both notopodial and neuropodial acicular lobes low, ridge or mound like; backed by foliose postchaetal lobes. Tentacular, dorsal and ventral cirri absent. Gills dorsal, simple and paired. Structure of epidermal papillae unknown. Two pairs of pygidial cirri present. Lateral organs and dorsal cirrus organs have not been observed. Stomodaeum with an eversible axial sac. Presence of gular membrane and structure of gut undocumented. Nephridial, reproductive and circulatory systems unknown. Aciculae absent. Chaetae variously ornamented capillaries and dentate, unprotected hooks. Chaetae of first segment somewhat longer than those of the next following chaetigers.

Families not considered

Families are missing from the above review for the following reasons. We may have accepted a recently proposed synonymy, or alternatively, the family is so poorly understood that even major morphological features (prostomium, parapodia, etc.) are difficult to interpret in standardized terms, or a proposed family cannot be clearly distinguished from other families.

Recent synonymies:

Antonbruunidae Fauchald, 1977 to Pilargidae by Glasby (1993).

Calamyzidae Hartmann-Schröder, 1971 to Syllidae by Glasby (1993).

Caobangiidae Jones 1974 to Sabellidae by Fitzhugh (1989).

Dinophilidae Remane, 1932 and Iphitimidae Fauchald 1970 to Dorvilleidae by Eibye-Jacobsen & Kristensen (1994).

Helmetophoridae Hartman 1978 to Flabelligeridae by Glasby & Fauchald (1991).

Levidoridae Perkins 1987 to Syllidae by Glasby (1993).

Other synonymies have been proposed, but are not accepted mostly due to problems with the analyses. We expect that as more detailed analyses are performed, many additional families will fall by the wayside; we have suggested some likely clusters in the overview of the taxa above.

Poorly known or poorly understood families

Archinomidae Kudenov 1991 was described to contain the genus *Archinome* Kudenov, 1991. The single species in this genus, *A. rosacea* (Blake 1985) was originally described in *Euphrosine* (Euphrosinidae). The species show features characteristic both of the euphrosinids and the closely related amphinomids; as suggested above, the relationship between these two families is uncertain and should be closely studied. The species mentioned here would be covered by the characterization of the amphinomids given above.

Euniphysidae Shen & Wu, 1988 may be a synonym of Eunicidae, but this synonymy has yet to be formally proposed. *Euniphysa*, as currently recognized, appears to make the genus *Eunice* paraphyletic (Lu & Fauchald, in prep.). The characterization of Eunicidae given above will include Euniphysidae as well; until the variability of major morphological features among the eunicids has been studied, the status of the euniphysids must be considered unsettled.

Laetmonectidae Buzhinskaya, 1986 was based on material collected in the northwestern part of the Indian Ocean. The single genus and species, *Laetmonecticus nigrum*, as noted by Buzhinskaya (1986), superficially resembles a terebellid without the uncini usually present in that family. Some terebellid genera are known to lack uncini (*Hauchiella*, *Biremis*) and indeed lack chaetae completely, so the absence of uncini is not *per se* a reason for excluding the genus from membership in the family Terebellidae. There are several very unusual features described by Buzhinskaya, making comparison with other taxa difficult without a detailed examination of well preserved material.

Pseudocirratulidae Petersen, 1994 is based on *Pseudocirratulus kingstonensis* Augener, 1924 from Jamaica. The family was named in a published abstract (Petersen 1994) after a study of Augener's types. The information presented in both Augener (1924) and Petersen (1994) is insufficient to detail most major morphological features.

Yndolaciidae Støp-Bowitz, 1987 was found in pelagic material from tropical Africa. Interpretation of the anterior end is difficult without a detailed analysis of well-preserved material.

Fossil polychaetes

Polychaetes lack most of the resistant structures present in organisms with an extensive fossil record. Polychaete jaws (scolecodonts) are common in deposits from certain periods (Robison 1987). Various kinds of tube- and burrow-structures have been referred to polychaetes (Howell 1962), but are far less diagnostic than are chaetae or jaws. Full-body fossils are rarer, but for example, those present in the Burgess Shales and Mazon Creek beds have demonstrated that polychaetes and polychaete-like organisms were well-represented in Paleozoic seas (Conway Morris 1979; Thompson 1979). This overview is not intended to be a complete review of the literature on fossil polychaetes; its purpose is to point out a few of the major findings and problems associated with identifying essentially soft-bodied organisms in the fossil record.

Allying any specimen, fossil or recent, with a described taxon must depend on recognizing features in the specimen uniquely linking it to that taxon. Many recent invertebrate clades are supported by soft-body autapomorphies which cannot reasonably be observed in a fossil specimen. Characteristic structures such as jaws, or in whole body fossils, bundles of chaetae segmentally arranged, have been found starting in mid-Paleozoic, and, as a consequence, several taxa have been described and linked to recent taxa.

The main point of the following overview is to record the earliest known fossils for major groups.

Several pre-Cambrian (Ediacran) fossils have been assigned to the polychaetes (e.g. Glaessner 1976*a*, 1976*b*, 1979). Certainly, some of these fossils might belong to a polychaete clade, but additional documentation is needed to resolve controversial findings. One of the best known, *Spriggina*, has been demonstrated to be an arthropod (Conway Morris 1991: 20; see also Bergström 1991: 27).

Lower-Cambrian sites in China have yielded several worm-like animals, one of which has been considered a polychaete; *Facivermis yunnanicus* has been compared to nereidid polychaetes (Hou & Chen 1989; Chen & Erdtmann 1991; Delle Cave & Simonetta 1991, fig. 33c). The reconstruction shows a slender worm with many segments and a wholly undifferentiated head; paired slender appendages are present along the body. Without demonstrated presence of at least one of the characteristic features of a nereidid (e.g. chaetae, jaws, paragnaths, head-structures), the presence of this family or even of polychaetes in Lower-Cambrian fossils cannot be accepted based on this record.

Conway Morris & Peel (1995), while describing full body fossils of a new halkieriid, demonstrated similarities between lower-Cambrian halkieriids from Greenland and *Wiwaxia* from the middle-Cambrian Burgess shales, and suggested that the latter might be a sister-taxon to the Polychaeta. *Wiwaxia* has been interpreted as a chrysopetalid-like polychaete (Butterfield 1990); the position of this genus has yet to be fully clarified, but it has several very chrysopetalid-like traits. However, *Canadia* and *Burgessochaeta* from Middle-Cambrian of Canada both have prostomium-like anterior ends; they are segmented with many apparently similar segments and have obvious tufts of chaetae along the body; they have been interpreted as polychaetes (e.g. Conway Morris 1979; Butterfield 1990). Both genera are similar to the Phyllodocida *sensu* Fauchald (1977). Thus, certainly by Middle-Cambrian, at least one of the major polychaete groups was present.

Scolecodonts are jaw pieces of euniceans (Ehlers 1868b), glycerids, goniadids and, possibly, nereidids (Howell 1962). They are present in various deposits at least from mid-Paleozoic, and are especially well known from the Ordovician and Silurian strata. Kielan-Jaworowska (1966) and Bergman (1989) gave good overviews of the literature. Orensanz (1990) related fossil euniceans to recent taxa at the family level. Eunicean genera are characterized mainly by soft structures, so further incorporation of the fossils must await better analysis of whole-body fossils when, or if, they become available.

Whole-body fossils of Devonian age were described by Thompson (1979). Recent families reported included Aphroditidae, Phyllodocidae, Hesionidae, Nephtyidae and Goniadidae, increasing the representation of the Phyllodocida (*sensu* Fauchald 1977) to include members of most major sub-groups. Thompson (1979) introduced an additional family, Fossundecimidae, which she assigned to the Phyllodocida and newly described an amphinomid extending the record of this family to the Devonian. Most of Thompson's evidence lies in a comparison of the body outlines present in the fossils with body outlines of recent polychaetes. While the body-outlines of the fossils certainly resemble outlines in the taxa to which they have been assigned, characteristic features of most of these families were not documented. The outlines themselves are not sufficiently unique to allow positive identification. These records must be considered dubious until the appropriate characters have been reported. The families Opheliidae and Flabelligeridae were also listed for the Devonian fauna by Thompson (1979) in a table; details of the records of these families remain unpublished.

Tubes and burrows assigned to polychaetes including serpulid tubes have been reported from the Paleozoic (Howell 1962). While many of these tubes may belong to the polychaetes, without confirmatory evidence of features unique to polychaetes, many remain doubtful.

Even this cursory survey shows that many and diverse polychaete groups were present before the end of the Paleozoic and that at least some of them go back well into middle Cambrian.

Fossil taxa cannot easily be incorporated in polychaete systematic schemes. Most fossils are too poorly preserved to allow characterization of many structures used in polychaete systematics. Not only are details of chaetal structures usually unavailable, but also relatively large structures, such as the shape of parapodial lobes, are difficult to observe, even in well-fossilized material (see illustrations in Thompson 1979). Recently, Orensanz (1990) included fossil taxa in his systematic treatment of the eunicemorphs. At the family level, he could group the fossil and recent families since the jaws are often used to characterize families in this group and fossilize well. However, even in this group, the number of characters that can be extracted from the fossils is small, and a phylogenetic analysis will be difficult for that reason. The fossil taxa may perhaps better be appended to an analysis developed on recent taxa.

Discussion

The morphology of the major polychaete families was described in large part in a series of taxon-oriented studies done in the middle of last century (e.g. Ehlers 1864, 1868*a*; Claparède 1868, 1870; Malaquin 1893; Darboux 1899) and during the first few decades of this century (e.g. Hessle 1917; Reimers 1933). A few major studies have been comparative (e.g. Meyer 1887, 1888; Racovitza 1896; Hanström 1928, 1929), and recently, the anterior nervous system of a great variety of polychaetes has been the subject of a series of studies by Orrhage (citations can be found in the References). At the ultramicroscopic level, Purschke has studied the ventral buccal organs in a variety of small-bodied taxa and demonstrated the variety of differences in structure present (see References for citations).

In early systematic schemes, two major polychaete taxa, Errantia and Sedentaria (Grube's Rapacia and Limivora, or Hatschek's Cirrophora and Acirra, or Benham's Gymnocephala and Cryptocephala) were recognized. The errants and sedentaries were originally recognized (e.g. Audouin & Milne Edwards 1834) before the class Polychaeta had been defined and thus the relationship between them acknowledged (Grube 1850). 'Errantia' and 'Sedentaria' were still used, especially in handbooks and general texts up to very recently (Hartmann-Schröder 1971, but see Hartmann-Schröder 1982; Barnes 1987, but see Ruppert & Barnes 1994 and Brusca & Brusca 1990; Appendix II). The presence of body-regions (Blainville 1825; Quatrefages 1865) is characteristic of certain 'sedentaries' (e.g. terebellids, serpulids), but other polychaetes also considered 'sedentaries' show little or no signs of tagmatization (the presence of body-regions; e.g. maldanids, scalibregmatids, cirratulids). Quatrefages' (1866, Appendix II) treatment of the spionids demonstrates the problems in using tagmatization as a character: Quatrefages listed most spionids among the 'errants'; those with modified segment 5 were assigned to the 'sedentaries'. The treatment of the orbiniids (as *Aricia* or as a family name based on that generic name) is another case in point. They were moved from 'errants' to 'sedentaries' and back in publications from the second half of the 19th century; since about 1890, they have consistently been considered 'sedentaries'. To complicate the problem even further, members of some 'errant' families, such as the onuphids, show distinct 'tagmatization', but are so obviously related to families that lack such separation (eunicids) in every other morphological feature that they have consistently been ranked among the 'errants.'

Grube (1850: 277) did not consider any morphological feature to be unique to one or the other of his 'suborders' and preferred for that reason to use the food uptake as the basic principle behind his classification. The Rapacia were supposed to be carnivores (Raubanneliden to use Grube's term) and the Limivora (Schlammfresser) feeding on detritus embedded in sand and mud. Grube (1850: 276–279) listed a series of morphological correlates, including among others, the attachment of the gut (loose in the body-cavity among the limivores, attached by mesenteries in the rapacians), the presence or absence of an eversible pharynx, the presence or absence of parapodial cirri, the presence or absence of compound chaetae, hooks and uncini.

Hatschek (1888, 1893) based his separation on the presence (Cirrophora) or absence (Acirra) of parapodial cirri, especially dorsal cirri. The presence of dorsal cirri characterizes a large group (essentially the 'Errantia'), but there is little that keeps the Acirra together except for the lack of cirri. Hatschek's scheme had an additional problem. Because he proposed a phylogenetic systematic scheme based on *a priori* assumptions (discussed below), he had to propose that the spionids and similar taxa had dorsal cirri; this has been found to be incorrect. Other, lower level groups proposed by Hatschek have been accepted, often in a setting completely different from the one in which they were originally proposed. Benham's (1896) proposed system has a somewhat similar basic problem: one of his groups, Cryptocephala, including as it does the sabellids, serpulids and sabellariids, contains taxa resembling each other in many features, but the other, Gymnocephala, does not.

In summary then, the separation of Polychaeta into two has been attempted repeatedly, but as delineated, none of the proposed taxa is adequate. Other characters might stabilize such a separation, but after more than 100years of searching, a two-group system has yet to be adequately characterized.

In this century, a group of scientists, not recognizing this primary split, have increased the number of primary groups without diagnosing relations among them (Dales 1963; Fauchald 1977; Appendix II; see also Pettibone 1982). Hartman (1968, 1969) belonged to this camp in that she could see no organizing features grouping the families into larger groups beyond what she considered obvious (e.g. euniceans and scale-worms). These authors often listed their orders in a sequence roughly reflecting their ideas of relationship among the taxa, but did not expressly relate them to each other. For example, Dales (1963), in a series of diagrams, suggested a relationship among the taxa, but did not link these organized units into a cohesive diagram; note that the diagrams are not consistent with his printed classification (see also Dales 1977); in Fauchald (1977), the suggested classification is easiest scanned in his table 1.

The sub-groups proposed by Hatschek (1893; Appendix II), below the levels of his Cirrifera and Acirra, have been accepted in part, or completely by many authors (Benham 1896; Hartmann-Schröder 1971; Dales 1963; Fauchald 1977; George in George & Hartmann-Schröder 1985 and under different names by Uschakov 1955). Fauvel (1923,1927) did not apply any intermediate taxa between Errantia and Sedentaria on one hand and the families on the other hand. Hartman (1968, 1969) accepted no intermediate taxa between Polychaeta and the families; even the scale-worm families and the eunicean families were listed separately, without a formal indication of a relationship between them (Hartman 1968: 3 referred to the superfamily Eunicea in a discussion of size of individuals). Parenthetically, Hartman divided the California Atlas into two, following the traditional lines, not because she accepted this classification, but because it divided what otherwise would have been a completely unwieldy volume into two roughly equal halves (O. Hartman, pers. commun. to K.F).

We are now in the situation that Polychaeta may be considered, for example, as a class with two subclasses with seven or eight orders (Uschakov 1955), or alternatively as two subclasses with no orders (Day). The Polychaeta are also treated as independent families (Hartman); or as referable to 12 (Dales), 17 (Fauchald), 22 (George), 25 (Pettibone) or 26 (Uschakov 1985) orders, without any other taxonomic structure proposed.

Some of these differences are trivial such as those related to choice of Linnean ranking, but a reorganization is obviously necessary and must be based on a better understanding of the phylogeny than any of the currently used systems exhibit.

Studies of evolution in the polychaetes have been based on one or another of a few *a priori* assumptions:

1. Evolution within the polychaetes may be described as a differentiation from homonomous segmentation to differentiated bodies based mainly on differentiation of soft-body structures (Fauvel 1923).
2. Evolution within the polychaetes has consisted mainly of a simplification from an initially complex structure (Storch 1968).
3. Evolution within the polychaetes has consisted mainly of a reduction in body-size accompanied by neoteny (Westheide 1987).

From the days of Cuvier and Lamarck, the annelid taxa with homonomous segmentation were listed before taxa with heteronomous segmentation. The assessment of what constituted homonomous and heteronomous segmentation was based on overall body structure and specifically the presence of two or more body regions. If regions were present, heteronomous segmentation was considered present (Quatrefages 1865, 1866). This notion has assumed evolutionary significance (Fauvel 1923). Provided that one expects the classification to reflect evolution, the association between a binary separation into errants and sedentaries and the evolutionary idea of increasing body-complexity appears contradictory. One would have expected an organization of families in order of increasing levels of complexity in external morphology. Instead, the group was divided into two groups not clearly matching the suggested increase in obvious morphological complexity: many simple-bodied organisms (e.g. opheliids and cirratulids) ended up among the sedentaries.

Furthermore, tagmatization is not obviously linked to structural complexity of other features, for example, parapodial lobes or chaetae. A sigalionid or a nephtyid has a far more complex system of lobes, lappets and ligules associated with the parapodia than do the sabellids or serpulids (compare illustrations in Pettibone 1970a,1970b or Rainer 1984,1989 with those of Rouse & Fitzhugh 1994). Structural complexity of chaetae, measured as different kinds of chaetae present, or as structurally complex individual kinds of chaetae, may be high (e.g. amphinomids, syllids, Fauchald 1977) or low (e.g. opheliids, cirratulids, Fauchald 1977) in polychaetes with homonomous segmentation. Chaetopterids, with arguably the most highly differentiated segments along the body, have only four different kinds of chaetae (Joyeux-Laffuie 1890), whereas the poecilochaetids, which have far less differentiation along the body, may have as many as seven different kinds of simple chaetae and spines (Mackie 1990: 359; a total of 14 kinds are known in the family, but the maximum for a given species is seven). Compound chaetae, consisting of shafts, a hinge region and an appendix, often with hoods or guards, are among the structurally most complex chaetae, but are present in polychaetes with relatively similar segments along the body (e.g. nereidids, syllids, phyllodocids, eunicids, acrocirrids and flabelligerids, Fauchald 1977). Invoking increasing complexity *per se* does not appear to be show a sufficiently consistent pattern to be useful as a explanatory model of polychaete phylogeny.

In the 1860s and 70s, increasing quality of microscopic equipment combined with an increased interest in examining live organisms led to the discovery of a number of very small annelids (e.g. Claparède 1868, 1870). Based on his own studies of very small annelids, Hatschek combined two notions as a basis for a phylogenetic scheme for the annelids. In addition to the notion of increasing complexity in morphological structure within the annelids, he added increased size as an evolutionary criterion (Hatschek 1878). The evolutionary progression went from the Archiannelida (Protodrilidae and Polygordiidae) through the Protochaeta (Saccocirridae) to the Polychaeta with Spionidae as the most primitive family of Polychaeta (*sensu* Hatschek).

Clark (1964) postulated that segmentation arose as an aid in burrowing and that, because of the physical properties of mud as a substrate, burrowing arose in a medium-sized to large organisms. Structurally, these ancestral annelids were simple-bodied, perhaps resembling earthworms externally, but without the hermaphroditic gonads present in that group (Fauchald 1974a). Consequently, the evolution of the polychaetes could be described as a differentiation of anterior structures, parapodia and chaetae (Fauchald 1974a). The 'archiannelids' were considered secondarily reduced or modified polychaetes (Hermans 1969, see also Fauchald 1974a). Hatschek's and Clark's (including Fauchald's version) explanatory models are untestable.

Dales (1962, 1963) showed the relationships among the families in bubble diagrams with a spatial arrangement that suggested a relationship among his orders. Dales did not link these organized units into a complete diagram that could be read as a statement of relationships. Clark (1969: 47) suggested that, despite this drawback, Dales' solution was the best available in that he collected together those families that could be regarded as related into separate and independent orders. Clark himself proposed the following 12 orders: Amphinomorpha, Eunicemorpha, Phyllodocemorpha, Spiomorpha, Drilomorpha, Terebellomorpha, Serpulimorpha, Archiannelida with the following families in separate orders: Oweniidae, Sternaspidae, Flabelligeridae and Poeobiidae (jointly) and Psammodrilidae.

Westheide (1985,1987) has argued that evolution within certain polychaetes could be described as progenesis associated with decreasing body-size and structural simplification. Indeed, within certain taxa, a reduction in size may be associated with increasing structural simplicity (Fransen 1980). Progenesis cannot be an explanation for all families since, in some, the plesiomorphic taxa are small-bodied and the most apomorphic forms include both large-bodied and small-bodied taxa (Fitzhugh 1989).

Storch (1968) studied segmental musculature of members of 23 polychaete families. He found that the most complicated muscle system represented a primitive stock from which the other polychaetes could be derived. He was able to show that the musculature of several polychaete families of the order Phyllodocida (*sensu* Fauchald 1977) could be derived as three separate paths of simplification from the pattern of musculature present in the scale-worms (Aphroditidae *sensu lato*). Storch (1968) also reported that while drilomorphs, terebellomorphs and spiomorphs were monophyletic groups, he was unable to link their pattern of segmental muscles to each other or to other polychaete families. He reported that eunicids and serpulimorphs were isolated in that both groups had a rather similar, simplified segmental musculature; however, Storch did not suggest that this similarity had any particular phylogenetic significance. Storch (1968: 256) gave a description of the 'primitive metameric organism'; in summary, he specified that it had to have numerous similar segments and, as a consequence, similar parapodia, complete coelomic segmental spaces, a nervous system without unusual concentrations, but with metamerically arranged ventral ganglia. Furthermore, nephridia had to be metamerically arranged, and the circulatory system was supposed to be closed and to show segmental vascular loops. Cephalization had to be minimal and aciculae absent. Storch acknowledged the theoretical nature of this characterization, but that the model was "nearly universally accepted".

Storch used a process described by Remane (1956) making it possible to interpret a theoretical model in terms of real taxa. The process consists of building series of taxa linked by increasing numbers of 'Spezialhomologien', a term that roughly corresponds to synapomorphies, if not in theory, at least in practice. These series can be linked to a central group. In some respects, this process can be said to be a pre-cladistic analysis with the very important exception that it starts out with a preconceived notion of how the primitive member of the taxon was constructed. Storch was only partially successful in his scheme in that he could link only members of the Phyllodocida (*sensu* Fauchald 1977) to each other, but was unable to relate the other polychaetes either to each other or to the one group that he could characterize. The mode of analysis used by Storch has been overtaken by developments in cladistics.

The studies cited above assume either that an *a priori* explanatory model or that an *a priori* starting point (the concept of a primitive annelid), or both, is needed before a phylogenetic/evolutionary study can be undertaken. Given these assumptions, the authors marshall evidence to show the applicability of the model of interest. We prefer to develop an observation-based, parsimonious analysis based on available information and subsequently test individual homology statements emerging from the tree(s). Such a model and suggested evaluations will be presented in the third paper in this series (Rouse & Fauchald 1997).

Conclusions

Current classifications can be grouped into two distinct patterns; in one, there is a primary split between two major groups; in the other, the families are grouped into orders, but the orders are not linked to each other. The families, genera and species recognized are similar, no matter what higher classifications are adopted. All classifications in current use are unsatisfactory for various reasons. The critical problem in the two current patterns of higher classification is that neither explicitly takes advantage of all morphological knowledge, but relies on a limited suite of characters considered important.

The lack of consistent morphological information is a major source of uncertainty in current classifications. Considering the number of species and the amount of missing information, morphological investigations need to be focused to resolve key problems. A competent analysis pointing to critical missing information is needed before a major added effort is undertaken. Increased morphological investigations are expected to lead to re-interpretation of problematic terminology and remove ambiguity in the use of morphological terms. Many problems will not be resolved exclusively by morphological studies; however, such studies supplemented by other kinds, especially molecular systematic studies, will probably decrease the residue of problem taxa.

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Appendix A

Some early classificatory schemes for annelids and related taxa comprising the period prior to recognition of Polychaeta as a distinc taxon. Only taxa of immediate interest have been included. Taxonomic levels have not been named. Content of each terminal taxon as listed is incomplete; it has been included only to suggest currently recognized organisms included in each of the proposed taxa

Linné 1758
Vermes
- Mollusca
  - *Nereis, Aphrodita*
- Intestina
  - *Lumbricus, Hirudo*
- Testacea
  - *Serpula*

Lamarck 1801
Vers
- Exterieurs
  - Avec des organes exterieurs
    - Polychaetes, earthworms, echiurans
  - Sans organes exterieurs
    - *Gordius, Hirudo, Planaria*
  - Intestins
    - Parasitic worms

Cuvier 1812
Vers a sang rouge
- Dorsibranchiata
  - Most free-living polychaetes
- Tubicoles
  - Sabellids, serpulids
- Abranches
  - Echiurans, *Lumbricus, Gordius, Hirudo*

Lamarck 1815
- Animaux apathique
  - Vers—Details in Lamarck 1816
- Animaux sensibles
  - Annélides—Details in Lamarck 1818

Lamarck 1816
Vers
- Mollasses
  - Turbellarians, plus various parasitic worms
- Rigidules
  - Acanthocephalans, nematodes
- Hispides
  - *Nais, Tubifex*

Blainville 1816
Vers—See also Blainville 1825,1828
- Sétipodes
  - Most polychaetes
- Apoda
  - Leeches, etc.

Cuvier 1816
Animaux articulées
- Annélides
  - Tubicoles
    - Serpulids, terebellids, *Penicillus, Dentalium*
  - Dorsibranches
    - Nereidids, eunicids, *Spio*, scale-worms, amphinomids, arenicolids
  - Abranches
    - Capitellids, leeches, earthworms

Lamarck 1818
Annélides
- Apodes
  - Leeches, Echiurans
- Antennées
  - Scale-worms, nereidids, eunicids, amphinomids
- Sédentaires
  - Arenicolids, maldanids, terebellids

Savigny 1822
Annélides
- Première Division
  - Annelida Nereideae
    - Aphroditae—Scale-worms
    - Nereides—Nereidids, glycerids, syllids, etc.
    - Eunicae—All euniceans
    - Amphinomae—Amphinomids and euphrosinids
  - Annelida Serpuleae
    - Amphitritae—Serpulids, sabellids, sabellariids, terebellids, pectinariids
    - Maldaniae—Maldanids
    - Telethusae—Arenicolids
  - Annelida Lumbricinae
    - Echiuri—Echiurans
    - Lumbrici—Earthworms
- Deuxième Division
  - Annelida Hirudineae
    - Hirudines—Leeches

Blainville 1825
Néréides
Néréides multidentées
Most euniceans
Néréides unidentées
Nereids, nephtyids, hesionids, syllids, phyllodocids, spionids, orbiniids, lumbrinerids and glycerids

Blainville 1828
Entomozoaires
Chaetopoda—Change of name
Hétérocriniens
Serpulides
Sabulaires—Sabellids, terebellids, pectinariids, flabelligerids, spionids and capitellids
Paromocriniens
Maldanies—Maldanids
Télethuses—Arenicolids
Homocriniens
Amphinomés—Amphinomids, euphrosinids
Aphrodités—Scale-worms
Néréidés
Zygocères
Néréiphylle—Phyllodocids
Néréimyre—Some hesionids
Néréides—Nereidids
Azygocères
Néréisylle—Syllids
Néréidice—*Lysidice* (Eunicidae)
Néréidonte—Other eunicids, onuphids
Microcères
Ophélie—Opheliids
Aonie—Some spionids
Aglaure—Some oenonids
Acères
Hésione—Hesionids
Aricie—Some orbiniids
Nephtys—Nephtyids
Glycère—Glycerids
Néréiscolés—Lumbrinerids, other oenonids, cirratulids and remaining orbiniids
Lombrincinées
Siphostome—Flabelligerid
Lombrie—Earthworms
Tubifex—Some "microdrile" oligochaetes
Nais—Other "microdrile" oligochaetes
Echiurides
Thalassème—Echiurans
Sternaspis—Sternaspids

Audouin & Milne Edwards 1834
Annélides
Annélides errantes
Aphrodisiens
Amphinomiens
Euniciens
Néréidiens
Ariciens
Péripatiens
Chétopteriens
Arénicoliens
Annélides tubicoles (ou sédentaires)—Serpulids, flabelligerids
Annélides terricoles—Capitellids, earthworms
Annélides souceuses—Leeches

Appendix B

Classifications of polychaetes from 1850 to today. The schemes were selected to show major differences among the schemes. Many schemes differing only in detail from those presented have been omitted, and differences in use of sub-families and families for certain taxa have not been presented in detail

Grube 1850
Annulata
Appendiculata Polychaeta
Rapacia
Aphroditea, Amphinomiacea, Nephthydea, Glycerea, Phyllodocea, Lycoridea, Amytidea, Eunicea, Ariciea, Syllidea
Limivora
Chaetopterea, Pherusea, Maldania, Opheliacea, Telethusa, Terebellacea, Hermellacea, Serpulacea
Gymnocopa
Tomopteridea
Onychophora
Peripatea
Oligochaeta
Naidea
Lumbricina
Discophora
Hirudinacea, Clepsinea, Branchiobdellea, Acanthobdellea

Ehlers 1864
Annelida
Annelida Chaetopoda
Nereidea
Amphinomea, Syllidea, Chrysopetalea, Eunicea, Aphroditea, Lycoridea, Phyllodocea, Nephthydea, Alciopea, Glycerea, Hesionea
Ariciea
Serpulea
Lumbricina
Annelida Discophora

Johnston 1865
Helmintha
Polypodous
Scoleces
Annelides
Rapacia
Aphroditaceae, Amphinomae, Eunicae, Nereidae, Nephthyaceae, Phyllodocidae, Glyceraceae, Syllidae, Amytiaceae, Aricidae, Chaetopteridae
Limivora
Opheliaceae, Siphonostomaceae, Telethusae, Maldaniae, Terebellidae, Sabellariad, Serpulidaeae, Campontiadae, ?Maeadae
Gymnocopa
Tomopteridae

Quatrefages 1866
Annelidae
A. Erraticae
A. Erraticae aberrantes
Aphroditiea, Palmyrea
A. Erraticae propriae
Eunicea, Lombrinerea, Amphinomea, Nephtydea, Nériniens, Cirrhatulea, Chloraemea, Nereidea, Syllidiea, Amytidea, Hesionea, Phyllodocea, Glycerea, Polyophthalmea
A. Sedentariae
A. Sedentariae aberrantes
Chetopterea
A. Sedentariae propriae
Tomopteridea, Clymenea, Arenicolea, Opheliea, Ariciea, Leucodoriea, Hermellea, Pectinarea, Terebellea, Serpulea
Gephyrea
G. armata
Sternaspidea
Echiurea
Bonelliea
G. inermia
Priapulea
Loxosiphonea
Aspidosiphonea
Sipunculea

Levinsen 1883
Annulata
Chaetopoda
Polychaeta
Aphroditiformia
A. vera, Palmyridae
Phyllodociformia
P. vera, Nephthiydae
Euniciformia
E. vera, E. glycerina
Syllidiformia
S. vera
Nereidae, Hesionidae, Syllidae, Nerillidae, Sphaerodoridae
S. spionina
Spionidae, Chaetopteridae, Cirratulidae, Ariciidae, Chloraemidae (?), Ophelidae (?)
Amphinomiformia

A. vera
Amphinomidae
Euphrosynidae
A. arenicolina
Telethusaea
Scalibregmidae
Maldaniformia
Maldanidae
Ammochariformia
Ammocharidae, Capitellidae
Terebelliformia
Terebellidae, Ampharetidae, Amphictenidae
Hermelliformia
Hermellidae
Sabelliformia
Sabellidae, Serpulidae
Sternaspiformia
Sternaspidae
Oligochaeta
Gymnocopa
Tomopteridae
Discophora

Hatschek 1893
Annelida
Archiannelida
Dinophilidae, Polygordiidae (incl, *Protodrilus*)
Chaetopoda
Protochaeta
Saccocirridae
Polychaeta
Cirrifera
Spiomorpha
Spionidae
Ariciidae
Anh. Chaetopteridae
Anh. Pherusiidae
Anh. Opheliidae
Amphinomorpha
Amphinomidae
Rapacia (= Nereimorpha)
Tribus a.
Glyceridae
Tribus b.
Nephthydidae
Tribus c.
Eunicidae
Tribus Nereipoda
Aphroditidae, Stephanidae, Nereidae (= Lycoridae), Hesionidae, Syllidae, Phyllodocidae, Anh. Myzostomidae
Acirra
Drilomorpha
Cirratulidae, Arenicolidae, Capitellidae, Maldanidae, Anh. Sternaspidae, Anh. Ctenodrilidae
Terebellomorpha
Amphictenidae, Terebellidae
Serpulimorpha
Hermellidae, Serpulidae
Oligochaeta
Hirudinea
Echiurida
Anh. Sipunculacea
Anh. Chaetognatha

Benham 1896
Chaetopoda
Archiannelida
Dinophilus, *Protodrilus* and *Polygordius*
Polychaeta
Phanerocephala
Nereidiformia
Syllidae, Hesionidae, Aphroditidae, Phyllodocidae, Tomopteridae, Nereidae, Nephthydidae, Amphinomidae, Eunicidae, Glyceridae, Sphaerodoridae, Ariciidae, Typhloscolecidae
Spioniformia
Spionidae, Polydoridae, Chaetopteridae, Magelonidae, Ammocharidae
Terebelliformia
Cirratulidae, Terebellidae, Ampharetidae, Amphictenidae
Capitelliformia
Capitellidae
Scoleciformia
Opheliidae, Maldanidae, Arenicolidae, Chlorhaemidae, Sternaspidae
Cryptocephala
Sabelliformia
Sabellidae, Eriographidae, Amphicorinidae, Serpulidae
Hermelliformia
Hermellidae
Myzostomaria
Myzostomatidae
Oligochaeta
Hirudinea

Perrier 1897
Annelés
Chètopodes
Polychètes (Annelida)
Errantia
Ctenodrilidae, Syllidae, Sphaerodoridae, Hesionidae, Nereidae, Phyllodocidae, Polygordiidae, Tomopteridae, Typhloscolecidae, Aphroditidae, Amphinomidae, Palmyridae, Glyceridae, Nephthydae, Eunicidae
Philocrinida
Stelechopidae, Myzostomidae
Sedentaria
Saccocirridae, Spionidae, Chaetopteridae, Ariciidae, Opheliidae, Scalibregmidae, Arenicolidae (Telethusidae), Capitellidae, Maldanidae, Ammocharidae, Cirratulidae, Sternaspidae, Flabelligeridae (Pherusidae),Terebellidae, Ampharetidae, Amphictenidae, Sabellariidae, Serpulidae
Oligochaeta (Lumbricina)
Discophores
Hirudinées
Trichotoma
Dinophilida

Uschakov 1955
Polychaeta
Errantia
Phyllodocemorpha
Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae, Aphroditidae, Chrysopetalidae, Glyceridae
Nereimorpha
Syllidae, Hesionidae, Pilargiidae, Nereidae, Nephthydidae, Sphaerodoridae
Amphinomorpha
Euphrosynidae, Spintheridae
Eunicemorpha
Eunicidae
Sedentaria
Spiomorpha
Ariciidae, Spionidae, Magelonidae, Disomidae, Paraonidae, Chaetopteridae, Cirratulidae
Drilomorpha
Chloraemidae, Scalibregmidae, Opheliidae, Capitellidae, Arenicolidae, Maldanidae, Oweniidae, Sabellariidae, Sternaspididae
Terebellomorpha
Pectinariidae, Ampharetidae, Trichobranchidae, Terebellidae
Serpulimorpha
Sabellidae, Serpulidae

Dales 1963
Annelida
Archiannelida
Polychaeta
Phyllodocida
Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae, Aphroditidae, *in sensu lato*, Chrysopetalidae, Glyceridae, Goniadidae, Sphaerodoridae, Pisionidae, Nephthyidae, Syllidae, Hesionidae, Pilargiidae, Nereidae
Capitellida
Capitellidae, Arenicolidae, Scalibregmidae, Maldanidae, Opheliidae
Sternaspida
Sternaspidae
Spionida
Spionidae, Disomidae, Poecilochaetidae, Longosomidae, Paraonidae, Apistobranchidae (mis-spelled), Chaetopteridae, Sabellariidae
Eunicida
Onuphidae, Eunicidae, Lumbrineridae, Arabellidae, Lysaretidae, Dorvilleidae, Histriobdellidae, (Ichthyotomidae)
Amphinomida

Amphinomidae *in sensu lato*
Magelonida
Magelonidae
Ariciida
Ariciidae
Cirratulida
Cirratulidae, Ctenodrilidae, (Stygocapitellidae)
Oweniida
Oweniidae
Terebellida
Pectinariidae, Ampharetidae, Terebellidae
Flabelligerida
Flabellgeridae
Psammodrilida
Psammodrilidae
Sabellida
Sabellidae
Serpulidae
Myzostomaria
Oligochaeta (sub-division not included here)
Hirudinea (sub-division not included here)

Fauchald 1977
Polychaeta
Orbiniida
Orbiniidae, Paraonidae, Questidae
Ctenodrilida
Ctenodrilidae, Parergodrilidae
Psammodrilida
Psammodrilidae
Cossurida
Cossuridae
Spionida
Spioniformia
Apistobranchidae, Spionidae, Magelonidae, Trochochaetidae, Poecilochaetidae, Heterospionidae
Chaetopteriformia
Chaetopteridae
Cirratuliformia
Cirratulidae, Acrocirridae
Capitellida
Capitellidae, Arenicolidae, Maldanidae
Opheliida
Opheliidae, Scalibregmidae
Phyllodocida
Phyllodociformia
Phyllodocidae, Alciopidae, Lopadorhynchidae, Pontodoridae
Aphroditiformia
Aphroditacea
Aphroditidae, Polynoidae, Polyodontidae, Pholoididae, Eulepethidae, Sigalionidae
Chrysopetalecea
Chrysopetalidae, Palmyridae
Pisioniacea
Pisionidae
Nereidiformia
Hesionidae, Pilargiidae, Syllidae, Calamyzidae, Nereidae, Antonbruunidae
Glyceriformia
Glyceridae, Goniadidae, Lacydoniidae
Suborder not recognized
Iospilidae, Nephtyidae, Sphaerodoridae, Tomopteridae, Typhloscolecidae
Amphinomida
Amphinomidae, Euphrosinidae
Spintherida
Spintheridae
Eunicida
Eunicea
Onuphidae, Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae, Dorvilleidae
Superfamily not recognized
Histriobdellidae, Ichthyotomidae
Sternaspida
Sternaspidae
Oweniida
Oweniidae
Flabelligerida
Flabelligeridae, Poeobiidae
Fauveliopsida
Fauveliopsidae
Terebellida
Sabellariidae, Pectinariidae, Ampharetidae, Terebellidae, Trichobranchidae, Bogueidae
Sabellida
Sabellidae, Sabellongidae, Caobangidae, Serpulidae, Spirorbidae
Families of uncertain affinities:
Dinophilidae, Nerillidae, Polygordiidae, Protodrilidae, Saccocirridae

George in George & Hartman-Schröder 1985
Annelida
Polychaeta
Phyllodocida
Palmyroidea
Palmyridae (incl. Chrysopetalidae)
Pisionoidea
Pisionidae
Aphroditoidea
Aphroditidae, Polynoidae, Polyodontidae, Peisidicidae, (= Pholoididae), Sigalionidae, Eulepethidae
Phyllodocoidea
Phyllodocidae, Lacydoniidae, Alciopidae, Lopadorrhynchidae, Pontodoridae
Iospiloidea
Iospilidae
Typhloscolecoidea
Typhloscolecidae
Tomopteroidea
Tomopteridae
Glyceroidea
Glyceridae, Goniadidae
Sphaerodoroidea
Sphaerodoridae
Neridoidea
Hesionidae, Helmeotphoridae, Pilargidae, Antonbruunidae, Syllidae, Calamyzidae, Nereididae (= Nereidae)
Nephtyoidea
Nephtyidae, Paralacydoniidae
Amphinomida
Amphinomidae, Euphrosinidae
Spintherida
Spintheridae
Eunicida
Eunicoidea
Onuphidae, Eunicidae, Hartmaniellidae, Lumbrineridae, Arabellidae, Lysaretidae, Dorvilleidae, Iphitimidae
Ichthyotomoidea
Ichthyotomidae
Histriobdelloidea
Histriobdellidae
Orbiniida
Orbiniidae, Paraonidae
Questida
Questidae
Spionida
Spionoidea
Apistobranchidae, Trochochaetidae (= Disomidae), Poecilochaetidae, Spionidae, Heterospionidae
Magelonoidea
Magelonidae
Chaetopteroidea
Chaetopteridae
Cirratuloidea
Cirratulidae
Ctenodrilida
Ctenodrilidae, Parergodrilidae
Psammodrilida
Psammodrilidae
Cossurida
Cossuridae
Flabelligerida
Flabelligeridae, Acrocirridae, Fauveliopsidae
Poeobiida
Poeobiidae
Sternaspida
Sternaspidae
Capitellida
Capitellidae, Arenicolidae, Maldanidae (incl. Bogueidae)
Opheliida
Opheliidae, Scalibregmatidae
Nerillida
Nerillidae
Dinophilida

Dinophilidae (incl. Diurodrilidae)
Polygordiida
Polygordiidae
Protodrilida
Protodrilidae, Saccocirridae
Oweniida
Oweniidae
Terebellida
Pectinariidae (= Amphictenidae), Sabellariidae, Ampharetidae, Trichobranchidae, Terebellidae
Sabellida
Sabellidae (incl. Sabellongidae), Caobangiidae, Serpulidae, Spirorbidae