

# **Taxonomy and phylogeny of polychaetes**

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**UNIVERSITY OF GOTHENBURG**

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*I love deadlines. I like the whooshing sound they make as they fly by.*

- Douglas Adams

# DISSERTATION ABSTRACT

Jenny Eklöf (2010). Taxonomy and phylogeny of polychaetes.  
University of Gothenburg, Department of Zoology, PO Box 463, SE-405 30 Göteborg, Sweden.

Polychaetes are a large group of segmented worms that display an enormous morphological diversity. Molecular data has shown in recent years that groups previously thought to be separate from polychaetes are actually part of the group. The relationships within polychaete groups have been difficult to discern, and molecular data only partly corroborate classifications done on morphological grounds. The main focus of this thesis is on Phyllodocidae, a family of polychaetes, and its phylogenetic relationships. Our results show that none of the phyllodocid subfamilies, as previously delineated by morphology, find support from molecular data. Instead groups previously not recognized receive high support. A number of polychaete families are holopelagic, and most of these have been regarded as closely related to phyllodocids. We have found that one of these holopelagic families, Alciopidae, is well nested within the phyllodocids, with its closest sister being *Eumida arctica*, making the genus *Eumida*, as delineated today, paraphyletic.

Part of this thesis also deals with cryptic species, which means that two or more species are virtually impossible to separate morphologically, but still represent separately evolving lineages, reproductively isolated from each other. We have found that Arctic and boreal populations of *Paranaitis wahlbergi* belong to two separate species, and the boreal populations are referred to a new species, *P. katoi* sp. n. We have also found that sympatric populations of *Notophyllum foliosum*, found in deep and shallow waters are two separate species, morphologically distinguished only by subtle details in their colouration, and the deep form is described as *N. crypticum* sp. n. A description is also provided for *Axiokebuita*, previously not found in European waters. Due to delineation problems with the two described species in the genus it was not possible to refer these new specimens to either of them or to a new species. A phylogenetic analysis of molecular data confirms the position of *Axiokebuita* among scalibregmatids.

Keywords: Polychaeta, Phyllodocidae, Alciopidae, pelagic polychaetes, phylogeny, cryptic species

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## LIST OF PAPERS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals (I–V).

- I. Jenny Eklöf, Fredrik Pleijel & Per Sundberg (2007). Phylogeny of benthic Phyllodocidae (Polychaeta) based on morphological and molecular data. *Molecular Phylogenetics and Evolution*, 45: 261–271.
- II. Jenny Eklöf, Arne Nygren, Karen Osborn, Per Sundberg & Fredrik Pleijel (manuscript). *Eumida* (Phyllodocidae, Annelida) goes pelagic.
- III. Arne Nygren, Jenny Eklöf & Fredrik Pleijel (2009). Arctic-boreal sibling species of *Paranaitis* (Polychaeta, Phyllodocidae). *Marine Biology Research*, 5: 315–327.
- IV. Arne Nygren, Jenny Eklöf & Fredrik Pleijel (2010). Cryptic species of *Notophyllum* (Polychaeta: Phyllodocidae) in Scandinavian waters. *Organisms Diversity & Evolution*, DOI 10.1007/s13127-010-0014-2.
- V. Jenny Persson & Fredrik Pleijel (2005). On the phylogenetic relationships of *Axiokebuita*, *Travisia* and *Scalibregmatidae* (Polychaeta). *Zootaxa*, 998:1–14.

This thesis is not to be regarded as a publication in the sense of the International Code of Zoological Nomenclature (ICZN, 1999), and scientific names mentioned in it should not be cited in any form.

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## INTRODUCTION

This thesis is about polychaetes and especially Phyllodocidae, which is a family of about 500 species of errant polychaetes. The main focus of the work has been to assess the phylogenetic relationship among the phyllodocids, including the position of the spectacular pelagic polychaete group Alciopidae, which long has been thought to be derived from phyllodocids. Another important part of this work has been to delineate and describe new as well as already described polychaete species using a combined molecular and morphological approach.

## AIMS

The objectives of this thesis are:

- To assess the phylogenetic relationships of the benthic Phyllodocidae using both molecular and morphological data, and to compare the results with previous classifications.
- To clarify the systematic position of the holopelagic alciopids among the phyllodocids.
- To examine if two allopatric populations of the phyllodocid *Paranaitis wahlbergi* belong to a single species or if they represent two separate, cryptic species.
- To assess whether a shallow and deep form of the phyllodocid *Notophyllum foliosum*, possibly separated by habitat and coloration, are conspecific or not.
- To give a comprehensive description of a scalibregmatid previously not found in European waters, and assess its phylogenetic position.

## POLYCHAETES

Polychaetes are a large group with about 14 000 species considered valid (Rouse & Pleijel 2006), and they are found in virtually all marine habitats, with sizes ranging from less than a millimetre to several

metres in lengths.

Polychaetes display an enormous morphological diversity, where different life-styles have given rise to many disparate forms, with everything from free-living predators to filter-feeding tube-builders and interstitial parasites represented. Polychaetes have historically been divided into Errantia and Sedentaria. Errantia comprised all errant (free-living) polychaetes, while Sedentaria contained both tube-builders and a variety of burrowing forms. This was mainly a convenient classification, which divided the polychaetes into two equally large groups, and was not, at least not explicitly, intended to show their evolutionary history. Later classifications based on these two major groups further divided polychaetes into a number of different orders that each contained one or several families, but without any further relationships specified (e.g. Fauchald 1977).

The first phylogenetic analysis based on morphological characters was conducted by Rouse & Fauchald (1997), and formed the basis for a new classification where polychaetes were divided into Scolecida, which are simple-bodied polychaetes, and Palpata. The latter taxon was in turn separated in Canalipalpata, named for the presence of grooved palps, and Aciculata, which by and large corresponded to the group Errantia. This has since then been the reigning classification, but with some modifications by later authors.

## **New additions to polychaetes**

Molecular data have in recent years made a huge impact on how we understand the evolutionary relationships of polychaetes, and have also changed our view on what should be included in the taxon Polychaeta to make it monophyletic. Polychaetes are part of the more inclusive group Annelida that also comprises the more well-known clitellates (e.g. earthworms and leeches), but in recent years it has been shown that clitellates probably has its closest relatives among polychaetes, making the taxon Polychaeta as currently delineated a paraphyletic group. To phrase it differently the polychaetes include the clitellates, which means that the taxon Polychaeta then would be synonymous to Annelida. To complicate things further, several other groups regarded as distinct phyla separate from Annelida, have been shown to have their origin within polychaetes too.



### *Clitellata*

It was already suggested, based on morphological data (Eibye-Jacobsen & Nielsen 1996, Purschke 1997) or functional considerations (Westheide 1997) that Clitellata probably belongs within polychaetes, Early molecular results (McHugh 1997, Kojima 1998) also pointed to that Clitellata are derived from a polychaete ancestor. Regarding the position of Clitellata within polychaetes, Nielsen (1995) suggested, based on morphology, that the simple-bodied polychaete family Capitellidae would be the sistergroup of clitellates. However, none of the molecular analyses have come to a conclusive result on which polychaete group is the sister to Clitellata, but Dinophilidae and Lumbrinereidae have been suggested in several analyses (Hall *et al.* 2004, Jördens *et al.* 2004, Colgan *et al.* 2006, Rousset *et al.* 2007). In a combined morphological and molecular analysis, Zrzavý *et al.* (2009) found that Clitellata and the clitellate-like polychaetes (Aeolosomatidae, Potamodrilidae, *Hrabeiella*) form a monophyletic group.

### *Siboglinidae*

The deep-sea pogonophoran tubeworms, and the vestimentiferan worms of deep-sea hydrothermal vents, were originally regarded as separate phyla, only distantly related to annelids. These taxa are now considered as closely related to annelids. Rouse & Fauchald (1997) found that Annelida was monophyletic only if Pogonophora (including vestimentiferans) was included among polychaetes. Molecular studies have given further support to the view that pogonophorans are derived annelids (McHugh 1997, Kojima 1998, Boore & Brown 2000, Bleidorn *et al.* 2003, Rousset *et al.* 2004, Colgan *et al.* 2006, Struck *et al.* 2007, Zrzavý *et al.* 2009). The pogonophorans and vestimentiferans are now referred to as the taxon Siboglinidae, in agreement with a recent revision of the group by Rouse (2001). The newly described genus *Osedax* (Rouse *et al.* 2004), which lives on and consumes the bones of dead whales via ramifying roots, also belong to the siboglinids. A detailed review of the taxonomic history of Siboglinidae can be found in Pleijel *et al.* (2008).

### *Echiura*

The phylogenetic position of Echiura has been discussed for a long time. The presence of chaetae and development through a trochophore

larvae have suggested a polychaete affinity, whereas the absence of segmentation has been the main reason for referring them to a separate phylum (Newby 1940). According to Rouse & Fauchald (1997) the echiurids are the sistergroup to all segmented taxa, but Nielsen (1995) and Eibye-Jacobsen & Nielsen (1996) suggested that the lack of segmentation in echiurids is a secondary loss, rather than a primary absence. Molecular data suggests that Echiura indeed are derived annelids (McHugh 1997, 1999, Brown *et al.* 1999, Bleidorn *et al.* 2003, Dunn *et al.* 2008), and give support to the view by Hessling & Westheide (2002) that the pattern of the nervous system in echiurids is homologous to that of polychaetes.

### *Sipuncula*

Another taxon that just recently has been thrown into the debate about what should be included in Annelida/Polychaeta is Sipuncula. Traditionally it has been associated with molluscs rather than annelids, based on the embryological development, where the micromeres during spiral cleavage form a molluscan cross. This has been considered a synapomorphic character for molluscs and sipunculans. However, molecular data (Brown *et al.* 1999, Martin 2001, Boore & Staton 2002, Bleidorn *et al.* 2003, 2006, Hall *et al.* 2004, Struck *et al.* 2007, Dunn *et al.* 2008, Shen *et al.* 2009) indicate that Sipuncula instead may be included in the annelids, although the more precise position is still unclear. In Bleidorn *et al.* (2003), it forms a clade with Clitellata, in Zrzavý *et al.* (2009) it is, in most analyses, found close to Dinophilidae, while Struck *et al.* (2007) suggests an affiliation with terebellomorphs.

## **Relationships within polychaete groups**

One of the major problems with the phylogenetic tree of polychaetes is the position of the root. One hypothesis is that the simple-bodied polychaetes such as Opheliidae and Questidae forms the basal grade making Scolecida paraphyletic (Fauchald 1977, Rouse & Fauchald 1997), while other hypotheses place taxa in Aciculata as a basal grade, making Aciculata and Phyllodocida paraphyletic (Storch 1968, Purschke 1997, Westheide 1997, Westheide *et al.* 1999).

The three major groups erected by Rouse & Fauchald (1997) have been difficult to confirm by molecular data (e.g. McHugh 1997,

Kojima 1998, Brown *et al.* 1999, Struck *et al.* 2007), but one may argue that this is mostly due to poor resolution in the molecular phylogenies. Among the three major recovered groups from Rouse & Fauchald (1977), Scolecida is arguably the weakest one, which is not surprising since these are “simple-bodied” polychaetes with few external characteristics. This will make them united by scores for absences in a morphological matrix, but the absence of features, such as palps, does not necessarily provide a reliable indication that they are closely related.

In paper V, in which we examined the phylogenetic position of the scalibregmatid *Axiokebuita*, Scolecida was found to be non-monophyletic, with the groups Orbiniidae and Questidae positioned well outside Scolecida. Bleidorn *et al.* (2003) came to same conclusion based on a much more inclusive set of scolecid taxa, where they failed to find a common ancestry for Scolecida. Instead, one of the included scolecid families, Capitellidae, clusters with Echiura, and notably, the group Orbiniidae (including Questidae) is distant from the other included members of Scolecida in all their analyses.

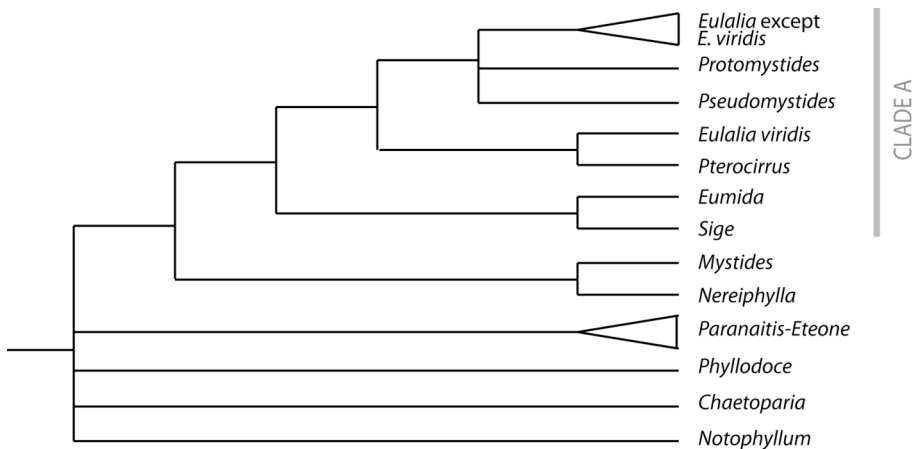
## PHYLLODOCIDS AND PELAGIC POLYCHAETES

Phyllodocidae is a family with about 500 species divided in 18 genera (Pleijel 1991). They are active free-living predators and belong within Aciculata. The benthic phyllodocids are fairly easy to recognize by their large flattened dorsal cirri and a single pair of eyes that usually is present (Fig. 1). Phyllodocids are long and slender and may reach a length of more than half a meter. They have a pair of palps, which are similar in size and shape to the paired antennae, and there is often also a median antenna or nuchal papilla present. Phyllodocids have, like many other errant polychaetes, an eversible pharynx, which is provided with a varying number of papillae. One character that has been considered important for classifying or identifying phyllodocids is the number and shape of the cirri on the first three segments (see below).



**Fig. 1.** *Phyllodoce citrina* with large fattened dorsal cirri.  
Photo by Fredrik Pleijel

In paper I, we analyzed a large number of phyllodocid taxa using both morphological and molecular data. We demonstrated high degrees in homoplasy in the traditionally used morphological phyllodocid characters, and showed that all the three current subfamilies Phyllodocinae, Eteoninae and Notophyllinae were non-monophyletic. The genera *Eulalia*, *Eumida*, *Protomystides*, *Pseudomystides*, *Pterocirrus* and *Sige* formed a well-supported group, as did a previously unrecognized group consisting of *Mystides* and *Nereiphylla*. *Eulalia* was found to be non-monophyletic and should be split, minimally into two groups. Another new clade with strong support included *Eteone* and *Paranaitis*, although with *Eteone* nested within a paraphyletic *Paranaitis* (Fig. 2).



**Fig. 2.** Phylogenetic tree of benthic phyllodocids, modified from paper I.

In terms of morphology this means that characters traditionally employed to delineate the major phyllodocid subgroups show high degrees of homoplasy. Three main patterns regarding the distribution of tentacular cirri on the first segments (see Fig. 3) can be identified among benthic phyllodocids (e.g. Pleijel 1991, Eibye-Jacobsen 1993):

- 1) One pair of tentacular cirri on segment 1, two pairs on segment 2, and one dorsal pair on segment 3 (e.g. *Eulalia*, *Phyllodoce*).
- 2) One pair of tentacular cirri on segment 1, two pairs on segment 2, but no dorsal or tentacular cirri in dorsal position on segment 3 (e.g. *Hesionura*, *Mystides*, *Pseudomystides*).
- 3) No cirri on segment 1 (assuming a reduction of the first segment), two pairs of cirri on segment 2, but no dorsal or tentacular cirri in dorsal position on segment 3 (*Eteone*).



**Fig. 3.** Three phyllodocids with different arrangements of the tentacular cirri on the first segments. From left to right *Eulalia clavigera*, *Pseudomystides limbata* and *Eteone barbata*. Photos by Fredrik Pleijel

Previous authors (e.g. Pleijel 1993, Orrhage & Eibye-Jacobsen 1998) have treated the presence of two pairs of cirri on segment 2 as a homology, as well as the reduced dorsal cirri on segment 3. In contrast, our phylogenetic analyses demonstrated high degrees of homoplasy in these two characters. For example, the reduction of dorsal cirri on segment 3 was maximally homoplastic and appears separately in *Eteone*, *Mystides* and *Pseudomystides*. Another highly homoplastic character is the absence or presence of a median antenna or nuchal papilla (regarding homology of median antenna and nuchal papillae, see Pleijel 1993, Eibye-Jacobsen 1993, Orrhage & Eibye-Jacobsen 1998). A median antenna may have been independently reduced in the groups *Mystides-Nereiphylla*, *Protomystides*, and within *Paranaitis*, although the polarity of the character state changes in some cases was equivocal due to uncertainties regarding the

ancestral conditions.

## The pelagic polychaetes

Most polychaetes are benthic with or without a pelagic larvae, some form pelagic epitokes (which means they are pelagic during the reproductive period), but a number of polychaetes are holopelagic, meaning that they live their whole life in the open water. Traditionally, holopelagic polychaetes have been classified into a number of separate families, including Alciopidae, Iospilidae, Lopadorhynchidae, Poeobiidae, Pontodoridae, Tomopteridae and Typhloscolecidae. Most of the holopelagic families have been regarded as closely related to phyllodocids (e.g. Uschakov 1972). However, not all pelagic polychaetes are derived from phyllodocids and some of them have evolved from sedentary polychaetes such as flabelligerids and acrocirrids (e.g. Osborn *et al.* 2009).

### *Alciopidae*

Alciopidae is a group of spectacular holopelagic polychaetes. They are active predators, and presumably hunt by sight (Fauchald & Jumars 1979). Alciopids share many morphological features with benthic phyllodocids, but differ most obviously in having exceptionally well developed eyes (Fig. 4). They also have a complex reproductive system, with sperm storing sacs, receptacula seminis, in females. There are strong morphological evidences for the monophyly of alciopids, with their large telescopic eyes as an apomorphy for the group, and this issue has never been questioned in the literature. Although it is usually assumed that alciopids are closely related to, or part of, phyllodocids, few of the authors dealing with phyllodocids have included alciopids.



**Fig. 4.** This alciopid was described as *Nauphanta celox* by Greeff (1876). It has since been synonymized with *Alciopa reynaudii*.

### *Lopadorhynchidae*

Lopadorhynchidae is a small group of holopelagic polychaetes with 15 species separated in four genera; *Lopadorhynchus*, *Pelagobia*, *Pedinosoma*, and *Maupasia*. Some authors have considered Lopadorhynchidae as a subfamily within Phyllodocidae (Fauvel 1923, Day 1967, Uschakov 1972), but it has mostly been treated as a separate taxon (e.g. Fauchald 1977, Pleijel & Dales 1991, Fauchald & Rouse 1997, Wilson 2000a). There is no real evidence of monophyly of the lopadorhynchids (Fauchald & Rouse 1997, Rouse & Pleijel 2001), and in fact Uschakov (1972) presented a tree in which they had different origins among the phyllodocid genera.

In Bergström's (1914) revision of Phyllodocidae, the taxon name Lopadorhynchidae was not used, and instead he placed the lopadorhynchids in several different phyllodocid subfamilies. *Lopadorhynchus* and *Chaetoparia* are illustrated as sister taxa based on the presence of hooks on the anteriormost segments, whereas *Maupasia* and *Pelagobia* were descendent from *Eteone*, while *Pedinosoma* was of uncertain origin. Uschakov (1972) also considered *Lopadorhynchus* to be closely related to *Chaetoparia* because of fusion of the cephalic lobe with the anterior segments and the presence of specialized chaetae on the first segments. Uschakov further thought *Pelagobia* and *Maupasia* to have an origin from *Eteone* because of the number of tentacular cirri on the first segment while he found *Pedinosoma*'s position unclear because of the ambiguous interpretations of the anterior segments. Dales (1955) had a different view on the phylogenetic position of *Lopadorhynchus* and considered that it had developed from *Protomystides* and *Mystides* since they in many ways resembled these bottom-living forms.

### *Tomopteridae*

Tomopteridae is probably the most familiar of the holopelagic taxa. Tomopterids live from surface waters to depths of at least 3000 meters (Wilson 2000b). Reviews of the literature and the taxa can be found in Dales (1972) and Uschakov (1972). Åkesson (1962) provided a study on the embryology and early development of *Tomopteris helgolandica*, which has been important for primary homology statements and comparisons with other polychaetes. The monophyly of Tomopteridae has never been questioned because of their unique

characters, but the position of the group is uncertain, although it has been referred to Phyllodocida. In several of the cladistic analyses of Rouse & Fauchald (1997) the Tomopteridae group together with Iospiliidae, and they are in turn closely related to *Lacydonia* and Phyllodocidae, but there is no strong evidence since the morphological homologies are difficult to assess.

Molecular analyses by Struck *et al.* (2007) place Tomopteridae as sister to Glyceridae and Goniadidae, and this clade is in turn sister to a clade of Phyllodocidae and Alciopidae. In Zrzavý *et al.* (2009) the position was highly unstable, probably due to long branches, but in the combined Bayesian analysis, it was found as sister to Glyceridae and Goniadidae.

### *Minor pelagic groups*

Iospilidae is a small and poorly known family that was initially described as a subfamily of Phyllodocidae, and it is still often considered as such. Uschakov (1972) suggested that they belong within Phyllodocidae, but Rouse & Fauchald (1997) placed them near Nereididae and Tomopteridae, while Fauchald (1977) recognized them as distinct from Phyllodocidae.

*Pontodora pelagica*, described by Uschakov (1972), is a relatively small worm with a cosmopolitan distribution. It has well developed parapodia and chaetae. Day (1967) considered *Pontodora* as related to Syllidae, whereas most other authors have treated them as close to Phyllodocidae (Fauchald 1977, George & Hartmann-Schröder 1985), or part of it (Uschakov 1972).

Typhloscolecidae is a small group of only three genera. Almost nothing is known of their biology, but based on their morphology they are considered to be ectoparasites, feeding on soft-bodied and gelatinous animals (Reibisch 1895, Uschakov 1972, Øresland & Pleijel 1991). Their relationship to other polychaetes have been uncertain, but they most likely belong within Phyllodocida (Rouse & Fauchald 1997).

Yndolaciidae is a relatively newly described family, originally based on a single species, *Yndolacia lopadorrhynchides*, from the Gulf of Guinea (Støp-Bowitz 1987). Since then, two more species have been described (Buzhinskaja 2004). Not much is known of their phylogenetic position, but they are believed to belong within Phyllodocida (Rouse & Pleijel 2001, Buzhinskaja 2004).



### *Non-Phyllodocidan pelagic polychaetes*

Most of the pelagic polychaetes are thought to have developed from within the group Phyllodocida. Among the non-phyllodocidan pelagic taxa are *Poeobius meseres*, Flotidae, and the newly discovered *Chaetopterus pugaporcinus* and genus *Swima*.

*Poeobius* differs dramatically from its benthic ancestors, and when it was first discovered, Heath (1930) thought it to be a link between Annelida and Echiura. It was later labelled a polychaete and Hartman (1955) pointed out the similarities to flabelligerids. Burnette *et al.* (2005) placed them within Flabelligeridae in a molecular analysis based on 18S rDNA and cytochrome *b*.

Flotidae is a family with three described species, which are all pelagic. They have been thought to be closely associated to Flabelligeridae (McIntosh 1885, Hartman 1967, Rouse & Pleijel 2003). Flotids are also sometimes linked to *Poeobius* (Rouse & Pleijel 2003, Halanych *et al.* 2007), and they have been proposed to be sister groups, with one single transformation to a pelagic lifestyle for both *Poeobius* and Flotidae (Rouse & Pleijel 2003). Osborn and Rouse (2008) examined the phylogenetic position of *Flota*, and found it to be nested within Flabelligeridae, however not with a common origin with *Poeobius*, thus there are two separate origins of holopelagic life-style in flabelligerids.

*Chaetopterus pugaporcinus* is a newly described species found in deep waters in California off Monterey Bay (Osborn *et al.* (2007)). A molecular analysis showed that it belonged within *Chaetopterus*, a normally benthic, tubicolous polychaete group. The worm exhibits a combination of both adult and larval characteristics, making it difficult to resolve if the specimens found are a suspended giant larval form, or if they indeed are a holopelagic paedomorphic species. Because of the presence of adult features, the authors considered it to be the first known representative of a holopelagic chaetopterid.

Other remarkable deep-sea pelagic polychaetes were found in the northeast and western Pacific Ocean (Osborn *et al.* 2009). Seven new species were discovered and referred to a new genus, *Swima*, with the type species being *Swima bombiviridis*. Five of the species produce bioluminescent bombs, which probably are used for defence. This new genus belongs within Acrocirridae, a family in Cirratuliformia, and thus represents the third pelagic group within cirratuliforms, *Poeobius* and Flotidae being the other two.

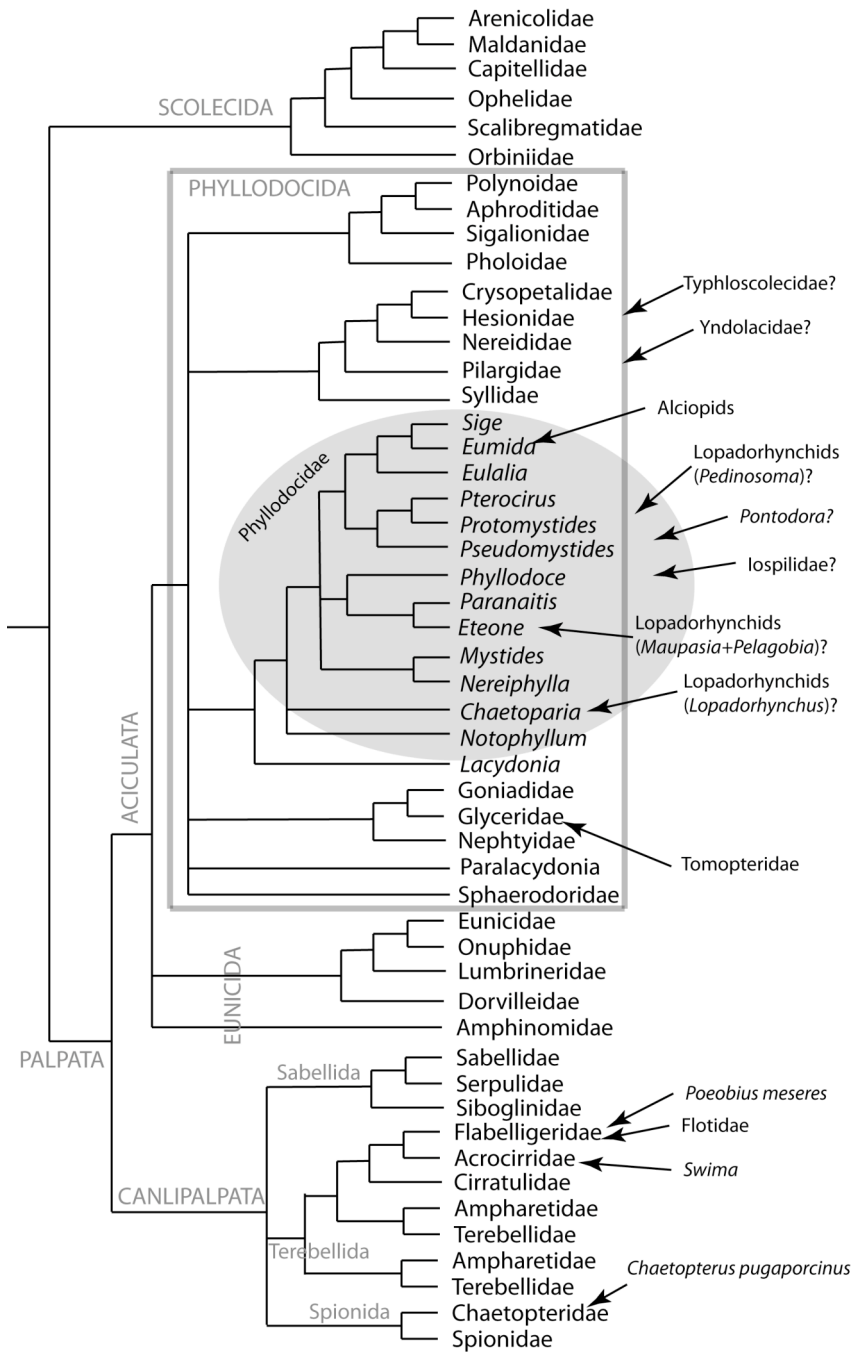
## On the position of Alciopidae and a few other pelagic polychaetes

That Alciopidae is closely related to the benthic Phyllodocidae and even has its closest relative within the group has never actually been questioned because of the large number of morphological similarities (Rouse & Fauchald 1997). Recent molecular studies carried out by Struck *et al.* (2007) and Halanych *et al.* (2007) also have confirmed that Alciopidae is closely related, or possibly belong within Phyllodocidae

In paper II, we concluded that alciopids are indeed a part of Phyllodocidae. The parsimony analysis based on morphology alone suggested that *Pterocirrus* is sister to alciopids, but when adding sequences from four genes Alciopidae was found nested within *Eumida*, with *E. arctica* as sister group. Alciopidae and *Eumida*, in turn, form a clade with *Sige*, *Eulalia*, *Pterocirrus*, *Protomystides* and *Pseudomystides*, a group corresponding to clade A from paper I (Fig. 2). This finding is in contrast to the results from Halanych *et al.* (2007), where Alciopidae was found as sister to *Eulalia viridis*, with *Sige fusigera* as the consecutive sister, while their *Eumida* sp. was not closely related to the two included alciopid taxa. We suggested that this most likely depends on misidentification of their *Eumida* sp.

Our analyses were based on a substantially larger number of taxa and data than earlier molecular studies. Even though our results shows with strong support that Alciopidae originated from within *Eumida* with *E. arctica* as its sister taxon, we could not find any obvious morphological character linking *Eumida* in general or *E. arctica* in particular to Alciopidae, other than the median antennae that is an apomorphy for the whole clade A from paper I.

In addition to the pelagic Alciopids I have sequenced a number of representatives from some of the other pelagic groups that are thought to be associated with Phyllodocidae, among them three members of Lopadorhynchidae, one member of Iospilidae, and one member of Typhloscolecidae. The unpublished results suggest a very interesting scenario with multiples of evolution of pelagisism among the phyllodocids and their closest relatives.



**Fig. 5.** Phylogenetic tree of Polychaeta, modified from Rouse & Pleijel (2001). Arrows indicate possible origins of the pelagic taxa.

Morphologically, there is nothing to suggest that Lopadorhynchidae is monophyletic, and my yet unpublished results from analyses of 18S rDNA, and cytochrome *c* oxidase subunit I (COI) indicate that Lopadorhynchidae consists minimally of two separate groups. Molecular data for the type genus *Lopadorhynchus* is lacking, but Uschakov (1972) presented a tree of phyllodocid relationships where *Lopadorhynchus* is sister to *Chaetoparia*. This was based on the fusion of the anterior segments and the hooks on the anterior segments are superficially similar to those of *Chaetoparia*. Dales (1955) on the other hand suggested that *Lopadorhynchus* had developed from *Protomystides* and *Mystides*. If either Uschakov or Dales is correct, lopadorhynchids is a polyphyletic assembly of pelagic taxa, with as much as three different origins from within or in close connection to Phyllodocidae (Fig. 5).

Preliminary analyses on unpublished molecular data from 18S of Iospilidae and Typhloscolecidae suggest that both groups may be closely related to Phyllodocidae, including alciopids and lopadorhynchids. However, all these preliminary findings need further investigation to draw any firm conclusions.

## CRYPTIC SPECIES

Species may be virtually impossible to separate morphologically but still represent separately evolving lineages that are reproductively isolated from each other. These species are called cryptic species. Cryptic species may be poorly studied organisms that actually have morphological differences, i.e. pseudo-cryptic species, or they may be inseparable to the human eye even after thorough investigations, i.e. true cryptic species (e.g. Westheide & Hass-Cordes 2001). The development of molecular analytical tools has made it possible to assess how common these cryptic species actually are. The marine environment has been suggested as hot spot for cryptic species in parity with tropical rain forest, and the implication of this is that the number of existing marine species is severely underestimated, and this is the case not the least for polychaetes.

There are several reasons why the sea seems to swarm with cryptic species. One reason is that marine organisms often rely on chemical signals in mate recognition, and thus members of two species may perceive themselves to be completely different but look similar to

us humans when we examine them visually. Furthermore, marine taxonomists rarely get the chance to study their organisms in living condition and thus lack knowledge on behaviour as well as of the appearance of live animals, which makes it more difficult to assess species boundaries (Knowlton 1993, 2000). Finally, many marine taxonomists have worked in an over-conservative tradition, in which large intraspecific variation and large distribution areas have been the norm.

In paper III and IV two cryptic species were described using a combined morphological and molecular approach. In one case, the two species were found allopatric (paper III), and in the other sympatric (paper IV). In the case of allopatric cryptic species, it can be difficult to assess whether the genetic distance is due to isolation by distance within a single species, or if the populations really are reproductively isolated. The allopatric study concerned the phyllodocid *Paranaitis wahlbergi* where the Arctic and boreal form morphologically may be separated by maximal size, with the Arctic *P. wahlbergi* reaching more than 10 cm in body length and boreal ones not exceeding 2 cm.

However, both our phylogenetic and population genetic analyses showed that the Arctic and boreal *P. wahlbergi* represented two non-nested clades with large genetic distances and should be treated as distinct species. To rule out that the differences we found were due only to spatial distance, we made a comparison with another phyllodocid, *Phyllodoce groenlandica*, with a similar geographic distribution. As we could not find any geographical separation of haplotypes for *P. groenlandica*, with an intraspecific variation that was comparable to that found within Arctic and boreal *P. wahlbergi*, we concluded that the geographic distance between Svalbard and the Scandinavian localities was unlikely to be the reason for the observed genetic distance, and therefore described the boreal form as *P. katoi* sp. n.

In paper IV we analysed a shallow and deep form of the phyllodocid *Notophyllum foliosum* where the shallow form tends to be more yellow orange and the deep form are more palish yellow to whitish. Both forms are speckled with patches of dark pigment on the dorsal cirri, and in addition the shallow form has white patches on the dorsal cirri, absent in the deep form. The results from our phylogenetic analyses confirmed that the deep and the shallow form of *N. foliosum* represent two genetically distinct species. Both mitochondrial and

nuclear data strongly supported two non-overlapping monophyletic groups, corresponding to one deep and one shallow form. The two forms can also be found sympatrically, which provides direct evidence that they indeed are reproductively isolated (Knowlton 2000). Thus, the shallow and the deep form represent separate species both under a phylogenetic (Mishler & Theriot 2000) and a biological (reproductive) species concept (Mayr 1963).

The phylogenetic relationships of the ingroup taxa of the two forms yielded contradictory results when comparing the mitochondrial COI with the nuclear ITS region. This is probably due to the difference in inheritance pattern between the mitochondrial and the nuclear genes (Avice 2000). Notably the deep form exhibited large intraspecific variation, and in the TCS analyses, the haplotypes formed disconnected networks. A reason for this large variation could have been cryptic species within the deep form, but as we used a combination of nuclear and mitochondrial data we could show that the large variation in COI in the deep form represented intraspecific variation, since the most divergent COI haplotypes were closest together in the ITS tree. Our findings underscore the importance of looking at both mitochondrial and nuclear genes when assessing species boundaries.

We concluded that *Notophyllum foliosum* sensu lato in Scandinavian waters, included two species: *N. crypticum* sp. n., which occurs in deeper waters (at 100–350 m), and *N. foliosum*, which occurs in shallow waters (at 20–125 m). The two species may morphologically be separated on their respective colouration.

Paper V is a study of a species found in western Norway and provides a slightly more complicated version of a common problem in current taxonomy. It can unequivocally be referred to the scalibregmatid genus *Axiokebuita* (based on the presence of well delineated prostomial processes and a bilobed pygidium without appendages). There are two species described in the genus, one from Antarctica, and one from mixed material from Antarctica and Canada (holotype from the latter region), and the genus has not previously been recorded from European waters. Based on morphology (including examination of the types) we were unable to separate, either the two previously described species from each other, or to state if the Norwegian populations are conspecific with either (or both). Phylogenetic analyses were performed based on 18S rDNA and 28S

rDNA to assess the position of the new specimens among scalibregmatids. However, in the absence of ethanol-preserved toptype material of either of the two previously described species, we could not allocate the new specimens to a new species or to any of the previously described ones. We therefore chose to refer them to as “*Axiokebuita*” but not to any known or new species.

## CONCLUSIONS AND FUTURE PROSPECTS

In this thesis I have come to the following conclusions:

- None of the phyllodocid subfamilies, previously defined by morphology, find support by the molecular data. Instead previously not recognized groups, such as “clade A”, “*Nereiphylla-Mystides*”, and “*Paranaitis-Eteone*” have high support.
- The holopelagic family Alciopidae is nested within the phyllodocids. Its closest sister is *Eumida arctica*, making the genus *Eumida*, as delineated today, paraphyletic.
- The Arctic and boreal populations of *Paranaitis wahlbergi* belong to two separate species. The boreal form is described as a new species, *P. katoi* sp. n.
- The sympatric populations of *Notophyllum foliosum*, found in deep and shallow waters are two separate species, morphologically distinguished by different colouration. The deep form is described as *N. crypticum* sp. n.
- A description is provided for *Axiokebuita*, previously not found in European waters. Phylogenetic analysis of molecular data confirms their position among scalibregmatids.

Regarding the benthic phyllodocids, the current classifications require thorough revision. For example, it is not clear which taxa that represent the most basal phyllodocid, and a larger taxon sampling is needed in order to clarify this.

The placement of the pelagic groups that are thought to be closely related to phyllodocids is another important issue. The phylogenetic positions of Lopadorhynchidae, Iospilidae, *Pontodora*, and Typhloscolecidae are uncertain, and they may very well be found

to belong within Phyllodocidae, or other closely related Phyllodocida families.

## SUMMARY OF INCLUDED PAPERS

### PAPER I

Jenny Eklöf, Fredrik Pleijel & Per Sundberg (2007). Phylogeny of benthic Phyllodocidae (Polychaeta) based on morphological and molecular data. *Molecular Phylogenetics and Evolution*, 45(1): 261-271.

A combined molecular (18S rDNA, 28S rDNA, 16S rDNA and COI) and morphological analysis of the benthic phyllodocids is presented for the first time. Nineteen phyllodocids and two outgroup taxa are assessed using parsimony, maximum likelihood and Bayesian analyses. We demonstrate high degrees in homoplasy in the traditionally used morphological phyllodocid characters, and show that all the three current subfamilies Phyllodocinae, Eteoninae and Notophyllinae are non-monophyletic. The genera *Eulalia*, *Eumida*, *Protomystides*, *Pseudomystides*, *Pterocirrus* and *Sige* form a well-supported group, as does *Mystides* and *Nereiphylla*. Another clade with strong support includes *Eteone* and *Paranaitis*, although with *Eteone* nested within a paraphyletic *Paranaitis*. The relationship between these two taxa indicate that the unusual arrangement of modified cirri on the first segments in *Eteone* is due to a fusion of segment 1 and 2 where the cirri of segment 1 have been reduced. *Eulalia* is non-monophyletic and should be split, minimally into two groups. Our results are ambiguous regarding the ancestral phyllodocid condition of absence–presence of median antenna or nuchal papilla and uniramous or biramous parapodia, but shows that the absence of cirri on segment 3 (previously an apomorphy, for e.g. *Mystides*, *Pseudomystides* and *Hesionura*) is maximally homoplastic.

### PAPER II

Jenny Eklöf, Arne Nygren, Karen Osborn, Per Sundberg & Fredrik Pleijel. *Eumida* (Phyllodocidae, Annelida) goes pelagic. (manuscript)



The spectacular holopelagic Alciopidae has long been thought to be closely related to Phyllodocidae. Recently, evidence that their origin is from within Phyllodocidae was presented. We add sequences from three more Alciopidae taxa and a much broader taxon sampling from the benthic members of Phyllodocidae. Our analysis based on four genes (18SrDNA, 28SrDNA, 16SrDNA and COI) and morphological characters shows surprisingly that Alciopidae belongs within the genus *Eumida*, where *Eumida arctica* constitutes the closest known relative to Alciopidae.

### **PAPER III**

Arne Nygren, Jenny Eklöf & Fredrik Pleijel. (2009). Arctic-boreal sibling species of *Paranaitis* (Polychaeta, Phyllodocidae). Marine Biology Research 5(4): 315–327

The phyllodocid polychaete *Paranaitis wahlbergi* occurs in Arctic and northern European boreal waters. Boreal populations are distinct from Arctic ones in having smaller maximal size and larger eggs; in all other respects we find them morphologically inseparable. Phylogenetic analyses and haplotype networks based on the mitochondrial genes 16S rDNA and COI, and the nuclear genes histone H3, ITS1, ITS2, 18S rDNA and 28S rDNA D1-D2 region confirm our suspicion that Arctic and boreal populations belong to different species. We describe the boreal form as a new species, *Paranaitis katoi*. It is presently known from the Swedish and Norwegian west coasts and from Scotland. Calibrated rates for COI indicate that *P. katoi* sp. nov. and *P. wahlbergi* may have been separate for as long as 29-56 million years.

### **PAPER IV**

Arne Nygren, Jenny Eklöf & Fredrik Pleijel. (2010) Cryptic species of *Notophyllum* (Polychaeta: Phyllodocidae) in Scandinavian waters. Organisms Diversity & Evolution, DOI 10.1007/s13127-010-0014-2.

The phyllodocid polychaete *Notophyllum foliosum* occurs in two colour morphs in Swedish and Norwegian waters, one palish yellow to grey form with black patches that is restricted to deeper waters and often associated with reefs of the deep-water coral *Lophelia pertusa*, and one usually yellow-orange form with black patches and white spots that is usually encountered on more shallow bottoms. We have

sampled the shallow form on the Swedish west coast, and both forms sympatrically in Norway. Phylogenetic and haplotype analyses based on the mitochondrial cytochrome *c* oxidase subunit I (COI) gene and the nuclear internal transcribed spacer region (ITS1-5.8SrDNA-ITS2) unequivocally indicate that the two forms represent different species. We apply the name *N. foliosum* (Sars, 1835) to the ‘shallow form’, and *N. crypticum* n. sp. for the ‘deep form’. A lectotype is designated for *N. foliosum*.

## PAPER V

Jenny Persson & Fredrik Pleijel. (2005). On the phylogenetic relationships of *Axiokebuita*, *Travisia* and Scalibregmatidae (Polychaeta). *Zootaxa*, 998 :1-14.

We provide a description of newly collected specimens of *Axiokebuita* from Norway, previously known only from east Canada and the Antarctic. Due to delineation problems between the only two described species, *A. minuta* and *A. millsii*, these new specimens cannot unambiguously be referred to either species. Previously unnoticed adhesive papillae on the pygidium are present in both species and may constitute an apomorphy for *Axiokebuita*. The taxon lacks many morphological features otherwise characteristic for scalibregmatids, and to assess its affinities we present 18S rDNA and 28S rDNA-based analyses together with six other scalibregmatids and twenty other polychaetes. A nemertean is used as out-group. All analyses support that *Axiokebuita* is a scalibregmatid. Furthermore, *Travisia*, traditionally referred to the Opheliidae, is nested within the scalibregmatids, as sister to *Neolipobranchius*. Arenicolidae and Maldanidae may constitute the sister group of scalibregmatids.

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## SVENSK SAMMANFATTNING

Havsborstmaskar är en stor grupp av segmenterade maskar som uppvisar en enorm morfologisk mångfald. Molekylära data har nyligen visat att grupper som tidigare ansetts vara skilda från havsborstmaskar istället ingår i denna grupp. Släktskapsförhållandena inom de olika havsborstmaskgrupperna har visat sig vara svårt att reda ut och analyser med DNA har bara delvis gett stöd till de grupper som tidigare klassificerats med hjälp av morfologi.

Målsättningen med den här avhandlingen har främst varit att undersöka familjen Phyllodocidae och deras fylogenetiska släktskap. Våra resultat visar att inga av de tidigare beskrivna underfamiljerna har stöd från molekylära data. Istället finns stöd för andra grupper, till exempel en där alla utom en av de arter som ingår har det gemensamt att de har en mittantenn.

De flesta havsborstmaskar är bottenlevande, många har dock ett frisimmande larvstadium. Det finns emellertid grupper av havsborstmaskar som lever hela sina liv i pelagialen, och en av dessa är gruppen Alciopidae. Vi har visat att Alciopidae har utvecklats från phyllodociderna, med en art av släktet *Eumida*, *Eumida arctica* som den närmsta systerarten.

Delar av denna avhandling handlar också om kryptiska arter, arter som är svåra eller omöjliga att skilja åt genom dess utseende men som ändå tillhör olika utvecklingslinjer och som är reproduktivt isolerade. Vi har visat att arktiska och skandinaviska populationer av *Paranaitis wahlbergi* tillhör två separata arter, och beskrev den skandinaviska som en ny art, *P. katoi*.

*Notophyllum foliosum* är en phyllodocid med två populationer som lever inom samma geografiska område, men som hittas på djupt (nedanför 100 meter) respektive grunt vatten (grundare än 100 meter). De kan särskiljas genom att de har olika färgteckning, och vi har även visat att dessa tillhör olika arter. Den form som hittas på djupt vatten beskrevs som *N. crypticum*.

I avhandlingen finns också en beskrivning av *Axiokebuita*, en art inom familjen Scalibregmatidae som tidigare inte hittats i europeiska vatten. Dessutom finns en fylogenetisk analys baserad på molekylära data som fastställer dess position bland scalibregmatiderna.

## REFERENCES

- Avise, J. (2000) Phylogeography. Cambridge University Press, Cambridge
- Bergström, E. (1914) Zur systematik der polychaetenfamilie der phyllodociden. *Zoologiska bidrag från Uppsala* 3:37–224
- Bleidorn, C., Podsiadlowski, L. & Bartolomaeus, T. (2006) The complete mitochondrial genome of the orbiniid polychaete *Orbinia latreillii* (Annelida, Orbiniidae) - A novel gene order for Annelida and implications for annelid phylogeny. *Gene* 370:96–103
- Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2003) New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 29:279–288
- Boore, J.L. & Brown, W.M. (2000) Mitochondrial genomes of *Galathealinum*, *Helobdella*, and *Platynereis*: Sequence and gene arrangement comparisons indicate Pogonophora is not a phylum and Annelida and Arthropoda are not sister taxa. *Molecular Biology and Evolution* 17:988–988
- Boore, J.L. & Staton, J.L. (2002) The mitochondrial genome of the sipunculid *Phascolopsis gouldii* supports its association with Annelida rather than Mollusca. *Molecular Biology and Evolution* 19:127–137
- Brown, S., Rouse, G., Hutchings, P. & Colgan, D. (1999) Assessing the usefulness of histone H3, U2 snRNA and 28S rDNA in analyses of polychaete relationships. *Australian Journal of Zoology* 47:499–516
- Burnette, A.B., Struck, T.H. & Halanych, K.M. (2005) Holopelagic *Poeobius meseres* ("Poeobiidae," Annelida) Is Derived From Benthic Flabelligerid Worms. *Biological Bulletin* 208:213–220
- Buzhinskaja, G. (2004) Two new genera of the pelagic family Yndolaciidae (Polychaeta) from the Arctic Ocean with an addition to the description of *Yndolacia lopadorrhynchoides* Støp-Bowitz. *Sarsia: North Atlantic Marine Science* 89:338–345
- Colgan, D.J., Hutchings, P.A. & Braune, M. (2006) A multigene framework for polychaete phylogenetic studies. *Organisms Diversity & Evolution* 6:220–235
- Dales, R.P. (1955) The evolution of the pelagic alciopid and phyllodocid polychaetes. *Proceedings of the Royal Society of London* 125:411–420
- Dales, R.P. (1972) A synopsis of the pelagic Polychaeta. *Journal of Natural History* 6:55–92
- Day, J.H. (1967) A Monograph on the Polychaeta of Southern Africa, pt. 1: Errantia. British Museum (Natural History), London
- Dunn, C.W., Hejnol, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., Sorensen, M.V., Haddock, S.H.D., Schmidt-Rhaesa, A., Okusu, A., Kristensen, R.M., Wheeler, W.C., Martindale, M.Q. & Giribet, G. (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452:745–749
- Eibye-Jacobsen, D. (1993) On the phylogeny of the Phyllodocidae (Polychaeta Annelida): an alternative. *Zeitschrift für Zoologische Systematik und*

- Evolutionsforschung* 31:174–197
- Eibye-Jacobsen, D. & Nielsen, C. (1996) The rearticulation of annelids. *Zoologica Scripta* 25:275–282
- Eklöf, J., Pleijel, F. & Sundberg, P. (2007) Phylogeny of benthic Phyllodoceidae (Polychaeta) based on morphological and molecular data. *Molecular Phylogenetics and Evolution* 45:261–271
- Fauchald, K. (1977) The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County. Science Series* 28:1–188
- Fauchald, K. & Jumars, P.A. (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review* 17:193–284
- Fauchald, K. & Rouse, G. (1997) Polychaete systematics: Past and present. *Zoologica Scripta* 26:71–138
- Fauvel, P. (1923) Polychètes Errantes. *Faune de France, Paris*. 5:1–488
- George, J.D. & Hartmann-Schröder, G. (1985) Polychaetes: British Amphinomida, Spintherida and Eunicida. Keys and notes for the identification of the species. EJ Brill & Dr. W. Backhuys, London
- Greiff, R. (1876) Untersuchungen über Alciopiden. *Nova Acta*. 39:33–132
- Halanych, K.M., Cox, L.N. & Struck, T.H. (2007) A brief review of holopelagic annelids. *Integrative and Comparative Biology* 47:872–879
- Hall, K.A., Hutchings, P.A. & Colgan, D.J. (2004) Further phylogenetic studies of the Polychaeta using 18S rDNA sequence data. *Journal of the Marine Biological Association of the UK* 84:949–960
- Hartman, O. (1955) Endemism in the North Pacific Ocean, with emphasis on the distribution of marine annelids, and descriptions of new or little known species. *Essays in the Natural Sciences in Honor of Captain Allan Hancock*. University of Southern California Press, Los Angeles, p 39–57
- Hartman, O. (1967) Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Foundation Monographs in Marine Biology* 2:1–387
- Heath, H. (1930) A connecting link between the Annelida and the Echiuroidea (Gephyrea Armata). *Journal of Morphology* 49:223–249
- Hessling, R. & Westheide, W. (2002) Are Echiura derived from a segmented ancestor? Immunohistochemical analysis of the nervous system in developmental stages of *Bonellia viridis*. *Journal of Morphology* 252:100–113
- Jördens, J., Struck, T. & Purschke, G. (2004) Phylogenetic inference regarding Parergodrilidae and *Hrabeiella periglandulata* ('Polychaeta', Annelida) based on 18S rDNA, 28S rDNA and COI sequences. *Journal of Zoological Systematics & Evolutionary Research* 42:270–280
- Knowlton, N. (1993) Sibling Species in the Sea. *Annual Review of Ecology and Systematics* 24:189–216
- Knowlton, N. (2000) Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* 420:73–90
- Kojima, S. (1998) Paraphyletic status of Polychaeta suggested by phylogenetic analysis based on the amino acid sequences of elongation factor-1 alpha. *Molecular Phylogenetics and Evolution* 9:255–261

- Martin, P. (2001) On the origin of the Hirudinea and the demise of the Oligochaeta. *Proceedings of the Royal Society of London, Series B-Biological Sciences* 268:1089–1098
- Mayr, E. (1963) Animal species and evolution. Harvard University Press, Cambridge
- McHugh, D. (1997) Molecular evidence that echiurans and pogonophorans are derived annelids. *Proceedings of the National Academy of Sciences of the United States of America* 94:8006–8009
- McHugh, D. (1999) Phylogeny of the Annelida: Siddall et al. (1998) rebutted. *Cladistics-the International Journal of the Willi Hennig Society* 15:85–89
- McIntosh, W.C. (1885) Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-76. *12:1–554*
- Mishler, B. & Theriot, E. (2000) The phylogenetic species concept (sensu Mishler and Theriot): monophyly, apomorphy, and phylogenetic species concepts. In: Q. Wheeler and R. Meier (eds) *Species concepts and phylogenetic theory. A debate*. Columbia University Press, New York, p 44–54
- Newby, W.W. (1940) The embryology of the echiuroid worm, *Urechis caupo*. *The American Philosophical Society* 16:1–219
- Nielsen, C. (1995) Animal evolution. Interrelationships of the living phyla. Oxford University Press, Oxford
- Nygren, A., Eklöf, J. & Pleijel, F. (2009) Arctic-boreal sibling species of *Paranaitis* (Polychaeta, Phyllodocidae). *Marine Biology Research* 5:315–327
- Nygren, A., Eklöf, J. & Pleijel, F. (2010) Cryptic species of *Notophyllum* (Polychaeta: Phyllodocidae) in Scandinavian waters. *Organisms Diversity & Evolution*
- Orrhage, L. & Eibye-Jacobsen, D. (1998) On the anatomy of the central nervous system of phyllodocidae (Polychaeta) and the phylogeny of Phyllodocid genera: a new alternative. *Acta Zoologica* 79:215–234
- Osborn, K.J., Haddock, S.H.D., Pleijel, F., Madin, L.P. & Rouse, G.W. (2009) Deep-Sea, Swimming Worms with Luminescent "Bombs". *Science* 325:964–964
- Osborn, K.J. & Rouse, G.W. (2008) Multiple origins of pelagicism within Flabelligeridae (Annelida). *Molecular Phylogenetics and Evolution* 49:386–392
- Persson, J. & Pleijel, F. (2005) On the phylogenetic relationships of *Axiokebuita*, *Travisia* and Scalibregmatidae (Polychaeta). *Zootaxa* 998:1–14
- Pleijel, F. (1991) Phylogeny and classification of the Phyllodocidae (Polychaeta). *Zoologica Scripta* 20:225–261
- Pleijel, F. (1993) Phylogeny of Phyllodoce (Polychaeta, Phyllodocidae). *Zoological Journal of the Linnean Society* 108:287–299
- Pleijel, F. (2008) A cladistic analysis of Siboglinidae Caullery, 1914 (Polychaeta, Annelida): formerly the phyla Pogonophora and Vestimentifera. *Zoological Journal of the Linnean Society* 132:55–80
- Pleijel, F. & Dales, R.P. (1991) British Phyllodocoideans, Typhloscolecoideans and Tomopteroideans. *Synopses of the British Fauna (New Series)* 45:1–202
- Purschke, G. (1997) Ultrastructure of nuchal organs in polychaetes (Annelida) - New results and review. *Acta Zoologica* 78:123–143
- Reibisch, J. (1895) Die pelagischer Phyllodociden und Typhloscoleciden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* 2:1–63

- Rouse, G.W. (2001) A cladistic analysis of Siboglinidae Caullery, 1914 (Polychaeta, Annelida): formerly the phyla Pogonophora and Vestimentifera. *Zoological Journal of the Linnean Society* 132:55-80
- Rouse, G.W. & Fauchald, K. (1997) Cladistics and polychaetes. *Zoologica Scripta* 26:139-204
- Rouse, G.W. & Pleijel, F. (2001) Polychaetes. Oxford University Press, Oxford
- Rouse, G.W. & Pleijel, F. (2003) Problems in polychaete systematics. *Hydrobiologia* 496:175-189
- Rouse, G.W. & Pleijel, F. (2006) Annelid phylogeny and systematics In: G.W. Rouse and F. Pleijel (eds) *Reproductive biology and phylogeny of Annelida*. Science Publishers Inc., Enfield, New Hampshire, p 3-21
- Rousset, V., Rouse, G.W., Siddall, M.E., Tillier, A. & Pleijel, F. (2004) The phylogenetic position of Siboglinidae (Annelida) inferred from 18S rRNA, 28S rRNA and morphological data. *Cladistics* 20:518-533
- Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007) A molecular phylogeny of annelids. *Cladistics* 23:41-63
- Shen, X., Ma, X., Ren, J. & Zhao, F. (2009) A close phylogenetic relationship between Sipuncula and Annelida evidenced from the complete mitochondrial genome sequence of *Phascolosoma esculenta*. *BMC Genomics* 10:136
- Storch, V. (1968) Zur vergleichenden Anatomie der segmentalen Muskelsysteme und zur Verwandtschaft der Polychaeten-Familien. *Zeitschrift für Morphologie und Ökologie der Tiere* 63:251-342
- Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D. & Halanych, K.M. (2007) Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology* 7:
- Støp-Bowitz, C. (1987) A new genus and species (*Yndolacia lopadorrhynchoides*) of pelagic polychaetes, representative of a new family, Yndolaciidae. *Bulletin of the Biological Society of Washington* 7:131-139
- Uschakov, P.V. (1972) Polychaeta 1. Polychaetes of the sub-order Phyllodociforma of the Polar Basin and the north-western part of the Pacific (translated from Russian by the Israel Program for Scientific Translation, Jerusalem 1974). *Fauna SSSR* 102:1-271
- Westheide, W. (1997) The direction of evolution within the Polychaeta. *Journal of Natural History* 31:1-15
- Westheide, W. & Hass-Cordes, E. (2001) Molecular taxonomy: description of a cryptic *Petitita* species (Polychaeta: Syllidae) from the island of Mahé (Seychelles, Indian Ocean) using RAPD markers and ITS2 sequences. *Journal of Zoological Systematics & Evolutionary Research* 39:103-111
- Westheide, W., McHugh, D., Purschke, G. & Rouse, G.W. (1999) Systematization of the Annelida: different approaches. *Hydrobiologia* 402:291-307
- Wilson, R.S. (2000a) Family Lopadorrhynchidae In: P.L. Beesley, G.J.B. Ross and G. C.J. (eds) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia*. CSIRO Publishing, Melbourne
- Wilson, R.S. (2000b) Family Tomopteriidae In: P.L. Beesley, G.J.B. Ross and G. C.J. (eds) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia*. CSIRO Publishing, Melbourne
- Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. (2009) Phylogeny of Annelida



- (Lophotrochozoa): total-evidence analysis of morphology and six genes.  
*BMC Evolutionary Biology* 9:189–203
- Åkesson, B. (1962) The embryology of *Tomopteris helgolandica* (Polychaeta). *Acta Zoologica* 43:135–199
- Øresland, V. & Pleijel, F. (1991) An ectoparasitic typhloscolecid polychaete on the chaetognath *Eukrohnia hamata* from the Antarctic Peninsula. *Marine Biology* 108:429–432