

# A brief review of holopelagic annelids

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**Synopsis** Annelids are one of the most successful major animal lineages in terms of number of species and of habitats occupied. Despite annelids being common in terrestrial, aquatic, and marine environments, only a limited number of lineages have evolved a holopelagic existence. Most of these holopelagic lineages belong to Phyllodocida (nereidids, syllids, scale worms, and jawed worms) and more particularly often within the family Phyllodocidae. These worms generally appear to retain many characteristics of adult annelids. Moreover, we provide molecular evidence showing that the well-known alciopids are derived from within Phyllodocidae. In contrast, at least two lineages, *Poebobius meseres/Flota flabelligera* and probably *Chaetopterus pugaporcinus*, are derived through paedomorphic processes acting on larvae from lineages that have sedentary adult forms. Herein, we will briefly review the known diversity of holopelagic annelids with discussion of their evolutionary origins.

## Introduction

Annelids are typically considered to be benthic organisms that spend all of their time either in the substrate or just on top of it, living out a slow and rather sedentary existence. However, this view clearly does not fit the wonderful diversity of annelids that is found throughout the world. Many annelids are, in fact, very active and several taxa spend their entire life cycle in the pelagic environment. Annelids comprise about 16,500 described species with numerous more awaiting description, or even discovery (Brusca and Brusca 2003). With the advent of molecular phylogenetic analyses, we now understand that several groups traditionally classified as distinct phyla actually fall within the annelid radiation. For example, echiurids, siboglinids (formerly vestimentiferans and pogonophorans), and even sipunculids are nested within Annelida (McHugh 1997; Halanych 2004; Bleidorn et al. 2006; Rousset et al. 2007; Struck et al. 2007). Although knowledge of annelids is increasing, some environments remain poorly sampled. One of these environments is the pelagic realm. Herein, we briefly review the diversity and evolutionary origins of known holopelagic annelids.

Evolutionary and environmental conditions under which holopelagic organisms originate and diversify certainly varies from lineage to lineage, and we expect organisms to be differentially adapted for pelagic versus benthic existence. In general,

holopelagic organisms can be derived from either a holopelagic ancestor or a benthic ancestor. Organisms with a biphasic life history are still typically considered to be benthic organisms, at least in the adult phase. From morphological and life-history perspectives, holopelagic species derived from holopelagic ancestors are less interesting than are species derived from benthic ancestors because the latter situation usually involves more drastic change in overall body plan and life history.

Furthermore, organismal evolution typically proceeds by modification of existing structures rather than by *de novo* inventions, and thus one might expect organisms to be “constrained by phyletic heritage” (*sensu* Gould and Lewontin 1979), thereby possessing clues of their ancestral forms. These clues can be important for elucidating selective regimes and circumstances under which holopelagic species originate. Considering that a benthic annelid life cycle may consist of a larva, a juvenile, an adult, and an epitoke (a terminal reproductive form), it is conceivable that evolutionary processes promoting holopelagogy could act on any (or all) of these forms. For example, pelagic larvae of a sessile organism may be subject to paedomorphic processes that, in essence, prolong a pelagic larval stage and ultimately abolish larval settlement. Alternatively, survival and regeneration of an actively swimming, but spawned, epitoke may have been the first steps on an evolutionary trajectory that led to

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**Table 1** Holopelagic annelid lineages

Taxon	Phylogenetic origins	Adult homologous to ancestral	Number of species
Alciopidae	Phyllodocidae	adult	30
Lopadorhynchidae	Phyllodocida—maybe within Phyllodocidae	adult	15
Tomopteridae	Phyllodocida—sister to Glyceriforms	adult	60
Typhloscolecidae	Phyllodocida	adult	13
Iospilidae	Phyllodocida—near Nerididae or Tomopteridae	adult	11
<i>Pontodora pelagica</i>	Phyllodocida—maybe within Phyllodocidae	adult	1
Yndolaciidae	Phyllodocidae	adult	3
<i>Poebius meseres/Flota flabelligera</i>	Flabelligeridae	larvae	2
<i>Chaetopterus pugaporcinus</i>	Chaetopteridae	larvae	1

a holopelagic existence. Even the adult phase of a more active species (e.g., a eunicid, nereidid, or phyllodocid) might possibly acquire a more holopelagic lifestyle in response to, for example, a dietary shift or predation.

In the case of annelids, holopelagic taxa are derived from both larval forms as well as adult (more generally postjuvenile) forms. Dale and Peter's (1972) review of holopelagic annelids gives basic taxonomic information and a sense of diversity, but a better treatment of their general biology is given by Uschakov (1972). We know of at least nine annelid lineages (Table 1) that have acquired a holopelagic existence. Some of these lineages have undergone evolutionary radiations once in the plankton or have established cosmopolitan populations. Below, we briefly review each of these taxa in turn. Herein, we use a mindset of phylogenetic taxonomy by referring to the most appropriate clade name that is nonredundant.

## Alciopidae

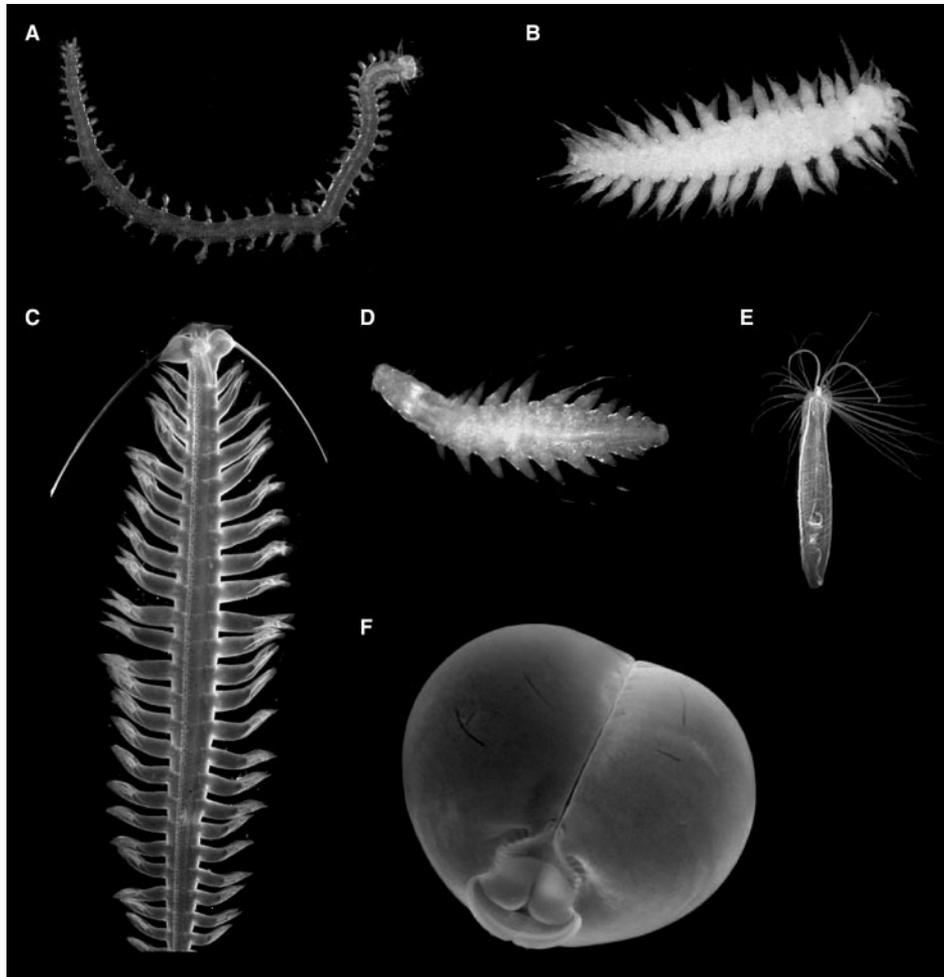
Alciopids are relatively long and slender holopelagic worms (Fig. 1A) whose most conspicuous feature is their pair of very large eyes. Segments, which can be more than a hundred, are clearly delineated, and they have well-developed biramous parapodia possessing both aciculae and chaetae. They are cosmopolitan in distribution and can occur in the upper and mid-water columns. As with many holopelagic organisms,

when collected by net, they are often broken or are in poor condition. In particular, Uschakov (1972), Rice (1987), and Wu and Lu (1993) provide information about these animals.

Ehlers (1864) erected the family Alciopidae for this group comprising about 30 species in nine genera. Although generally treated as a valid family (Fauchald 1977; Rice 1987; Fauchald and Rouse 1997), more recent workers regard the taxon as within Phyllodocidae (Rouse and Pleijel 2001). A recent molecular analysis by Struck et al. (2007) support phyllodocid affinities, but their taxonomic sampling was not sufficient to resolve if alciopids were sister to, or within, Phyllodocidae.

In order to address this issue, we performed a phylogenetic analysis using available 18S nuclear ribosomal gene data from GenBank. Table 2 indicates the taxa employed and their GenBank accession numbers. Details of data collection (e.g., DNA extraction, PCR, and sequencing) and more thorough phylogenetic methods are given by Struck et al. (2006). Outgroups were chosen based on the annelid phylogeny of Struck et al. (2007). Sequences were aligned with Clustal W (Thompson et al. 1994) and corrected by eye. The data matrix is available from TreeBase ([www.treebase.org](http://www.treebase.org)). Regions that could not be aligned with certainty were excluded from analysis. Bayesian inference analyses were performed with MrBayes (Huelsenbeck and Ronquist 2001) using the model suggested by MrModeltest (Nylander 2002; see Fig. 2 legend). Two sets of four Markov chains (three heated and one cold) ran simultaneously for one million generations with trees being sampled every 100 generations. The first 1000 trees from each set were discarded as "burn in" based on the convergence of likelihood scores. The majority-rule consensus tree and posterior probabilities of the phylogeny were determined from the remaining 18,002 trees (9001 from each set).

The 18S tree (Fig. 2) placed alciopid taxa within Phyllodocidae with strong support as judged by posterior probabilities. This result strengthens arguments (Rouse and Pleijel 2001) that alciopids should be regarded as a derived phyllodocid lineage. Thus, this group should be recognized as Alciopini and not Alciopidae. Given the taxon sampling here, the position of alciopids within Phyllodocidae is uncertain. Alciopids have several features that are associated with an adult morphology (i.e., well-developed parapodia, numerous segments, well-developed eyes, nuchal organs) and, like some phyllodocids, alciopids are strong swimmers. Therefore, there is no reason to suspect alciopids



**Fig. 1** Photographs of holopelagic annelids (A) Alcipodidae, (B) Lopadorhynchidae, (C) Tomopteridae, (D) Iospilidae, (E) *Poeobius meseres*, and (F) *Chaetopterus pugaporcinus*. Note the posterior and the long second-segment cirri are not fully pictured in the tomopterid image. Karen Osborn of MBARI deserves photo credit for the *Poeobius meseres* image. The *C. pugaporcinus* image is from Osborn et al. (2007). Permission to reprint both these latter images was kindly provided by *Biological Bulletin*.

are the product of pedomorphic processes acting on larvae. In other words, the adult alciopid form is homologous to the adult form of their phyllodocid ancestors.

### Lopadorhynchidae

Lopadorhynchids are relatively small, up to 5 cm, dorso-ventrally flattened holopelagic worms with up to approximately 40 segments (Fig. 1B). In general, these worms have well-developed parapodia with chaetae and their body tapers slightly at both ends. The group may be nonmonophyletic (Fauchald and Rouse 1997; Rouse and Pleijel 2001) making discussion of the group's morphological apomorphies awkward. In general, there are two groups within this recognized family, mainly distinguished by anterior features including degree of prostomium–peristomium fusion, degree of

muscularization of anterior segments, and variable presence of chaetae. The head and parapodia are generally well-developed. There are four recognized genera with about 15 species which, taken together, have a cosmopolitan distribution (Dales and Peter 1972; Fauchald 1977). Rouse and Pleijel (2001) reported Lopadorhynchids to be more common in warm waters, but they are rather common in Antarctic waters as well (K.M.H., personal observation).

Lopadorhynchidae has previously been considered to be within Phyllodocidae (Uschakov 1972), but they are more typically considered a family within Phyllodocida (Fauchald 1977; Fauchald and Rouse 1997; Rouse and Pleijel 2001). Morphological analyses place them near Phyllodocidae and Lacydoniidae (Rouse and Fauchald 1997). To our knowledge they have not yet been molecularly characterized.

**Table 2** Taxa used in the phylogenetic analysis of Alciopidae based on 18S

Taxon	Species	GenBank accession
Alciopidae	<i>Alciopina</i> sp.	DQ790073
	<i>Torrea</i> sp.	DQ790096
Phyllodocidae	<i>Eulalia viridis</i> 1	AY340428
	<i>Eulalia viridis</i> 2	AY525627
	<i>Sige</i> sp.	AY894305
	<i>Phyllodoce maculata</i>	AY176302
	<i>Phyllodoce groenlandica</i>	DQ790092
	<i>Phyllodoce</i> sp.	AB106249
	<i>Notophyllum foliosum</i>	DQ779662
	<i>Eteone picta</i>	DQ779648
	<i>Eteone longa</i>	AF448155
	<i>Eumida</i> sp.	AY894296
	<i>Anatides</i> sp.	AY894293
Outgroups		
Tomopteridae	<i>Tomopteris</i> sp.	DQ790095
Glyceridae	<i>Glycera dibranchiata</i>	AY995208
Goniadidae	<i>Glycinde amigera</i>	DQ790079
	<i>Goniada brunnea</i>	DQ790080

## Tomopteridae

Common in near-shore waters and relatively large (up to 10 cm), tomopterids are perhaps the most familiar holopelagic annelid (Fig. 1C). Comprising about 60 species in two recognized genera, these dorso-ventrally flattened worms are cosmopolitan in distribution (Dales and Peter 1972). Their conspicuous palps, long parapodial cirri on the second segment, and fusion of the prostomium with the first two segments, make the head of tomopterids very distinctive (Fauchald 1977). Parapodia are well-developed but lack chaetae as adults. Åkesson's (1962) report on the development of *Tomopteris helgolandica* shows that these worms bear chaetae as juveniles. Tomopterids, along with alciopids, are among the most transparent annelids, but they can have some pigmentation (Fig. 1C).

Tomopterids have traditionally been treated as within Phyllodocida, but their exact placement has been uncertain (Rouse and Pleijel 2001). Morphological analyses (Rouse and Fauchald 1997) place them close to the holopelagic Iospilidae and near *Lacydonia* and Phyllodocidae. In comparison, the multigene analysis of Struck et al. (2007) place tomopterids as sister to a Glyceridae/Goniadidae clade. This tomopterid/glyceriform clade is, in turn, sister to a phyllodocid/alciopid clade. Thus, when

additional molecular data are available, Iospilidae and *Lacydonia* may be part of this larger clade. Given that tomopterids are usually very active swimmers and have morphology similar to other adult annelids, there is little doubt that the adult form of tomopterids is directly homologous to the adult form of their ancestors.

## Typhloscolecidae

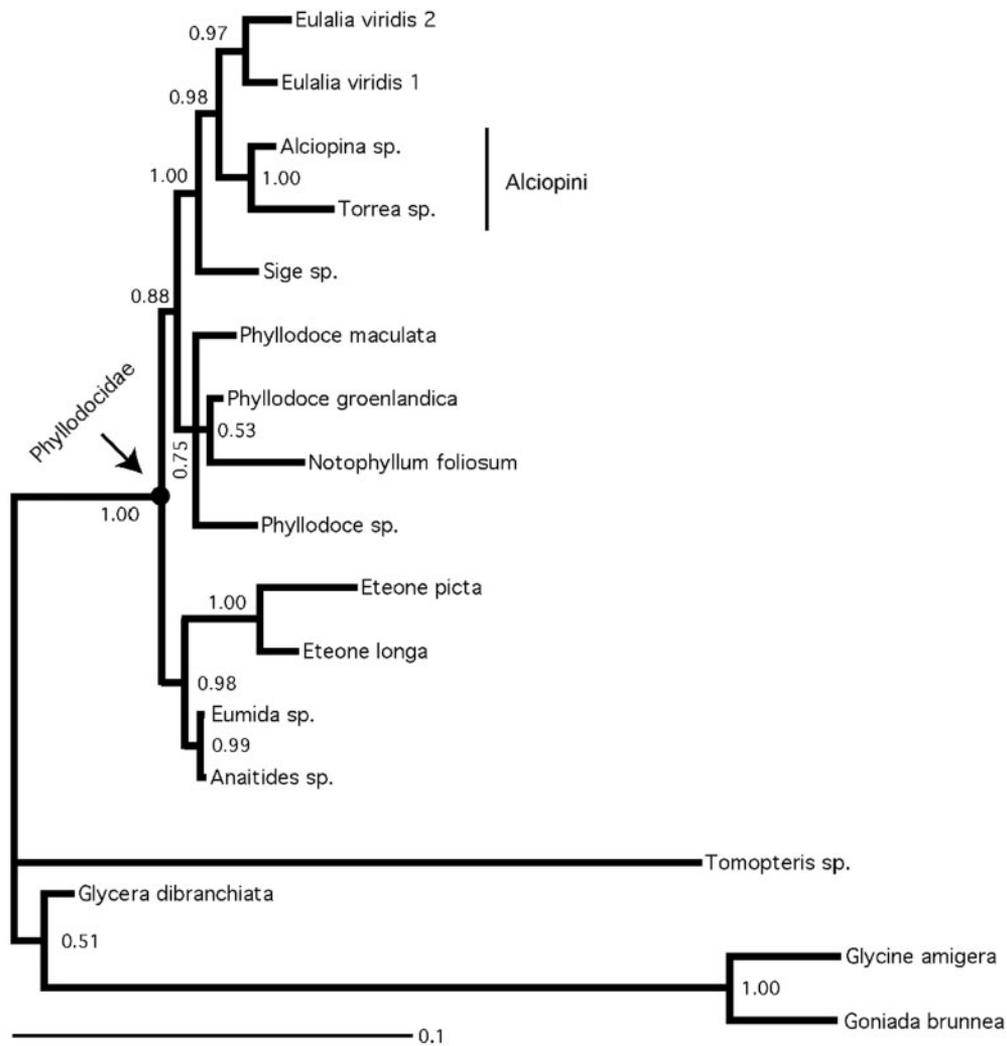
These transparent holopelagic annelids are roughly cylindrical with the body tapering from the anterior to the posterior. Approximately 13 species in three genera are known ranging in length from 0.5 to 4 cm with up to 50 segments (Rouse and Pleijel 2001). Throughout most of the worm's length, dorsal and ventral cirri are broad and foliose, reminiscent of phyllodocids. Only very limited information exists on the biology of this group. Some reports on feeding are given (Feigenbaum 1979; Øresland and Pleijel 1991) suggesting that some species may prey on chaetognaths. Chaetae are present. Although clearly within Phyllodocida, more exact placement is not clear (Rouse and Fauchald 1997; Rouse and Pleijel 2001).

## Iospilidae

Comprising about 11 species in four recognized genera, Iospilidae are small (<1 cm) holopelagic polychaetes that may have eyes and, in some cases, a pair of lateral jaws (Fig. 1D; Fauchald 1977; Fauchald and Rouse 1997; Rouse and Pleijel 2001). Upon collection they appear to be relatively good swimmers compared to some similar, small-sized holopelagic annelids (e.g., *Poebobius meseres*) and possess well-developed parapodia. They are apparently cosmopolitan, and are not too uncommon in Southern Ocean surface waters (down to 200 m) near the Antarctic Peninsula (K.M.H., personal observation). Although morphology suggest origins in Phyllodocida, Fauchald (1977) notes that they are rather distinct from Phyllodocidae. Given that Uschakov (1972) suggests they are within Phyllodocidae and Rouse and Fauchald's (1997) cladistic study suggests placement near Nereididae and Tomopteridae, it is safe to say we have little idea where they fit in phyllodocid phylogeny.

## *Pontodora pelagica*

As with other holopelagic polychaetes, little is known about the biology of *Pontodora pelagica*. This relatively small worm (up to 5 mm) can have about 17–18 segments, a pair of small eyes and antennae (Fauchald 1977; Rouse and Pleijel 2001).



**Fig. 2** Results of Bayesian analysis of alciopid phylogenetic origins. The analysis used a GTR+G+I model with two sets of three heated and one cold chain run for one million generations and sampled each 100 generations. From each set, 1000 trees were discarded as burn in. The majority-rule tree of the remaining 18,002 total trees is shown with posterior probability values given next to the relevant node.

This organism, described by Uschakov (1972), has been found to have a wide, almost cosmopolitan, distribution. The one other species, *Epitoka pelagica* that has been described appears to be a junior synonym (Berkeley and Berkely 1960). This organism has well-developed parapodia and chaetae, all of which are compound. Based on overall morphology, *P. pelagica* appears to be close to, or within, Phyllocidae (Uschakov 1972; Fauchald 1977; Rouse and Pleijel 2001).

### Yndolaciidae

This group of holopelagic worms was originally collected in 1960 and 1961 but first described in 1987 by Støp-Bowitz. The original material, from the Gulf of Guinea off the Atlantic coast of Africa, was

in poor shape. Støp-Bowitz (1987) described the anterior end as reduced, but other authors have interpreted the drawings as showing a damaged or missing anterior (Rouse and Pleijel 2001). Upon reexamination of the original material, however, Buzhinskaja (2004) commented that specimens have a distinct protostomium that were not evident from the drawings by Støp-Bowitz. Buzhinskaja (2004) described two novel species, including one in a new genus based on a single specimen missing an anterior end. Thus, there are currently three nominal species within the Yndolaciidae (*Yndolacia lopadorrhynchoides*, *Yndolaciella polarsterni*, and *Paryndolacia tomopteroides*). These worms are most likely within Phyllocida (Rouse and Pleijel 2001; Buzhinskaja 2004), but they lack cephalic appendages on their

protostomium, unlike other Phyllodocida. This group, with generally well-developed parapodia and chaetae, are seemingly derived from an adult-like ancestor. Buzhinskaja (2004), however, discussed the resemblance of these worms to larval tomopterids (Åkesson 1962). Because so little is known about these worms, assessing if paedomorphosis contributed to their evolution is currently not possible. If this is the case, they would be derived from holopelagic ancestors.

### ***Poeobius meseres* and *Flota flabelligera***

*Poeobius meseres* is perhaps one of the best-studied species of holopelagic annelids, in part because it is easily accessible off the coast of California (Burnette et al. 2005). *Poeobius meseres* is a mid-water organism that resembles a small floating green sac with tentacles (Fig. 1E). It lacks chaetae and obvious segmentation, but the nervous system is iterated with 11 mid-ventral ganglia. *Flota flabelligera*, described by Hartman (1967) closely resembles *P. meseres*, except the former has chaetae. She originally placed *F. flabelligera* within Flabelligeridae but later (Hartman 1971) moved it to Fauveliopsidae.

Burnette et al. (2005) conducted a molecular phylogenetic analysis using 18S ribosomal gene and cytochrome *b* subunit I that placed *P. meseres* within Flabelligeridae and as sister to *Therochaete collarifera* (given the taxa sampled). Flabelligerids are slow sedentary worms that tend to be infaunal or epifaunal. Given the biology of adult flabelligerids and the morphology of *P. meseres*, selective pressures apparently acted on the larval form placing *P. meseres*'s ancestors on an evolutionary trajectory that led to a holopelagic species. In terms of paedomorphic mechanisms, *P. meseres* appears to be a case of progenesis, where timing of gamete development accelerates (Burnette et al. 2005). However, more needs to be known about flabelligerid larvae to completely assess how such a transition may have occurred.

### ***Chaetopterus pugaporcinus***

Chaetopterid worms are well-studied benthic worms that live in parchment tubes and whose bodies show tagmosis into three regions. Recently, Osborn and colleagues (2007) discovered an apparently holopelagic member of the group, *Chaetopterus pugaporcinus*, in mid-water depths off California. (Fig. 1F). These animals resemble the very characteristic larva of *Chaetopterus*, but also possess some adult features. They tentatively concluded that these animals are most likely a novel holopelagic species

because morphology and the combination of larval and adult features were consistent in several individuals representing a broad size range. However, they also consider the possibility that these organisms were very unusual larvae. These organisms are several times larger than known polychaete larvae. Additionally, Osborn et al. (2007) used nucleotide sequence data to clearly place this curious organism within *Chaetopterus*. As discussed by the authors, resemblance to a larval form and the absence of some adult features (e.g., dorsal-ventral flattening of the anterior region and the absence of modified chaetae on segment A4) suggest paedomorphosis during the evolution of this lineage.

### **Discussion**

Holopelagic annelids generally fall into two broad categories (Table 1). Holopelagic worms that are easily recognizable as annelids, with segmentation and relatively well-developed parapodia, are derived from within Phyllodocida. This first category includes Alciopidae, Lopadorhynchidae, Tomopteridae, Typhoscolecidae, Iospilidae, *Pontodora pelagica*, and possibly Yndolaciidae. In these cases, there appears to be some degree of homology between the ancestral and derived adult forms. The fact that many holopelagic lineages seem to be within, or closely related specifically to, Phyllodocidae is most intriguing from an evolutionary perspective. What is so special about that lineage in terms of the propensity to evolve a holopelagic lifestyle? Why do not we find nereidids or eunicids producing holopelagic lineages? We can speculate that jaws of eunicids were too heavy or conspicuous for a holopelagic existence, but they presumably could be lost. In the case of holopelagic lineages of Phyllodocidae, we can assert that foliose cirri found in members of that family may have aided swimming in early holopelagic forms, but typhoscolecids are the only holopelagic group with similar foliose appendages. Even though phyllodocids are an energetically active group of worms, why they have been successful at producing holopelagic lineages is not obvious.

The second category includes worms that are so highly derived that upon initial inspection, they may not look like annelids. In both the case of *Poeobius meseres* (and by extension *Flota flabelligera*) and *Chaetopterus pugaporcinus*, there is considerable evidence suggesting that paedomorphic evolutionary processes acted on a larval form of the ancestral lineage. The reason these taxa look so highly

modified is that they have lost, or never ontogenetically developed, many of the features (e.g., segmentation, parapodia, and chaetae) we consider diagnostic of an adult annelid. [Note that there are many examples of these features being modified or lost through paedomorphic processes in benthic species as well (Struck 2006).] These taxa, which have experienced paedomorphosis, are related to sedentary benthic adults that have indirect development. Thus, to some degree, natural selection acting on the pelagic larval form, rather than upon the adult, to produce a holopelagic species is more likely.

Given that *C. pugaporcinus* was only recently discovered and the realization that little is known about the biology of the pelagic realm, there is no doubt that more interesting holopelagic annelids will be discovered. Whether they fit into one of these broad categories, or not, remains to be seen. Nonetheless, many holopelagic annelids already known to science are very poorly studied or characterized in just about every aspect of their biology. We politely urge the scientific community to begin, in earnest, to work on some of these taxa as there will clearly be many interesting findings.

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## References

- Åkesson B. 1962. The embryology of *Tomopteris helgolandica* (Polychaeta). *Acta Zool* 43:135–200.
- Berkeley E, Berkeley C. 1960. Some further records of pelagic Polychaeta from the northeast Pacific north of latitude 40°N and east of longitude 175°W, together with records of Siphonophora, Mollusca, and Tunicata from the same region. *Can J Zool* 42:121–33.
- 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.
- Brusca RC, Brusca GJ. 2003. *Invertebrates*. 2nd Edition. Sinauer Press.
- Burnette AB, Struck TH, Halanych KM. 2005. Holopelagic *Poebobius meseres* (Poebobiidae, Annelida) is derived from benthic flabelligerid worms. *Biol Bull* 208:213–20.
- Buzhinskaja GN. 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* 89:338–45.
- Dales RP, Peter G. 1972. A synopsis of the pelagic Polychaeta. *J Nat Hist* 6:55–92.
- Ehlers E. 1864. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Leipzig: Wilhelm Engelmann. p 1–268.
- Fauchald K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera. *Nat Hist Mus Los Angeles County Sci Ser* 28:1–188.
- Fauchald K, Rouse GW. 1997. Polychaete systematics: past and present. *Zool Scripta* 26.
- Feigenbaum D. 1979. Predation on chaetognaths by typhlocolecoid polychaetes: one explanation for headless specimens. *J Mar Biol Assoc UK* 59:631–3.
- Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. *Proc Roy Soc Lond B, Biol Sci* 205:581–98.
- Halanych KM. 2004. The new view of animal phylogeny. *Ann Rev Ecol Syst* 35:229–56.
- Hartman O. 1967. Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from the Antarctic sea. *Allan Hancock Monogr Mar Biol* 2:1–387.
- Hartman O. 1971. Abyssal polychaetous annelids from the Mozambique basin off southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide area. *J Fish Res Board Can* 28:1407–28.
- Huelsenbeck JP, Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–5.
- McHugh D. 1997. Molecular evidence that echiurans and pogonophorans are derived annelids. *Proc Natl Acad Sci USA* 94:8006–9.
- Nylander J. 2002. MrModeltest. 1.1 edn: <http://morphbank.ebc.uu.se/MR.BAYES>.
- Osborn KJ, Rouse GW, Goffredi SK, Robison BH. 2007. Description and relationships of *Chaetopterus pugaporcinus*, and unusual pelagic polychaete (Annelida, Chaetopteridae). *Biol Bull* 212:40–54.
- Øresland V, Pleijel F. 1991. An ectoparasitic typhlocolecoid polychaete on the chaetognath *Eukrohnia hamata* from the Antarctic peninsula. *Mar Biol* 108:429–32.
- Rice SA. 1987. Reproductive biology, systematics and evolution in the polychaete family Alciopidae. *Bull Biol Soc Wash* 7:114–27.
- Rouse GW, Fauchald K. 1997. Cladistics and polychaetes. *Zool Scripta* 26:139–204.
- Rouse GW, Pleijel F. 2001. *Polychaetes*. Oxford University Press.
- Rousset V, Pleijel F, Rouse GW, Erséus C, Siddall M. 2007. A molecular phylogeny of annelids. *Cladistics* 23:41–63.
- Støp-Bowitz C. 1987. A new genus and species (*Yndolacia lopadorrhynchoides*) of pelagic polychaetes, representative of a new family, Yndolaciidae. *Bull Biol Soc Wash* 7:128–30.

- Struck TH. 2006. Progenetic species in polychaetes (Annelida) and problems assessing their phylogenetic affiliation. *Int Comp Biol* 46:558–68.
- Struck TH, Purschke G, Halanych KM. 2006. Phylogeny of Eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA). *Approach Syst Biol* 55:1–20.
- Struck TH, Schult N, Kusen T, Hickman E, Bleidorn C, McHugh D, Halanych KM. 2007. Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evol Biol* 7:57.
- Thompson JD, Higgins DG, Gibson TJ. 1994. Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res* 22:4673–80.
- Uschakov PV. 1972. Polychaeta 1. Polychaetes of the suborder Phyllodociformia of the Polar Basin and the northwestern part of the Pacific. *Fauna SSSR* 102:1–271.
- Wu B, Lu H. 1993. Phylogeny of Alciopidae (Polychaeta): a cladistic analysis. *Acta Zool Sinica* 39:23–9.