

## A multigene framework for polychaete phylogenetic studies

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### Abstract

Producing a robust phylogenetic reconstruction for Polychaeta using either morphological or molecular data sets has proven very difficult. There remain many conflicts between morphological analyses and hypotheses based on DNA data, the latter principally derived from 18S rRNA sequences. For the present study a data set covering a broad range of polychaete diversity was assembled, including 38 new sequences from 21 species. Besides available 18S rRNA data, five additional gene segments were examined: the D1 and D9-10 expansion regions of 28S rRNA, histone H3, snU2 RNA and cytochrome *c* oxidase subunit I. Maximum parsimony, maximum likelihood and Bayesian analyses were conducted.

Annelida and Mollusca were reciprocally monophyletic in maximum likelihood analyses, but Polychaeta included a cephalopod in maximum parsimony analyses, and a patellogastropod in Bayesian analyses. When rooted on the Mollusca, optimal topologies from maximum likelihood analyses showed a recognisable basal group of taxa, including Oweniidae, Chaetopteridae and Amphinomidae. The six studied phyllodocidan families plus Orbiniidae (as the sister group of the scale-worms) formed the next most basal group. All analyses support the inclusion of Echiura, Clitellata and Siboglinidae within polychaetes. Bayesian analyses show Echiura as the sister group of Capitellidae, in agreement with previous 18S rRNA results. In contrast, Echiura formed the sister group to Trichobranchidae in maximum likelihood and maximum parsimony analyses.

Supra-familial groupings consistently recovered within Polychaeta in the analyses are: (i) Terebellida without Ampharetidae; (ii) Scolecida (excepting Orbiniidae); (iii) Eunicidae, Lumbrineridae and Clitellata; and (iv) “Cirratuliformia” (including Sternaspidae) plus Sabellidae, Serpulidae and Spionidae.

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### Introduction

The interaction of molecular and morphological approaches has produced substantial progress in understanding the deeper phylogeny of most major invertebrate groups. This is only partly true for the

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Lophotrochozoa which, although first identified as a clade by molecular analyses (Halanych et al. 1995), have not been resolved into monophyletic phyla by subsequent investigations of 18S ribosomal DNA (Winne-penninckx et al. 1995; Giribet et al. 2000; Halanych et al. 2002). Polychaeta is a particularly problematic taxon. Consequently, there has been extensive recent interest in the group's membership and higher classification from the perspectives of both morphology (e.g. Bartolomaeus 1995; Nielsen 1995; Eibye-Jacobsen and Nielsen 1996; Rouse and Fauchald 1997; Rouse and Pleijel 2001, 2003; Purschke 2002; Bartolomaeus et al. 2005) and DNA sequencing (e.g. McHugh 1997, 2000; Brown et al. 1999; Martin 2001; Struck et al. 2002a, b; Bleidorn et al. 2003a, b; Hall et al. 2004).

Discussion about the membership of Polychaeta has recently focussed on the inclusion of Clitellata (Oligochaeta and Hirudinea), Pogonophora, Vestimentifera and Echiura. There are good morphological (Purschke et al. 1993; Westheide 1997; McHugh 2000) and molecular data (Moon et al. 1996; Erséus et al. 2000; Martin 2001; Siddall et al. 2001) that Clitellata forms a monophyletic group, as do several of its constituent taxa (Erséus and Källersjö 2004).

The division of Annelida into two reciprocally monophyletic sister groups, Polychaeta and Clitellata, was maintained by Rouse and Fauchald (1997), Rouse (1999) and Rouse and Pleijel (2001). In contrast, Purschke et al. (2000) suggested an unspecified subclade of Polychaeta as the sister taxon of Clitellata. Molecular studies support this suggestion but have not clarified potential relationships with polychaete subgroups (McHugh 2000; Martin et al. 2000; Purschke et al. 2000; Rota et al. 2001; Martin 2001; Struck et al. 2002a, b; Bleidorn et al. 2003a, b; Hall et al. 2004; Erséus 2005).

Taxa previously recognised as the phyla Pogonophora and Vestimentifera are now generally considered, with some dissent (Salvini-Plawen 2000), to form a single clade within the polychaete family Siboglinidae (Bartolomaeus 1998; Rouse 2001; Halanych et al. 2001). Molecular studies generally concur but have not been able to establish its sister taxon (Halanych et al. 2001; Halanych 2005; Bleidorn et al. 2003b).

Recent studies by Hessling and Westheide (2002) and Hessling (2003) on the development of the nervous system of *Bonellia* (Echiura) have shown elegantly that these worms are derived from segmented ancestors and belong within Annelida. This is supported by molecular studies (Aguinaldo et al. 1997; McHugh 1997, 2000; Bleidorn et al. 2003a, b; Hall et al. 2004). Studies using in situ hybridisation (Hessling and Westheide 1999; Hessling 2003) strongly suggest that the absence of segmentation in echiurans is secondary, as the organisation of characters such as neuronal ganglia and the organisation of the suboesophageal ganglion is consis-

tent with that found in most annelids. This implies that the trunk is a modified segmental structure and not a single large segment. Hessling and Westheide (1999) suggest that the pattern of the nervous system in larval and juvenile Echiura is homologous with that of Annelida. This was supported by Hessling and Westheide (2002) who used antibodies against the neurotransmitters serotonin (5-hydroxytryptamine) and FMRFamide to demonstrate the presence of paired, discrete repetitive units in the ventral nerve cord during echiuran larval development. Hessling (2003) used computer-aided 3-D reconstruction to show that the organisation of the nervous system is truly metameric, supported by a corresponding arrangement of peripheral nerves. Echiuran cleavage patterns, chaetal formation and sperm ultrastructure closely resemble those found in polychaetes (Newby 1940; Franzén and Ferraguti 1992; Pilger 1993). In 18S rRNA analyses, Echiura is shown as the sister group of the Polychaete family Capitellidae, with considerable bootstrap support (Bleidorn et al. 2003a, b; Hall et al. 2004).

While a lot of progress has been made during the past decade using morphological and/or molecular data to investigate relationships within the annelidans, many questions remain. These concern the relationships among the polychaete annelids, what group is sister to the Clitellata, and what extant group is the most basal on the annelid tree. The low resolution of annelid phylogenies may be due to a rapid radiation of the group. This has been discussed at length by McHugh (2000) and Rota et al. (2001). McHugh (2000) commented on the problems with using morphological characters for interpreting deep annelid relationships. These include determining homology between character states and the prevalence of convergence or parallel secondary losses. Halanych (1998) has argued that the hypothesised rapid radiation resulted in short internodes with few informative sites at the molecular level. Over time, subsequent evolution has led to an erosion of even this relatively small amount of information (Abouhelf et al. 1998). This may explain why analyses of single genes, such as the 18S rRNA data, have not robustly resolved the branching patterns among annelid lineages. The solution may be to use combined data from multiple genes, hoping that phylogenetic signals from the different data sets will be concordant and noise not correlated. This strategy has been adopted in the present study.

Rouse and Fauchald (1997) studied the majority of the approximately 80 polychaete families, including all those for which data were available to code most characters. They separated polychaetes into two main divisions, Scolecida and Palpata. The latter was divided into two groups: (i) Aciculata containing Phyllodocida and Eunicida, and (ii) Canalipalpata containing the major subclades Sabellida, Terebellida and Spionida.

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