

## 1. General Introduction

A subdivision of the Annelida in Polychaeta and Clitellata can be found in recent textbooks (Ax, 1999, Westheide & Rieger, 1996). Whereas the monophyly of the Clitellata is supported by a vast number of autapomorphies (Purschke, 2002), the monophyly of the polychaetes remains contentious (Nielsen, 2001). The polychaetes comprise a group of about 13,000 described species with a generally marine distribution (Glasby et al., 2000). Fauchald (1977) listed 80 families in his seminal work on higher polychaete taxa. This reflects the huge morphological variety of this taxon. Polychaetes are traditionally classified into two groups, Errantia and Sedentaria. This classification goes back to the 19<sup>th</sup> Century (Audouin & Milne Edwards, 1834; Quatrefages, 1866) and is mainly based on the life habits of the included specimens. While errant polychaetes are usually free-living, and predacious, and may be armed with jaws, the sedentaries comprise mainly the tubicolous and burrowing species which are typically deposit- or filter-feeders (Fauchald, 1977). This classification has been rejected by many authors (e.g. Dales, 1962; Fauchald, 1977; Pettibone, 1982). The currently widely-used classification of polychaetes is based on the cladistic analysis by Rouse & Fauchald (1997). They suggest that the Polychaeta comprise two major clades, the Scolecida and the Palpata. The scolecids comprehend sedentary palp-lacking forms with two or more pairs of pygidial cirri. The highest ranked taxa within the Palpata are the Canalipalpata (comprising the remaining so-called “Sedentaria”) and the Aciculata (the formerly Errantia). This view was challenged by Bartolomaeus (1998) and Hausen (2001), who question the monophyly of these taxa.

Besides the question about the relationships of annelid taxa, it is highly controversial whether some enigmatic protostome taxa should be included (Halanych et al., 2002). Whereas the placement of Vestimentifera and Pogonophora as derived polychaetes with sabellid affinity is consensus of many investigations (Bartolomaeus, 1995; McHugh, 1997; Rouse & Fauchald, 1997), the evolutionary relationships of the unsegmented Echiura and Sipunculida are in debate. The key question in both cases is whether the lack of segmentation should be regarded as a primary absence or as secondary loss (e.g. Purschke et al., 2000). Hessling and Westheide (2002) show that Echiura possess serially repeated units in their nervous system which correspond to typical metameric ganglia of the Annelida. This supports the hypothesis of a secondary loss of segmentation in Echiura.

Considering all these questions it must be held in mind that morphology is subject to natural selection. It is therefore likely that losses of certain characters evolve convergent when the considered taxa live under similar selective pressures (Purschke et al., 2000). The same holds true for the correspondence of the reproductive biology of terrestrial polychaetes and Clitellata, which do not reflect common ancestry (Purschke, 2002).

Many more or less well supported examples for convergent evolution due to similar selective pressures are described in the annelid literature.

Molecular markers can be used as independent data for resolving questions regarding convergent evolution of morphological characters, for judging if an absent character represents a primary or secondary condition. Thus it is an independent test for hypotheses which have been evaluated on morphological data.

Another major advantage of using molecular data is the extent of the dataset, which means that the maximum number of characters of an organism is limited by the number of nucleotid pairs in its genom (Hillis, 1987). However, only a small fraction of the genom is usually used in phylogenetic studies. The best studied gene is the 18S rRNA gene, which is available for nearly all higher Metazoan taxa (Giribet, 2002).

In the attempt to investigate the monophyly of the polychaetes and to infer annelid ingroup relationships several molecules have been used. McHugh (1997) and Kojima (1998) analyzed the elongation factor-1 $\alpha$  gene. Both analyses conclude that Clitellata, Echiura, and Pogonophora (incl. vestimentiferans) represent annelid taxa which are derived from polychaetes. The paraphyly of the Polychaeta was also recovered in an analysis by Brown et al. (1999). In this paper the usefulness of histone H3, U2 snRNA and fragments of the 28S rDNA sequence data for inferring polychaete relationships was assessed. The resolution of the separate analyses of each gene was very poor and even in a combined dataset no high bootstrap support could be obtained for the recovered relationships between polychaete families. The 18S rRNA gene is frequently used in investigations regarding clitellate ingroup relationships (e.g. Apakupakul et al., 1999; Trontelj et al., 1999; Martin et al., 2000; Martin, 2001; Siddall et al., 2001; Erséus & Källersjö, 2004) and therefore for almost all major clitellate taxa 18S sequence data is available. In contrast to this the polychaetes were stepmotherly treated. Before 2001, 18S sequence data of polychaetes was only found in analyses concerning protostome relationships (e.g. Winnepeninckx et al., 1998) or have been used as outgroup taxa in studies on clitellate relationships (Siddall et al., 2001).

The first papers dealing with questions on polychaete ingroup relationships were that by Rota et al. (2001) and Struck et al. (2002a). Both papers try to resolve the phylogenetic position of meiofaunal polychaete taxa with simplified anatomy. Struck et al. (2002b) investigated the phylogeny of the errant Eunicida. Despite all these attempts it was obvious that the inference of polychaete phylogeny lacks from a sufficient taxon sampling, which was particularly true for sedentary taxa.

In Chapter 2: *A contribution to sedentary polychaete phylogeny using 18S rRNA sequence data*, Chapter 3: *New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences*, and Chapter 4: *18S rDNA and polychaetes*, polychaete phylogeny is investigated using a larger taxon sampling. The aim of this studies is to test the hypotheses

of polychaete phylogeny which have been developed on the basis of morphological data (see above), as well as to investigate the phylogenetic position of taxa with a hitherto uncertain annelid affinity (e.g. Echiura).

Recent studies have shown that 18S sequence data is also useful for inferring ingroup relationships of polychaete families. In these studies the 18S is used as a backbone for the analysis and is combined with other genes (Nygren & Sundberg, 2003; Borda & Siddall, 2004), like mt 16S rDNA, which are known to have a faster rate of evolution and which are appropriate for the resolution of younger speciation events.

For a proper understanding of the phylogeny of Annelida, the phylogenetic position of the Orbiniidae represents a key position. Traditionally this group was interpreted as an intermediate between errant (with whom they share the prominent parapodia) and sedentary polychaetes (which share the same life habit). In the cladistic analysis of Rouse & Fauchald (1997) they are placed at a basal position within the polychaetes. In Chapter 5: *Phylogenetic relationships and evolution of Orbiniidae (Annelida, Polychaeta) based on molecular data*, the phylogenetic relationships of orbiniids are inferred by two genes (18S and 16S). Chapter 6: *Molecular phylogeny of lugworms (Annelida, Arenicolidae) inferred from three genes*, deals with the relationships of arenicolids. These worms are one of the few polychaete taxa with economic importance. Large individuals are collected for sea angling bait (McLusky *et al.*, 1983) and recent studies on *Arenicola marina* have shown that its haemoglobin might be a promising blood substitute for human medicine (Zal *et al.*, 2002).

In Chapter 7 a summarising discussion of the most important results of my thesis is given.