

## Phylogeny of Catenulida and support for Platyhelminthes

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### Abstract

Molecular studies have shown that Platyhelminthes is polyphyletic, placing Rhabditophora within Lophotrochozoa, whereas Acoela and Nemertodermatida are separate early bilaterian branches. However, there has been little evidence to support the position of Catenulida, a group that was traditionally classified within Platyhelminthes. In Ehlers' pioneering cladistic system of the Platyhelminthes they were placed as the earliest clade. Other morphologists have considered the Catenulida as an early bilaterian clade separate from Rhabditophora, a position that was supported in an early molecular study. Subsequent molecular phylogenetic studies, which placed Catenulida as the sister group of Rhabditophora with no or low branch support, included 18S rDNA data from only one or two catenulid species. The aims of the present study were (1) to test the putative sister-group relationship of Catenulida and Rhabditophora by improving the taxon sampling of molecular data spanning a larger part of catenulid taxonomic diversity and (2) to provide a phylogenetic framework for the systematization of Catenulida. Twelve catenulid species were sampled around Sweden. Both the 18S rDNA gene and the 28S rDNA gene were sequenced and analysed in a Metazoa-wide data set within parsimony and Bayesian frameworks. The results unambiguously support Catenulida as the sister group of Rhabditophora within Lophotrochozoa. Parsimony-based inferences about the common ancestor of Catenulida and Rhabditophora are presented. A definition of the name Platyhelminthes is suggested.

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### Introduction

Catenulida is a group of small worms comprising about 100 species worldwide. Most live in freshwater habitats such as mires, ponds, streams and moist terrestrial habitats where they often are very abundant, whereas the members of the marine Retronectidae are very rare. Catenulids have a simple anatomy and lack sclerotized parts such as copulatory stylets, which makes species

identification problematic. Many currently recognized species are regarded as cosmopolitan, perhaps due to the paucity of distinguishing morphological features.

The monophyly of Catenulida is undisputed, with an unpaired, dorsomedially located protonephridium, anterodorsal testes and male genital pore, and aciliary nonmobile sperm as proposed synapomorphies (Ehlers 1985). On the other hand, the phylogenetic position of Catenulida within Bilateria is more controversial. Conventionally the group was classified as a basal clade within the Platyhelminthes (Ehlers 1985). However, Smith et al. (1986) pointed out that there are no known

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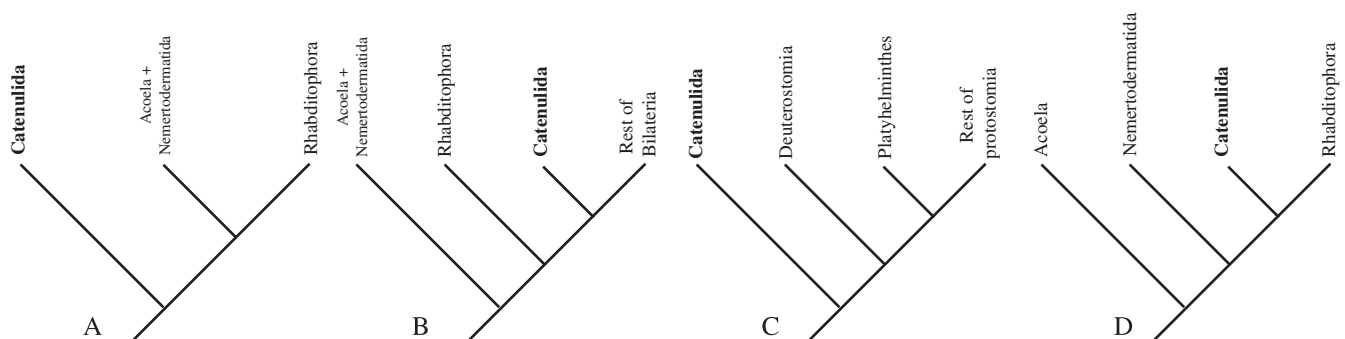
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morphological synapomorphies uniting the main platyhelminth clades Catenulida, Acoela, Nemertodermatida and Rhabditophora. In a study of bilaterian phylogeny based on morphological characters, Haszprunar (1996) considered Platyhelminthes as paraphyletic, with Acoela, Nemertodermatida and Rhabditophora as the most basal bilaterian clades, followed by Catenulida as sister to the remaining bilaterians.

Attempts to determine the phylogenetic position of Catenulida using rDNA were based on no more than two catenulid species. In the first study using ribosomal 18S rDNA data (Carranza et al. 1997), the single catenulid species *Stenostomum leucops* (Dugs) branched first within Bilateria, separately from Rhabditophora. Zrzavy et al. (1998) proposed a new phylum Catenulida based on parsimony analysis of 18S rDNA and morphological characters (branch support was not evaluated), again involving a single *S. leucops* sequence. The internal phylogeny of Platyhelminthes was analysed by Littlewood et al. (1999a), based on 82 platyhelminth and 13 non-platyhelminth bilaterian 18S rDNA sequences. In their study the four sequences derived from *S. leucops* formed a monophyletic sister group to the Rhabditophora in the most parsimonious tree, but this relationship received no bootstrap support greater than 50%. Subsequent studies, including one *S. leucops* sequence (Peterson and Eernisse 2001) or one *S. leucops* plus one sequence identified as derived from a *Suomina* sp. (Jondelius et al. 2002), also reported no support for a sister-group relationship between Catenulida and Rhabditophora. Partial 28S rDNA sequences from two catenulid species did support such a relationship (Littlewood et al. 1999b), but the Catenulida + Rhabditophora grouping was again not supported by the 18S rDNA data partition in the same study. Telford et al. (2003) found low bootstrap support for a sister-group relationship between Catenulida and Rhabditophora when using the 18S rDNA sequences from *S. leucops* and *Suomina* sp. in combination with

new 28S rDNA sequences in a model-based analysis. These conflicting hypotheses are summarized in Fig. 1. The results placing Catenulida and Rhabditophora as sister groups (Peterson and Eernisse 2001; Jondelius et al. 2002; Telford et al. 2003) have been cited as strongly supported by “denser sampling” in a review of the phylogeny of Platyhelminthes (Baguña and Riutort, 2004). It should be clear from the above that the claim of a strongly supported monophylum consisting of Catenulida and Rhabditophora is a grave distortion of our current understanding of catenulid phylogeny. Low or non-existent bootstrap support based on one or two terminals is not an example of strong support derived from dense taxon sampling. On the contrary, the clade Catenulida + Rhabditophora is highly tentative and needs further testing through acquisition and analysis of more data from a wider diversity of catenulids, so that truly dense taxon sampling can be obtained. New data (from new catenulid taxa) may improve consistency of the tree topology in parsimony analyses (Rydin and Källersjö 2002), whereas inadequate sampling may lead to statistical support for erroneous groupings (Wallberg et al. 2004). Denser taxon sampling of catenulid sequences is clearly desirable.

In the present study we analyse 18S rDNA from a minimum of 12 catenulid species represented by 21 terminals, and 28S rDNA from 10 catenulid species. In order to reconstruct the position of Catenulida we compile a data set spanning as many higher bilaterian groups as possible. Compared to previous studies, the Bilateria-wide combined 18S/28S rDNA data set represents a substantial increase in number of catenulid taxa as well as number of characters. Our aim is to test whether the tentatively preferred hypothesis of a Catenulida + Rhabditophora clade will withstand falsification attempts with more than five times as many catenulid terminals as previously available. In other words: are Catenulida the sister group of Rhabditophora or a high-ranking bilaterian clade? We



**Fig. 1.** Schematic illustration of conflicting hypotheses regarding the phylogenetic position of Catenulida. (A) Sister group of all other Platyhelminthes, including Acoela and Nemertodermatida, according to Ehlers (1985). (B) Sister group to all Bilateria except Acoela, Nemertodermatida and Rhabditophora, according to Haszprunar (1996). (C) Sister group to Bilateria according to Carranza et al. (1997). (D) Sister group to Rhabditophora, according to Peterson and Eernisse (2001), Jondelius et al. (2002) and Telford et al. (2003).

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