



The phylogenetic position of Neogosseidae (Gastrotricha: Chaetonotida) and the origin of planktonic Gastrotricha

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Abstract Planktonic forms of Gastrotricha have been known since the 1850s, despite the fact that they are rather uncommon and difficult to collect. They are characterized by a round sack-shaped body, an absence of furcal adhesive tubes, and a different distribution of the locomotory ciliation compared to epibenthic and periphytic gastrotrichs. Today, planktonic gastrotrichs are classified into the three taxa—Dasydytidae, Neogosseidae, and *Undula*—but their origin and whether they share a recent common ancestor remain largely unknown. A long-held view is that planktonic taxa are derived from benthic ancestors related to *Chaetonotus* (*Zonochaeta*), but the hypothesis has never been properly tested. Here, in order to elucidate the phylogeny and origin of planktonic Gastrotricha, we provide the first molecular data on the very rare genera *Kijanebalola* and *Neogosseia*, both members of the family Neogosseidae. We use Bayesian and maximum likelihood phylogenetics to analyze sequences of 18S rDNA, 28S rDNA, and COI mtDNA spanning 71 taxa in total. We find high support for a common origin of planktonic gastrotrichs, with monophyly of both Dasydytidae and Neogosseidae. Planktonic forms have evolved from epibenthic or periphytic ancestors, and the closest extant clade comprises members of *Chaetonotus* (*Zonochaeta*) + *Chaetonotus heteracanthus* Remane, 1927. These results further imply that the motile spines and underlying muscle patterns that control them in

species of Dasydytidae are adaptations to the planktonic environment that evolved independently of those in other species of Gastrotricha.

Keywords Meiofauna · Freshwater · Planktonic · Phylogeny · Paucitubulatina

Introduction

Gastrotricha is a small phylum of aquatic acoelomate animals with approximately 850 species (see Balsamo et al. 2009, 2013, 2014; Hummon and Todaro 2010; Kieneke and Schmidt-Rhaesa 2014; Todaro et al. 2014; and references therein). The group is a common component of the meiofauna and is hypothesized to act as an important link between the microbial loop and larger invertebrate predators (Balsamo and Todaro 2002). The phylum is divided into the two orders Chaetonotida and Macrodasyida. Chaetonotida, present in both freshwater and marine habitats, are generally tenpin-shaped with adhesive tubes confined to the posterior end and with the cuticle generally sculptured into various arrangements of scales and spines. Macrodasyida, with few exceptions, are entirely marine and vermiform, with adhesive tubes not confined to the posterior end, and with a smooth or sculptured cuticle.

Freshwater gastrotrichs within Chaetonotida are very small, ranging from 60 to 770 µm in total body length. Most species are not only epibenthic, periphytic, or interstitial but some also have a planktonic lifestyle. The first records of planktonic gastrotrichs were those of *Dasydytes goniathrix* Gosse, 1851 and *Dasydytes antenniger* Gosse, 1851 (now *Neogosseia antennigera*). In the years leading up to the twentieth century, several findings of new planktonic gastrotrichs were published, e.g., *Chitonodytes longisetosus*

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