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AUTHORS: Tobias K  nneby^{1*} & M. Antonio Todaro²

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

¹*Department of Zoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden. E-mail: tobias.kanneby@nrm.se; tobiaskanneby@gmail.com*

²*Department of Life Sciences, University of Modena and Reggio Emilia, via Campi 213/d, I-41100 Modena, Italy. E-mail: antonio.todaro@unimore.it*

**Corresponding author. E-mail: tobias.kanneby@nrm.se; tobiaskanneby@gmail.com. Phone: +46851954294*

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 remains largely unknown. A long held view is that planktonic taxa derive 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; 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 Macrodasysida. 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. Macrodasysida, 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 μm to 770 μm in total body length. Most species are epibenthic, periphytic or interstitial, but some also have a planktonic life-style. 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 20th century several findings of new planktonic gastrotrichs were published, e.g. *Chitonodytes longisetosus* (Metschnikoff, 1865), *Haltidytes saltitans* (Stokes, 1887), *Stylochaeta fusiformis* (Spencer, 1890) and *Setopus bisetosus* (Thompson, 1891). Zelinka (1889) separated *N. antennigera* (Gosse, 1851) from the rest of the planktonic gastrotrichs based on the cephalic tentacles. Daday (1905) erected the families Dasydytidae and Gosseidae (now Neogosseidae) and gave diagnostic characters for each group. The very rare *Kijanebalola* was described from an Ugandan lake by Beauchamp (1932), and regarded as a close relative to *Neogosseia*. A leap in the knowledge of planktonic forms was made during the 1980s by Kisielewski (1991), who found several new and very interesting semi-planktonic gastrotrichs from an evolutionary point of view, among them *Undula*, *Ornamentula* and *Kijanebalola*. Common features of the planktonic species are the absence of the furcal adhesive tubes and a rearrangement of the locomotory ciliation. In planktonic taxa the ciliation includes discrete tufts along the trunk region and at least a band of long strong propelling cilia, which more or less completely encircles the head. Today planktonic gastrotrichs are classified into three taxa: (i) the monotypic *Undula*, forming the subfamily Undulinae, which is provisionally considered a sister group of the

1 subfamily Chaetonotinae (Kisielewski 1991); (ii) Dasydytidae, which is characterized
2 by long and movable spines (Kisielewski 1991; Kieneke and Ostmann 2012); and (iii)
3 Neogosseidae, characterized by long posterior spines, either distributed in an unpaired
4 median group (*Kijanebalola*) or in a paired lateral group (*Neogossea*), and a pair of
5 club-shaped cephalic tentacles (Todaro et al. 2013).
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9 The origin and evolution of planktonic gastrotrichs remain largely unknown
10 (Hochberg and Litvaitis 2000; Kieneke et al. 2008a). However, the long-held
11 hypothesis that at least some planktonic forms may have been derived from benthic
12 ancestors (e.g. related to *Chaetonotus* (*Zonochaeta*) Remane, 1927a; see Kisielewski
13 1991) has gained support in a recent phylogenetic study based on molecular data
14 (K  nneby et al. 2013). In the latter study the authors showed that the planktonic
15 Dasydytidae is nested within a non-monophyletic Chaetonotidae. However, the non-
16 monophyly of Chaetonotidae had been known for quite some time prior to that study,
17 based on morphological data (e.g. Hochberg and Litvaitis 2000; Kieneke et al.
18 2008a). It should be emphasized that the systematics of the entire order Chaetonotida,
19 and especially within the largest group Chaetonotidae, is unstable. This is mainly due
20 to the classification's heavy reliance on cuticular structures and ornamentation,
21 characters that are extremely variable and thereby inconsistent on higher levels of
22 classification (e.g. genus, family etc.) (see K  nneby et al. 2013). A phylogenetic
23 approach based on molecular data may prove to be helpful in the process of re-
24 systematization of chaetonotidan taxa, similar to what is happening in the
25 systematization of the Macrotrichida (Todaro et al. 2012; 2014) However, several
26 groups of chaetonotidans have not yet been sampled for molecular data; this includes
27 Dichaeturidae, Neogosseidae and Proichthyidiidae, mainly because of lack of material.
28 It should be emphasized that members of these groups are very uncommon, with
29 some species only reported from their respective, often remote, type localities; as a
30 consequence, information on these animals is generally very poor and their origin and
31 phylogenetic alliances remain obscure.
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35 In this study, in order to shed some light on the hypothesized relationship
36 between Dasydytidae and Neogosseidae suggested by previous authors, we have
37 obtained specimens and sequences of 18S rDNA, 28S rDNA and COI mtDNA for the
38 uncommon planktonic genera *Kijanebalola* and *Neogossea*, comprising Neogosseidae
39 (Table 1). We also hope, if possible, to shed light on the origin of planktonic
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Gastrotricha. Although efforts were made to find *Undula paraënsis* Kisielewski, 1991, at its type localities in Brazil, these attempts were fruitless.

MATERIALS AND METHODS

Collection and documentation

Kijanebalola devestiva Todaro et al. 2013 (Fig. 1A) and *Neogosseia acanthocolla* Kisielewski, 1991 (Fig. 1B) were collected in February 2013 from a freshwater pond in the iSimangaliso wetland park (Kwazulu-Natal, South Africa); for details on specimen sampling, recording and storage prior to DNA processing refer to Todaro et al. (2013). Individuals of *Neogosseia antennigera* (Fig. 1C, D) were collected with a plankton net with a mesh size of 25 µm at Bryan Country Club Lake, Bryan, Texas, USA (30°38'32.18"N; 96°21'44.05"W) on two occasions, May 23, 2012 and June 26, 2012. Collected samples contained *Ceratophyllum* spp. and *Lemna* spp. It is also noteworthy that the water of the lake as well as ambient sediment contain arsenic levels that exceed the human health criterion and are not optimal for aquatic life (Clark et al. 1998). Subsamples were treated with a 1% MgCl₂-solution and subsequently studied under an Olympus LMS225R dissecting microscope. Gastrotrichs were picked out with a micropipette, mounted on a slide and documented alive with an Olympus BH-2 microscope equipped with DIC optics and a Canon EOS Rebel T1i digital camera or a Nikon Eclipse 80i DIC microscope equipped with a Nikon Digital Sight DS-Fi1 digital camera. For molecular studies, specimens were recovered from the slide and put in 95-100% EtOH and stored at -18 to -20°C until further treatment. The specimens of Neogosseidae used in the phylogeny have been photographed and the photos have been deposited as collection 855412 in Morphbank (<http://www.morphbank.net/855412>) (Table 1). Also refer to collection 799280 in Morphbank (<http://www.morphbank.net/799280>) for photographs of the other specimens used in our analysis (Table 1).

Phylogenetic analyses

DNA extraction, amplification and sequencing of 18S rDNA, 28S rDNA and COI mtDNA follow the protocol presented in Kånneby et al. (2012). The new sequences were analyzed together with most of the sequences obtained by Kånneby et al. (2013). However, to keep the dataset more manageable, only a single sequence per morphological species per gene was included, with the exception of Neogosseidae

where in some instances two sequences from the same morphological species were used (Table 1).

The nuclear genes were aligned with Muscle (Edgar 2004) implemented in Geneious v. 7.1.8 (Kearse et al. 2012) using the default settings. COI was aligned in the same way as the nuclear genes using the translation align option, ensuring that gaps in the alignment correspond to the translated amino acid sequences. The concatenated dataset (18S rDNA, 28S rDNA and COI mtDNA) was analyzed with MrBayes v.3.2.3 (Ronquist *et al.* 2012) on the CIPRES Science Gateway v. 3.3 (Miller et al. 2010) under the mixed model setting with gamma distributed rate variation across sites and an estimated proportion of invariable sites. The gamma shape parameter, the substitution rates for the GTR-model, the proportion of invariable sites and the character state frequencies were all unlinked. The dataset was partitioned according to each nuclear gene and by codon position for COI. To ensure sufficient mixing and a reliable sample from the posterior distribution the dataset was analyzed with 8 MCMC chains for each run and a heating parameter of 0.1. The analysis started from a random starting tree and was run for 40 million generations. Convergence of the two runs was ascertained by checking the log likelihood graphs, the average standard deviation of split frequencies and the potential scale reduction factor (PSRF+) (Gelman & Rubin 1992). After a burn-in of 5 million generations, chains were sampled every 1000th generation. *Musellifer delamarei* (Renaud-Mornant, 1968) within Muselliferidae, a group hypothesized to be the sister group of all other Paucitubulatina (e.g. Hochberg and Litvaitis 2000; Todaro et al. 2006; Leasi and Todaro 2008; K  nneby et al. 2014), was used as outgroup. The alignments of the concatenated dataset and the resulting consensus trees from the Bayesian and the maximum likelihood analyses has been deposited in TreeBASE at <http://purl.org/phylo/treebase/phyloids/study/TB2:S17533>

Maximum likelihood (ML) analyses were performed with RaxML GUI v. 1.3 (Stamatakis 2006; Silvestro and Michalak 2012) on the concatenated dataset as well as datasets of individual genes, to check for congruence with the Bayesian analysis.

RESULTS

The final alignment of the concatenated dataset yielded 7109 positions, with 1830, 4612 and 667 positions for 18S rDNA, 28S rDNA and COI mtDNA, respectively.

1 In general the concatenated phylogenies based on both the Bayesian and the
2 maximum likelihood alignments follow the results obtained by K  nneby et al. (2013).
3 Given the included data, none of the currently recognized subgenera appear
4 monophyletic except for *Chaetonotus* (*Zonochaeta*). *Lepidochaetus*, considered a
5 subgenus within *Chaetonotus* by Balsamo et al. (2009), is also monophyletic. The
6 hypothesized reinvasion of certain Chaetonotidae (*Halichaetonotus* and marine
7 *Heterolepidoderma* in a sister group relation to the freshwater taxon *Chaetonotus*
8 *schantzei* Metschnikoff, 1865) from a limnic environment to a marine environment by
9 K  nneby et al. (2013) also gains high support in this study (pp=0.98) (Fig. 2).

16 For individual gene trees there are no major conflicts when taking into account
17 bootstrap support values above 70. Deeper nodes within the Chaetonotidae +
18 Dasydytidae + Neogosseidae clade generally have very low bootstrap support (results
19 not shown).

23 With regard to the main aims of the current study, the Bayesian analysis gives
24 high support for monophyly of the planktonic gastrotrichs
25 (Dasydytidae+Neogosseidae) in our study (pp=1). Within this clade both Dasydytidae
26 (pp=0.99) and Neogosseidae (pp=1) are monophyletic (Fig. 2). For Neogosseidae,
27 both *Kijanebalola* (*K. devastiva*, n=2) and *Neogosseia* (*N. acanthocolla*, n=1 + *N.*
28 *antennigera*, n=2) are monophyletic with high bootstrap support (pp=1). *N.*
29 *acanthocolla* and *N. antennigera* are sister taxa. Within Dasydytidae two major clades
30 can be discerned: *Haltidytes squamosus* + *Ornamentula para  nsis* and *Dasydytes* +
31 *Stylochaeta* (Fig. 2). Within the latter clade *Stylochaeta fusiformis* and *Stylochaeta*
32 *scirtetica* are in a sister group relation to *Dasydytes* (*Prodasydytes*) *elongatus*
33 Kisi  lewski, 1991 and *Dasydytes* (*P.*) *papaveroides* Kisi  lewski, 1991 (pp=1). The
34 subgenus *Dasydytes* (*Prodasydytes*) is non-monophyletic, because of the sister group
35 relationship of *Dasydytes* (*P.*) *carvalhoae* Kisi  lewski, 1991 to *D. (P.) elongatus* + *D.*
36 (*P.*) *papaveroides* and *Stylochaeta* (pp=1).

42 The sister group of the planktonic gastrotrichs (Dasydytidae + Neogosseidae)
43 appears as *Chaetonotus* (*Zonochaeta*) spp. + *Chaetonotus heteracanthus* Remane,
44 1927 (pp=0.99). *Polymerurus* is the sister group of the latter clade and the planktonic
45 gastrotrichs (Fig. 2).

51 The maximum likelihood analysis of the concatenated dataset supports
52 monophyly of planktonic Gastrotricha (bs=90). However, Dasydytidae appear non-
53 monophyletic, although with very low support (bs=55), since *Stylochaeta*+*Dasydytes*

1 is in a sister group relationship to Neogosseidae. *Haltidytes squamosus* Kisielewski,
2 1991 and *Ornamentula paraënsis* Kisielewski, 1991 form the sister group of
3 *Stylochaeta*+*Dasydytes*. Further, the support for *Chaetonotus* (*Zonochaeta*) as the
4 sister clade of planktonic gastrotrichs is also very low (bs=45). The deeper nodes of
5 the maximum likelihood phylogeny generally have very low support.
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10 DISCUSSION

11 Inside the primarily benthic phylum Gastrotricha, the occurrence of planktonic taxa is
12 in many respects of particular interest. For instance, within an evolutionary
13 framework these animals may prove to be excellent for studies dealing with the origin
14 and evolution of adaptations to the planktonic environment. Knowledge of the co-
15 location of pelagic dwellers along the gastrotrich evolutionary tree would benefit
16 studies dealing with, for example, ancestral character patterns and evolution of traits
17 such as movable spines and muscle systems arrangement (Kieneke and Ostmann
18 2012).
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27 Unfortunately, the origin and phylogenetic alliances of planktonic Gastrotricha
28 has not been studied to any great extent. Kisielewski (1991) considered Dasydytidae
29 and Neogosseidae as two separate lineages, and discussed their possible origin from a
30 benthic ancestor within Chaetonotidae. This hypothesized ancestor would have
31 developed a sack-shaped body, by reduction of the caudal lobes and adhesive tubes.
32 The ventral ciliation would also have been modified into tufts and bands encircling
33 the head. However, whether the two groups arose from a common ancestor or not was
34 left open.
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42 Based on morphological observations, both Remane (1927a) and Kisielewski
43 (1991) agree on a close relationship between *Chaetonotus* (*Zonochaeta*) and
44 Dasydytidae (and possibly Neogosseidae). In fact, members of *Chaetonotus*
45 (*Zonochaeta*) and Dasydytidae both possess movable spines of similar structure and
46 function, e.g. strongly cuticularised, scaleless spines with a notched apex, used for
47 locomotion and/or defence (Schwank 1990; Kisielewski 1991; Kieneke and Ostmann
48 2012). In his 1991 authoritative paper on Brazilian freshwater Gastrotricha,
49 Kisielewski described the subgenus *Dasydytes* (*Prodasydytes*), whose members he
50 considered to have retained the plesiomorphic character states among the planktonic
51 Gastrotricha. Comparing morphology it is evident that *Dasydytes* (*P.*) *carvalhoae*,
52 *Dasydytes* (*P.*) *elongatus* and *Dasydytes* (*P.*) *papaveroi* exhibit several similarities
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with members of the putative Dasydytidae sister taxon, *Chaetonotus (Zonochaeta)*. These traits are: (i) long and specialized spines with denticles and bifurcated tips; (ii) similar shape of scales; and (iii) long parafurcal spines. In addition, dasydytids possess long ventrolateral and/or dorsolateral motile spines. To be more specific, dasydytids, by virtue of a peculiar complex system made up of serially arranged oblique muscles and segmental longitudinal muscles, can quickly raise their spines, which causes the animal to leap through the water, e.g. in response to a predator or other threat (Kieneke et al. 2008a; Kieneke and Ostmann 2012). On the other hand, species of *Chaetonotus (Zonochaeta)* are further characterized by a peculiar transverse row of spines, commonly known as the girdle, across the trunk. These spines can also be raised by muscle action. Consequently, the combination of movable spines and the associated musculature can be seen as potentially homologous characters shared by the dasydytids and species of *Chaetonotus (Zonochaeta)* (e.g. Kisielewski 1991).

The first cladistic analysis of Gastrotricha, based on 81 morphological characters, showed a sister group relationship between Dasydytidae and Neogosseidae in close alliance to Proichthyridae and Dichaeturidae (Hochberg and Litvaitis 2000). A subsequent, more inclusive analysis based on 135 morphological characters found a monophyletic Neogosseidae nested within Dasydytidae, although with low statistical support at nodes (Kieneke et al. 2008b). In the latter work, planktonic Gastrotricha appeared as a subset of Chaetonotidae, with low statistical support at nodes, although not in a close relationship with *Chaetonotus (Zonochaeta)*. In the recent phylogenetic analysis, based on three molecular markers, K  nneby et al. (2013) found a sister group relation between Dasydytidae (*Dasydytes*, *Haltidytes*, *Ornamentula* and *Stylochaeta*) and a clade containing *Chaetonotus (Zonochaeta)*, and thereby somewhat confirming the early hypothesis by Remane (1927a) and Kisielewski (1991).

The current study supports the general phylogenetic scenario obtained by K  nneby et al. (2013) and provides further evidence, on a molecular basis, for a common origin of Dasydytidae and Neogosseidae. The major findings of our study are: (i) Dasydytidae and Neogosseidae both appear as monophyletic groups; (ii) Dasydytidae and Neogosseidae are in a sister group relation; and (iii) the planktonic lineage evolved from a benthic or periphytic ancestor within Chaetonotidae. Strong nodal support and congruence with previous phylogenies (e.g. K  nneby et al. (2013)

for the general scenario and Hochberg and Litvaitis (2000) for the sister group relationship between Dasydytidae and Neogosseidae) make our findings very likely.

Neogosseidae is monophyletic and the clade has high support in our analyses. Neogosseidae can be separated from Dasydytidae morphologically by the presence of a pair of club-shaped cephalic tentacles in neogosseids. Within Neogosseidae, *Kijanebalola* and *Neogosseia* (Fig. 1) are sister groups in our phylogeny, and can be separated morphologically from each other based on distinct autapomorphic traits of the posterior end, which appears truncate and provided with a pair of tufts in *Neogosseia*, and rounded with a median group of spines in *Kijanebalola* (Todaro et al. 2013).

Dasydytidae also appears monophyletic in our analysis (Fig. 2). Morphologically, the presence of groups of motile spines along the trunk, that aid ciliary swimming can be considered an autapomorphy for the family (e.g. Kieneke and Ostmann 2012). Likewise, the peculiar system of somatic oblique and segmented lateral muscles associated with the cuticular movable spines, may at least provisionally be considered an additional autapomorphy of Dasydytidae (Kieneke and Ostmann 2012). Within Dasydytidae two major clades can be distinguished (Fig. 2). The first contains two species, *Haltidytes squamosus* and *Ornamentula paraënsis*. The second contains five species, *D. (P.) elongatus*, *D. (P.) carvalhoae*, *D. (P.) papaveroi*, *Stylochaeta fusformis* and *Stylochaeta scirtetica*. The grouping of *Haltidytes* + *Ornamentula* in one clade and *Dasydytes* in another provides support to the in-group evolutionary scenario envisioned by Kisielewski (1991) on the basis of the structure and organization of the cuticular apparatus (scales and spines), but is in contrast to the phylogenetic hypothesis put forward by Kieneke and Ostmann (2012; see position of *Ornamentula* and *Stylochaeta* in Fig. 10) based mainly on characters of the muscular system. All the sampled species in our phylogeny belong to the subgenus *Dasydytes* (*Prodasydytes*), which is, according to the results, non-monophyletic due to the early divergence of *D. (P.) carvalhoae* along the *Dasydytes* + *Stylochaeta* branch. By virtue of the highly uniform anatomy of species of *Dasydytes*, and the strong difference compared to species of *Stylochaeta*, we consider this result quite unlikely and perhaps an artifact due to contamination.

Our phylogeny supports the existence of a monophyletic planktonic clade, as shown by Hochberg and Litvaitis (2000) and Kieneke et al. (2008b). However, in

contrast to the latter study, Neogosseidae appear to be the sister taxon of Dasydytidae and not nested within it.

In the present study the planktonic clade appears as an offshoot of the Chaetonotidae as repeatedly indicated in the literature, for example, by Kisielewski (1991). Due to lack of material we did not include specimens of Dichaeturidae nor Proichthyridae, and because of this, the hypothesis by Hochberg & Litvaitis (2000), where the planktonic taxa are most closely related to these groups, cannot be properly tested. It should be emphasized that Dichaeturidae and Proichthyridae are very rare, that the original descriptions are poor, and that both these conditions could make the very existence of these taxa as independent evolutionary lines open to doubt. For instance, the recent and most accurate description of a third species of Dichaeturidae (Suzuki et al. 2013), reports characteristics that could well fit for a taxon belonging to the current Chaetonotidae. However, a taxonomic revision of Dichaeturidae and Proichthyridae lies beyond the scope of the present paper; yet in agreement with Kisielewski (1991), we consider our finding very likely. According to our results the evolution of the genuine planktonic life-style in Chaetonotida occurred only once (Dasydytidae+Neogosseidae) and probably from a benthic/periphytic ancestor.

From a morphological point of view, a lineage originally affiliated with the Chaetonotidae and evolving to the split between Dasydytidae and Neogosseidae, would have undergone several morphological adaptations to cope with the change from a benthic or periphytic life-style to a permanent planktonic life-style. Both Dasydytidae and Neogosseidae lack a furca and adhesive tubes, and have a rounded posterior end. There are also reductions and rearrangements of the locomotory ciliature: while benthic chaetonotids commonly have ventral longitudinal bands of cilia, planktonic taxa possess transverse bands or tufts of cilia along the trunk and around the head, which may increase speed and maneuverability when swimming.

These dramatic changes would also have involved the ancestors that the Dasydytidae + Neogosseidae clade share with the sister group revealed by the Bayesian analysis in our study, e.g. *Chaetonotus* (*Zonochaeta*) spp. + *Chaetonotus heteracanthus*. The maximum likelihood analysis does not show high support for this sister group relation, suggesting *Polymerurus* as a possible alternative sister group. However, we note that the most relevant autapomorphic trait of *Polymerurus* is the extraordinarily long furca, which makes it hard to unite taxa lacking a furca (planktonic gastrotrichs) with taxa possessing a particularly long furca. On the other

hand the presence of strong scaleless spines could testify in favor for a close relationship between Dasydytidae + Neogosseidae and *Chaetonotus (Zonochaeta)* spp. + *C. heteracanthus*. In this scenario we acknowledge the possible independent origin of the musculature, associated with the movable spines, in dasydytids and *Chaetonotus (Zonochaeta)*, respectively. Future morpho-functional studies on the musculature of species of *Chaetonotus (Zonochaeta)* could support or disprove this hypothesis.

To summarize, the phylogenetic hypothesis generated by this study gives strong support for a common origin of Dasydytidae and Neogosseidae, and also a hypothesized common origin of planktonic Gastrotricha. It also appears very plausible that the planktonic clade has evolved from a benthic or periphytic ancestor, by morphological adaptations to a life in the water column. Morphology and molecular data prefers *Chaetonotus (Zonochaeta)* spp. (and *C. heteracanthus*) as the sister group of planktonic Gastrotricha. The close relationship of these groups to *Polymerurus* is somewhat confusing and should be evaluated in future studies.

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REFERENCES

- Balsamo, M. (1978). Prime ricerche sui Gastrotrichi dulciacquicoli italiani. *Atti della Societa Toscana di Scienze Naturali Memorie, Serie B*, 84, 87–150. (1977).
- Balsamo, M. (1983). *Gastrotrichi. Guide per il riconoscimento delle specie animali delle acque interne italiane*. Italy: Consiglio Nazionale delle Ricerche.
- Balsamo, M. & Fregni, E. (1995). Gastrotrichs from interstitial fresh water, with a description of four new species. *Hydrobiologia*, 302, 163–175.

- Balsamo, M., d'Hondt, J. L., Pierboni, L. & Grilli, P. (2009). Taxonomic and nomenclatural notes on freshwater Gastrotricha. *Zootaxa*, 2158, 1–19.
- Balsamo, M., Grilli, P., Guidi, L. & d'Hondt, J. L. (2014). Gastrotricha: Biology, ecology and systematics, families Dasydytidae, Dichaeturidae, Neogosseidae, Proichthyidiidae. In H. J. F. Dumont (Ed.), *Identification guides to the plankton and benthos of inland waters*, 24. (187 pp.) Weikersheim: Backhuys Publishers.
- Balsamo, M., Guidi, L. & d'Hondt, J. L. (2013). Phylum Gastrotricha. In Z. Q. Zhang, (Ed.), *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness* (Addenda 2013). *Zootaxa*, 3703, 79–82.
- Balsamo, M. & Todaro, M. A. (1987). *Aspidiophorus polystictos*, a new marine species (Gastrotricha, Chaetonotida) and its life cycle. *Bollettino di Zoologia*, 54, 147–153.
- Balsamo, M. & Todaro, M. A. (1995). Gastrotrichi del Trentino: le Viotte del Monte Bondone. *Studi Trentini di Scienze Naturali–Acta Biologica*, 70, 9–22.
- Balsamo, M. & Todaro, M. A. (2002). Gastrotricha. In S. D. Rundle, A. L. Robertson, & J. M. Schmid-Araya (Eds.), *Freshwater meiofauna: biology and ecology* (pp. 45–61). Leiden: Backhuys Publishers.
- Beauchamp P. (1932). Scientific results of the Cambridge Expedition to the East African Lakes. *Journal of the Linnean Society of London, Zoology*, 38, 241–248.
- Brehm, V. (1917). Ergebnisse einiger im Franzensbader Moor unternommener Exkursionen. *Archiv für Hydrobiologie*, 11, 306–323.
- Brunson, R. B. (1950). An introduction to the taxonomy of the Gastrotricha with a study of eighteen species from Michigan. *Transactions of the American Microscopical Society*, 69, 325–352.
- Clark, D. R., Cantu, R., Cowman, D. F. & Maxson, D. J. (1998). Uptake of arsenic and metals by tadpoles at an historically contaminated Texas site. *Ecotoxicology*, 7, 61–67.
- Daday, E. von. (1905). Untersuchungen über die Süsswasser Mikrofauna Paraguays. *Zoologica*, 44, 1–374.
- Dujardin, F. (1841). *Histoire Naturelle des Zoophytes Infusoires*. Paris: Libraire Encyclopedique de Roret.

- Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
- Ehrenberg, C. G. (1838). *Die Infusionstierchen als vollkommene Organismen. Ein Blick in des tiefere organische Leben der Natur*. Leipzig: Leopold Voss.
- Gelman, A. & Rubin, D. B. (1992). "Inference from Iterative Simulation using Multiple Sequences". *Statistical Science*, 7, 457–511.
- Gerlach, S. A. (1953). Gastrotrichen aus dem Küstengrundwasser des Mittelmeeres. *Zoologischer Anzeiger*, 150, 203–211.
- Greuter, A. (1917). Beiträge zur Systematik der Gastrotrichen in der Schweiz. *Revue Suisse de Zoologie*, 25, 35–76.
- Grünspan, T. (1908). Beiträge zur Systematik der Gastrotrichen. *Zoologischer Jahrbücher Abteilung für Systematik*, 26, 214–256.
- Gosse, P. H. (1851). A catalogue of Rotifera found in Britain with descriptions of five new genera and thirty-two new species. *Annals and Magazine of Natural History*, 2, 197–203.
- Hochberg, R. & Litvaitis, M. K. (2000). Phylogeny of the Gastrotricha: a morphology-based framework of gastrotrich relationships. *Biological Bulletin*, 198, 299–305.
- Hummon, W. D. (1974). Gastrotricha from Beaufort, North Carolina, U.S.A. *Cahiers de Biologie Marine*, 15, 431–446.
- Hummon, W. D. & Todaro, M. A. (2010). Analytic taxonomy and notes on marine, brackish water and estuarine Gastrotricha. *Zootaxa*, 2392, 1–32.
- Kåanneby, T., Atherton, S. & Hochberg, R. (2014). Two new species of *Musellifer* (Gastrotricha: Chaetonotida) from Florida and Tobago and the systematic placement of the genus within Paucitubulatina. *Marine Biology Research*, 10, 983–995.
- Kåanneby, T., Todaro, M. A. & Jondelius, U. (2009). One new species and records of *Ichthyidium* Ehrenberg, 1830 (Gastrotricha: Chaetonotida) from Sweden with a key to the genus. *Zootaxa*, 2278, 26–46.
- Kåanneby, T., Todaro, M. A. & Jondelius, U. (2012). A phylogenetic approach to species delimitation in freshwater Gastrotricha from Sweden. *Hydrobiologia*, 683, 185–202.

- Kånneby, T., Todaro, M. A. & Jondelius, U. (2013). Phylogeny of Chaetonotidae and other Paucitubulatina (Gastrotricha: Chaetonotida) and the colonization of aquatic ecosystems. *Zoologica Scripta*, 42, 88–105.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P. & Drummond, A. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28(12), 1647–1649.
- Kieneke, A. & Ostmann, A. (2012). Structure, function and evolution of somatic musculature in Dasydytidae (Paucitubulatina, Gastrotricha). *Zoomorphology*, 131, 95–114.
- Kieneke, A., Martínez Arbizu, P. & Riemann, O. (2008a). Body musculature of *Stylochaeta scirtetica* Brunson, 1950 and *Dasydytes (Setodytes) tongiorgii* (Balsamo, 1982) (Gastrotricha: Dasydytidae): A functional approach. *Zoologischer Anzeiger*, 247, 147–158.
- Kieneke, A., Riemann, O. & Ahlrichs, W. H. (2008b). Novel implications for the basal internal relationships of Gastrotrich revealed by an analysis of morphological characters. *Zoologica Scripta*, 37, 429–460.
- Kieneke, A. & Schmidt-Rhaesa, A. (2014). Gastrotricha. In A. Schmidt-Rhaesa (Ed.), *Handbook of Zoology. Vol. 3 Gastrotricha and Gnathifera* (pp. 1–134). Berlin, Boston: De Gruyter.
- Kisielewski, J. (1981). *Gastrotricha from raised and transitional peat bogs in Poland*. Monografie Fauny Polski, 11. Warszawa: Polska Akademia Nauk.
- Kisielewski, J. (1986). Taxonomic notes on freshwater gastrotrichs of the genus *Aspidiophorus* Voigt (Gastrotricha, Chaetonotoidea) with description of four new species. *Fragmenta Faunistica*, 30, 139–156.
- Kisielewski, J. (1987). Two new interesting genera of Gastrotricha (Macrodasyida and Chaetonotida) from the Brazilian freshwater psammon. *Hydrobiologia*, 153, 23–30.
- Kisielewski, J. (1991). Inland-water Gastrotricha from Brazil. *Annales Zoologici Warszawa*, 43, Supplement 2, 1–168.
- Leasi, F. & Todaro, M. A. (2008). The muscular system of *Musellifer delamarei* (Renaud-Mornant, 1968) and other chaetonotidans with implications for the

- phylogeny and systematization of the Paucitubulatina (Gastrotricha).
Biological Journal of the Linnean Society, 94, 379–398.
- Marcolongo, I. (1910). Primo contributo allo studio dei Gastrotrichi del lago-stagno craterico di Astroni. *Monitore Zoologico Italiano*, 21, 315–318.
- Metschnikoff, E. (1865). Über einige wenig bekannte niedere Thierformen. *Zeitschrift für Wissenschaftliche Zoologie*, 15, 450–463.
- Miller, M. A., Pfeiffer, W. & Schwartz, T. (2010). “Creating the CIPRES Science Gateway for inference of large phylogenetic trees” in *Proceedings of the Gateway Computing Environments Workshop (GCE)* (pp. 1–8), 14 Nov. 2010, New Orleans, LA.
- Preobrajenskaja, E. N. (1926). Zur Verbreitung der Gastrotrichen in den Gewässern der Umgebung von Kossino. *Arbeiten der Biologischen Station zu Kossino (Moskau)*, 4, 1–14.
- Remane, A. (1927a). Beiträge zur Systematik der Süßwassergastrotrichen. *Zoologischer Jahrbücher Abteilung für Systematik, Oekologie, und Geographie der Tiere*, 53, 269–320.
- Remane, A. (1927b) Gastrotricha. In: G. Grimpe and Wagler, E. (Eds.), *Die Tierwelt der Nord- und Ostsee*, Lieferung X. VII (d) (pp. 1–56). Leipzig: Akademische Verlagsgesellschaft.
- Remane, A. (1927c) *Xenotrichula velox* nov. gen. nov. spec., ein chaetonotoides Gastrotrich mit männlichen Geschlechtsorganen. *Zoologischer Anzeiger*, 71, 289–294.
- Remane, A. (1934). Die Gastrotrichen des Küstengrundwassers von Schilksee. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein*, 20, 473–478.
- Remane, A. (1935–36). Gastrotricha und Kinorhyncha. In H. G. Bronn (Ed.), *Klassen und Ordnungen des Tierreichs*, Band 4, Abteilung 2, Buch 1, Teil 2, Lieferungen 1–2 (pp. 1–385). Leipzig: Akademie Verlagsgesellschaft.
- Renaud-Mornant, J. (1968). Présence du genre *Polymerurus* en milieu marine, description de deux espèces nouvelles (Gastrotricha, Chaetonotidae). *Pubblicazioni della Stazione Zoologica di Napoli*, 36, 141–151.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. (2012). MrBayes 3.2:

- Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
- Schrom, H. (1972). Nordadriatische Gastrotrichen. *Helgoländer wissenschaftlicher Meeresuntersuchungen*, 23, 286–351.
- Schwank, P. (1990). Gastrotricha. In A. Brauer, J. Schwoerbel & P. Zwick (Eds.) *Süßwasserfauna von Mitteleuropa. Band 3, Heft 1–2: Gastrotricha und Nemertini* (252 pp.). Stuttgart, Jena, New York: Gustav Fischer Verlag.
- Silvestro, D. & Michalak, I. (2012). raxmlGUI: a graphical front-end for RaxML. *Organisms Diversity and Evolution*, 12, 335–337.
- Spencer, T. (1890). On a new rotifer. *Journal of the Quekett Microscopical Club, Series 2*, 4, 59 + pl. 5.
- Stamatakis, A. (2006). RaxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
- Stokes, A. C. (1887a). Observations on a new *Dasydytes* and a new *Chaetonotus*. *The Microscope (Detroit)*, 7, 261–265.
- Stokes, A. C. (1887b). Observations on *Chaetonotus*. *The Microscope (Detroit)*, 7, 1–9; 35–43.
- Suzuki, T. G., Maeda, M. & Furuya, H. (2013). Two new Japanese species of Gastrotricha (Chaetonotida, Chaetonotidae, *Lepidodermella* and Dichaeturidae, *Dichaetura*), with comments on the diversity of gastrotrichs in rice paddies. *Zootaxa*, 3691(2), 229–239.
- Thompson, P. G. (1891). A new species of *Dasydytes*, order Gastrotricha. *Science Gossip*, 319, 160–162.
- Todaro, M. A. (1992). Contribution to the study of the Mediterranean meiofauna: Gastrotricha from the Island of Ponza. *Bollettino di Zoologia*, 59, 321–333.
- Todaro, M. A., Dal Zotto, M., Jondelius, U., Hochberg, R., Hummon, W. D., Kåanneby, T. & Rocha, C. E. F. (2012). Gastrotricha: A marine sister for a freshwater puzzle. *PLoS ONE*, 7(2), e31740.
- Todaro, M. A., Kåanneby, T., Dal Zotto, M. & Jondelius, U. (2011). Phylogeny of Thaumastodermatidae (Gastrotricha: Macrodasysida) inferred from nuclear and mitochondrial sequence data. *PLoS ONE*, 6(3), e17892.
- Todaro, M. A., Leasi, F. & Hochberg, R. (2014). A new species, genus and family of marine Gastrotricha from Jamaica, with a phylogenetic analysis of

- Macrodasysida based on molecular data. *Systematics and Biodiversity*, 12, 473–488.
- Todaro, M. A., Perissinotto, R. & Bownes, S. J. (2013). Neogosseidae (Gastrotricha, Chaetonotida) from the iSimangaliso Wetland Park, Kwazulu-Natal, South Africa. *ZooKeys*, 315, 77–94.
- Todaro, M. A., Telford, M. J., Lockyer, A. E. & Littlewood, D. T. J. (2006). Interrelationships of the Gastrotricha and their place among the Metazoa inferred from 18S rRNA genes. *Zoologica Scripta*, 35, 251–259.
- Valkanov, A. (1937). Rotatorien und Gastrotrichen der Umgebung von Plönsbiotopen. *Forschungsberichte aus der Biologischen Station zu Plön*, 11, 1–178.
- Voigt, M. (1901). Mittheilungen aus der Biologischen Station zu Plön, Holstein. Über einige bisher unbekannte Süßwasserorganismen. *Zoologischer Anzeiger*, 24, 191–195.
- Voigt, M. (1902). Drei neue *Chaetonotus*-Arten aus Plöner Gewässern. *Zoologischer Anzeiger*, 25, 116–118.
- Wilke, U. (1954). Mediterrane Gastrotrichen. *Zoologischer Jahrbücher Abteilung für Systematik (Jena)*, 82, 497–550.
- Zelinka, C. (1889). Die Gastrotrichen. Eine monographische Darstellung ihrer Anatomie, Biologie und Systematik. *Zeitschrift für Wissenschaftliche Zoologie*, 49, 209–384.

FIGURE LEGENDS

Figure 1. Species of Neogosseidae included in this study. A. *Kijanebalola devestiva*, habitus of adult specimen. Note the rounded posterior end with single median group of spines. B. *Neogossea acanthocolla*, habitus of adult specimen. Note the truncate posterior end with a pair of tufts. C. *Neogossea antennigera*, anterior two thirds of body of adult specimen. D. *N. antennigera*, posterior end of body of adult specimen. Note the truncate posterior end with a pair of tufts. Scale bars: A and B, 50 μm ; C and D, 25 μm .

Figure 2. Majority rule consensus tree based on the Bayesian analysis of the concatenated dataset. Numbers at nodes represent posterior probability. Asterisks indicate a bootstrap support value above 75, obtained from the maximum likelihood analysis of the concatenated dataset. The star indicate the clade where a permanent planktonic life-style has evolved. The clades containing members of Muselliferidae (outgroup) and Xenotrichulidae have been collapsed for esthetic reasons (see Table 1 for full set of taxa).

Table 1. Taxa used in the phylogenetic analyses in this study with Genbank accession numbers and reference. The Morphbank Id number is given in parentheses for most specimens and photographs can be accessed at <http://www.morphbank.net/799280> or at <http://www.morphbank.net/855412>. Na, Not available.

Taxon (Morphbank ID)	Genbank Accession #			Reference
	18S	28S	COI	
Family Chaetonotidae				
<i>Arenotus strixinoi</i> Kisielewski, 1987 (791776)	JQ798537	JQ798608	JQ798677	K��nneby et al. 2013
<i>Aspidiophorus ophiodermus</i> Balsamo, 1983 (791777–791778)	JN185463	JN185510	NA	K��nneby et al. 2012
<i>Aspidiophorus paramediterraneus</i> Hummon, 1974 (791779)	JQ798538	JQ798609	JQ798678	K��nneby et al. 2013
<i>Aspidiophorus polystictos</i> Balsamo & Todaro, 1987	JQ798598	JQ798665	JQ798727	K��nneby et al. 2013
<i>Aspidiophorus tentaculatus</i> Wilke, 1954 (791780)	JQ798553	JQ798625	JQ798690	K��nneby et al. 2013
<i>Aspidiophorus tetrachaetus</i> Kisielewski, 1986 (791781)	JN185505	JN185540	JN185576	K��nneby et al. 2012
<i>Aspidiophorus</i> sp. 3	JQ798559	JQ798629	NA	K��nneby et al. 2013
<i>Chaetonotus acanthocephalus</i> Valkanov, 1937 (791825–791826)	JQ798569	NA	JQ798701	K��nneby et al. 2013
<i>Chaetonotus acanthodes</i> Stokes, 1887 (791828– 791830)	JQ798552	JQ798624	NA	K��nneby et al. 2013
<i>Chaetonotus aemilianus</i> Balsamo, 1978 (791819)	JQ798556	JQ798626	JQ798693	K��nneby et al. 2013
<i>Chaetonotus armatus</i> Kisielewski, 1981 (791832–791835)	JQ798594	NA	JQ798723	K��nneby et al. 2013
<i>Chaetonotus (Zonochaeta) bisacer</i> Greuter, 1917 (791848– 791849)	JQ798565	JQ798635	NA	K��nneby et al. 2013
<i>Chaetonotus</i>	JQ798549	JQ798621	JQ798687	K��nneby et al.

<i>daphnes</i> Balsamo & Todaro, 1995 (791782–791784)				2013
<i>Chaetonotus</i> cf. <i>dispar</i> Wilke, 1954 (791844–791846)	JQ798561	JQ798631	JQ798696	Kånneby et al. 2013
<i>Chaetonotus heideri</i> Brehm, 1917 (791836–791837)	JQ798547	JQ798619	JQ798685	Kånneby et al. 2013
<i>Chaetonotus heteracanthus</i> Remane, 1927 (791840–791842)	JQ798543	JQ798615	JQ798681	Kånneby et al. 2013
<i>Chaetonotus</i> cf. <i>hystrix</i> Metschnikoff, 1865 (791821)	JQ798603	JQ798670	JQ798732	Kånneby et al. 2013
<i>Chaetonotus</i> cf. <i>laroides</i> Marcolongo, 1910 (791788–791789)	JQ798602	JQ798669	JQ798731	Kånneby et al. 2013
<i>Chaetonotus mariae</i> Todaro, 1992 (791824)	JQ798558	JQ798628	NA	Kånneby et al. 2013
<i>Chaetonotus</i> cf. <i>maximus</i> Ehrenberg, 1838 (791793)	JQ798574	JQ798646	JQ798706	Kånneby et al. 2013
<i>Chaetonotus microchaetus</i> Preobrajenskaja, 1926 (791801)	JQ798583	JQ798651	JQ798714	Kånneby et al. 2013
<i>Chaetonotus neptuni</i> Wilke, 1954	JQ798595	JQ798662	JQ798724	Kånneby et al. 2013
<i>Chaetonotus</i> cf. <i>novenarius</i> Greuter, 1917 (791822–791823)	JQ798566	JQ798636	JQ798699	Kånneby et al. 2013
<i>Chaetonotus</i> cf. <i>oculifer</i> Kisielewski, 1981 (791802)	JQ798576	JQ798647	JQ798708	Kånneby et al. 2013
<i>Chaetonotus polyspinosus</i> Greuter, 1917 (791804–791805)	JQ798563	JQ798633	JQ798698	Kånneby et al. 2013
<i>Chaetonotus schultzei</i> Metschnikoff, 1865	JQ798596	JQ798663	JQ798725	Kånneby et al. 2013
<i>Chaetonotus similis</i> Zelinka, 1889 (791808–791809)	JQ798578	JQ798648	JQ798710	Kånneby et al. 2013
<i>Chaetonotus</i> cf. <i>sphagnophilus</i> Kisielewski, 1981	JQ798604	JQ798671	JQ798733	Kånneby et al. 2013

<i>Chaetonotus uncinus</i> Voigt, 1902 (791847)	JQ798540	JQ798611	NA	Kånneby et al. 2013
<i>Chaetonotus (Zonochaeta)</i> sp. 1 (791852–791853)	JQ798593	JQ798661	NA	Kånneby et al. 2013
<i>Chaetonotus (Zonochaeta)</i> sp. 2 (791854–791856)	JQ798587	JQ798655	JQ798718	Kånneby et al. 2013
<i>Chaetonotus</i> sp. 1 (791817–791818)	JQ798601	JQ798668	JQ798730	Kånneby et al. 2013
<i>Halichaetonotus aculifer</i> (Gerlach, 1953)	JQ798550	JQ798622	JQ798688	Kånneby et al. 2013
<i>Halichaetonotus euromarinus</i> Hummon & Todaro, 2010 (791857–791859)	JQ798551	JQ798623	NA	Kånneby et al. 2013
<i>Halichaetonotus paradoxus</i> (Remane, 1927)	JQ798599	JQ798666	JQ798728	Kånneby et al. 2013
<i>Halichaetonotus</i> sp. 2	JQ798600	JQ798667	JQ798729	Kånneby et al. 2013
<i>Halichaetonotus</i> sp. 4	JQ798560	JQ798630	JQ798695	Kånneby et al. 2013
<i>Heterolepidoderma acidophilum</i> Kånneby et al., 2012 (791871–791872)	JN185462	JN185509	JN185543	Kånneby et al. 2012
<i>Heterolepidoderma loricatum</i> Schrom, 1972	JQ798541	JQ798612	NA	Kånneby et al. 2013
<i>Heterolepidoderma macrops</i> Kisielewski, 1981 (791860–791863)	JN185469	JN185515	JN185548	Kånneby et al. 2012
<i>Heterolepidoderma ocellatum</i> (Metschnikoff, 1865) (791867–791868)	JN185476	JN185520	JN185555	Kånneby et al. 2012
<i>Heterolepidoderma</i> sp. 2 (791875–791876)	JN185485	JQ798644	JN185563	Kånneby et al. 2013
<i>Heterolepidoderma</i> sp. 3 (791877–791879)	JQ798572	JQ798641	JQ798704	Kånneby et al. 2013
<i>Ichthydium skandicum</i> Kånneby et al., 2009 (791880–791881)	JQ798573	JQ798645	JQ798705	Kånneby et al. 2013
<i>Ichthydium squamigerum</i> Balsamo & Fregni, 1995 (791882–791883)	JQ798607	JQ798674	JQ798736	Kånneby et al. 2013

<i>Lepidochaetus brasilese</i> Kisielewski, 1991 (791884–791887)	JN185495	JQ798658	JN185568	Kånneby et al. 2012; 2013
<i>Lepidochaetus zelinkai</i> (Grünspan, 1908) (791897– 791899)	JN185486	JN185527	JN185564	Kånneby et al. 2012; 2013
<i>Lepidodermella intermedia</i> Kånneby et al., 2012 (791904– 791906)	JN185468	JN185514	JN185547	Kånneby et al. 2012
<i>Lepidodermella minor minor</i> (Remane, 1936) (791907–791908)	JN185474	NA	JN185553	Kånneby et al. 2012
<i>Lepidodermella squamata</i> (Dujardin, 1841) (791915–791917)	JN185479	JN185523	JN185558	Kånneby et al. 2012
<i>Polymerurus nodicaudus</i> (Voigt, 1901)	JN185502	JN185537	JN185573	Kånneby et al. 2012
<i>Polymerurus rhomboides</i> (Stokes, 1887) (791931–791933)	JN185493	JN185533	JN185567	Kånneby et al. 2012
Family Dasydytidae				
<i>Dasydytes carvalhoae</i> Kisielewski, 1991 (791934–791937)	JQ798570	JQ798639	JQ798702	Kånneby et al. 2013
<i>Dasydytes elongatus</i> Kisielewski, 1991 (791938–791941)	JQ798568	JQ798638	JQ798700	Kånneby et al. 2013
<i>Dasydytes papaveri</i> Kisielewski, 1991 (791948–791950)	JQ798571	JQ798640	JQ798703	Kånneby et al. 2013
<i>Haltidytes squamosus</i> Kisielewski, 1991 (791951–791954)	JQ798567	JQ798637	NA	Kånneby et al. 2013
<i>Ornamentula paraënsis</i> Kisielewski, 1991 (791955–791956)	JQ798562	JQ798632	JQ798697	Kånneby et al. 2013
<i>Stylochaeta fusiformis</i> (Spencer, 1890) (791957–791959)	JN185471	JN185517	JN185550	Kånneby et al. 2012
<i>Stylochaeta scirtetica</i> Brunson, 1950 (791960– 791962)	JN185492	JN185532	NA	Kånneby et al. 2012
Family				

Muselliferidae				
<i>Musellifer delamarei</i> (Renaud-Mornant, 1968)	AM231775	NA	NA	Todaro et al. 2006
<i>Musellifer reichardti</i> Kånneby et al., 2014	KF578503	NA	NA	Kånneby et al. 2014
Family Neogosseidae				
<i>Kijanebalola devestiva</i> Todaro et al. 2013 (855405–855406)	KR822112	KR822117	KR822120	This study
<i>Kijanebalola devestiva</i> Todaro et al. 2013 (855405–855406)	KR822113	KR822118	NA	This study
<i>Neogosseia acanthocolla</i> Kisieleski, 1991 (855408)	KR822114	KR822119	KR822121	This study
<i>Neogosseia antennigera</i> (Gosse, 1851) (855197-855198)	KR822110	KR822115	NA	This study
<i>Neogosseia antennigera</i> (Gosse, 1851) (855197-855198)	KR822111	KR822116	NA	This study
Family Xenotrichulidae				
<i>Draculiciteria tessellata</i> (Renaud-Mornant, 1968) (791964–791967)	JN185470	JN185516	JN185549	Kånneby et al. 2012
<i>Heteroxenotrichula squamosa</i> Wilke, 1954 (791968)	JQ798542	JQ798613	NA	Kånneby et al. 2013
<i>Xenotrichula intermedia</i> Remane, 1934	JF357664	JF357712	JF432047	Todaro et al. 2011
<i>Xenotrichula punctata</i> Wilke, 1954	JN185464	JN185511	NA	Kånneby et al. 2012
<i>Xenotrichula velox</i> Remane, 1927 (791969–791971)	JN185488	JQ798652	NA	Kånneby et al. 2012

Figure 1 Neogosseidae
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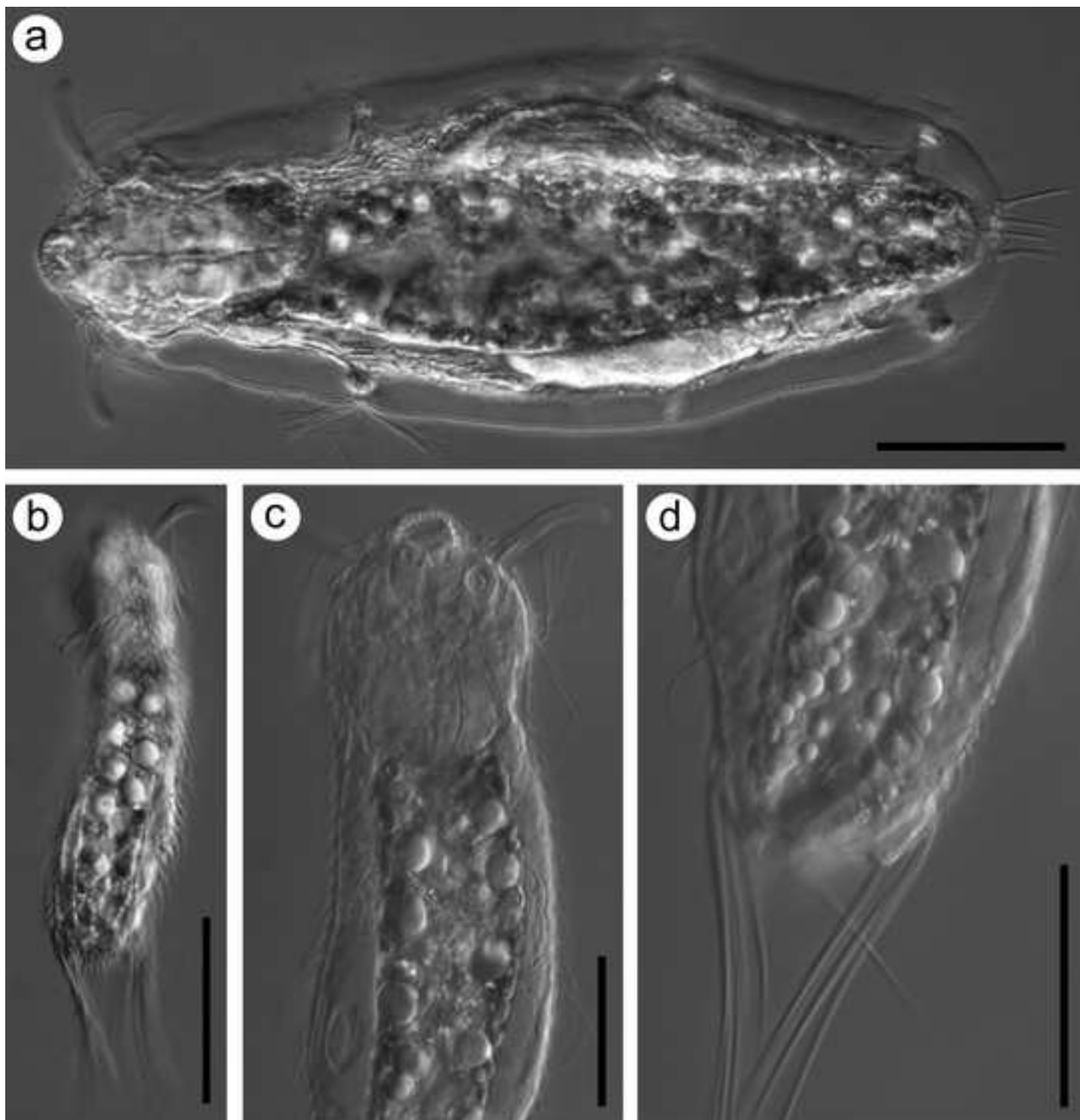


Figure 2 Phylogeny

