AUTHORS: Tobias Kånneby[1*] & M. Antonio Todaro[2]

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 *Neogossea*, 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 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 cuticule.

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 *Neogossea 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 *Neogossea*. 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

subfamily Chaetonotinae (Kisielewski 1991); (ii) Dasydytidae, which is characterized by long and movable spines (Kisielewski 1991; Kieneke and Ostmann 2012); and (iii) Neogosseidae, characterized by long posterior spines, either distributed in an unpaired median group (*Kijanebalola*) or in a paired lateral group (*Neogossea*), and a pair of club-shaped cephalic tentacles (Todaro et al. 2013).

The origin and evolution of planktonic gastrotrichs remain largely unknown (Hochberg and Litvaitis 2000; Kieneke et al. 2008a). However, the long-held hypothesis that at least some planktonic forms may have been derived from benthic ancestors (e.g. related to *Chaetonotus (Zonochaeta)* Remane, 1927a; see Kisielewski 1991) has gained support in a recent phylogenetic study based on molecular data (Kånneby et al. 2013). In the latter study the authors showed that the planktonic Dasydytidae is nested within a non-monophyletic Chaetonotidae. However, the non-monophyly of Chaetonotidae had been known for quite some time prior to that study, based on morphological data (e.g. Hochberg and Litvaitis 2000; Kieneke et al. 2008a). It should be emphasized that the systematics of the entire order Chaetonotida, and especially within the largest group Chaetonotidae, is unstable. This is mainly due to the classification's heavy reliance on cuticular structures and ornamentation, characters that are extremely variable and thereby inconsistent on higher levels of classification (e.g. genus, family etc.) (see Kånneby et al. 2013). A phylogenetic approach based on molecular data may prove to be helpful in the process of re-systematization of chaetonotidan taxa, similar to what is happening in the systematization of the Macrodasyida (Todaro et al. 2012; 2014) However, several groups of chaetonotidans have not yet been sampled for molecular data; this includes Dichaeturidae, Neogosseidae and Proichthydiidae, mainly because of lack of material. It should be emphasized that members of these groups are very uncommon, with some species only reported from their respective, often remote, type localities; as a consequence, information on these animals is generally very poor and their origin and phylogenetic alliances remain obscure.

In this study, in order to shed some light on the hypothesized relationship between Dasydytidae and Neogosseidae suggested by previous authors, we have obtained specimens and sequences of 18S rDNA, 28S rDNA and COI mtDNA for the uncommon planktonic genera *Kijanebalola* and *Neogossea*, comprising Neogosseidae (Table 1). We also hope, if possible, to shed light on the origin of planktonic

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 *Neogossea 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 *Neogossea 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% $MgCl_2$-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; Kånneby 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/phylows/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.

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

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

With regard to the main aims of the current study, the Bayesian analysis gives high support for monophyly of the planktonic gastrotrichs (Dasydytidae+Neogosseidae) in our study (pp=1). Within this clade both Dasydytidae (pp=0.99) and Neogosseidae (pp=1) are monophyletic (Fig. 2). For Neogosseidae, both *Kijanebalola* (*K. devestiva*, n=2) and *Neogossea* (*N. acanthocolla*, n=1 + *N. antennigera*, n=2) are monophyletic with high bootstrap support (pp=1). *N. acanthocolla* and *N. antennigera* are sister taxa. Within Dasydytidae two major clades can be discerned: *Haltidytes squamosus* + *Ornamentula paraënsis* and *Dasydytes* + *Stylochaeta* (Fig. 2). Within the latter clade *Stylochaeta fusiformis* and *Stylochaeta scirtetica* are in a sister group relation to *Dasydytes (Prodasydytes) elongatus* Kisielewski, 1991 and *Dasydytes (P.) papaveroi* Kisielewski, 1991 (pp=1). The subgenus *Dasydytes (Prodasydytes)* is non-monophyletic, because of the sister group relationship of *Dasydytes (P.) carvalhoae* Kisielewski, 1991 to *D. (P.) elongatus* + *D. (P.) papaveroi* and *Stylochaeta* (pp=1).

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

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

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

DISCUSSION

Inside the primarily benthic phylum Gastrotricha, the occurrence of planktonic taxa is in many respects of particular interest. For instance, within an evolutionary framework these animals may prove to be excellent for studies dealing with the origin and evolution of adaptations to the planktonic environment. Knowledge of the co-location of pelagic dwellers along the gastrotrich evolutionary tree would benefit studies dealing with, for example, ancestral character patterns and evolution of traits such as movable spines and muscle systems arrangement (Kieneke and Ostmann 2012).

Unfortunately, the origin and phylogenetic alliances of planktonic Gastrotricha has not been studied to any great extent. Kisielewski (1991) considered Dasydytidae and Neogsseidae as two separate lineages, and discussed their possible origin from a benthic ancestor within Chaetonotidae. This hypothesized ancestor would have developed a sack-shaped body, by reduction of the caudal lobes and adhesive tubes. The ventral ciliation would also have been modified into tufts and bands encircling the head. However, whether the two groups arose from a common ancestor or not was left open.

Based on morphological observations, both Remane (1927a) and Kisielewski (1991) agree on a close relationship between *Chaetonotus (Zonochaeta)* and Dasydytidae (and possibly Neogosseidae). In fact, members of *Chaetonotus (Zonochaeta)* and Dasydytidae both possess movable spines of similar structure and function, e.g. strongly cuticularised, scaleless spines with a notched apex, used for locomotion and/or defence (Schwank 1990; Kisielewski 1991; Kieneke and Ostmann 2012). In his 1991 authoritative paper on Brazilian freshwater Gastrotricha, Kisielewski described the subgenus *Dasydytes (Prodasydytes)*, whose members he considered to have retained the plesiomorphic character states among the planktonic Gastrotricha. Comparing morphology it is evident that *Dasydytes (P.) carvalhoae*, *Dasydytes (P.) elongatus* and *Dasydytes (P.) papaveroi* exhibit several similarities

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 Proichthydidae 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, Kånneby 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 Kånneby 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. Kånneby 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 *Neogossea* (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 *Neogossea*, 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 Proichthydidae, 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 Proichthydidae 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 Proichthydidae 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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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				
Arenotus strixinoi Kisielewski, 1987 (791776)	JQ798537	JQ798608	JQ798677	Kånneby et al. 2013
Aspidiophorus ophiodermus Balsamo, 1983 (791777–791778)	JN185463	JN185510	NA	Kånneby et al. 2012
Aspidiophorus paramediterraneus Hummon, 1974 (791779)	JQ798538	JQ798609	JQ798678	Kånneby et al. 2013
Aspidiophorus polystictos Balsamo & Todaro, 1987	JQ798598	JQ798665	JQ798727	Kånneby et al. 2013
Aspidiophorus tentaculatus Wilke, 1954 (791780)	JQ798553	JQ798625	JQ798690	Kånneby et al. 2013
Aspidiophorus tetrachaetus Kisielewski, 1986 (791781)	JN185505	JN185540	JN185576	Kånneby et al. 2012
Aspidiophorus sp. 3	JQ798559	JQ798629	NA	Kånneby et al. 2013
Chaetonotus acanthocephalus Valkanov, 1937 (791825–791826)	JQ798569	NA	JQ798701	Kånneby et al. 2013
Chaetonotus acanthodes Stokes, 1887 (791828–791830)	JQ798552	JQ798624	NA	Kånneby et al. 2013
Chaetonotus aemilianus Balsamo, 1978 (791819)	JQ798556	JQ798626	JQ798693	Kånneby et al. 2013
Chaetonotus armatus Kisielewski, 1981 (791832–791835)	JQ798594	NA	JQ798723	Kånneby et al. 2013
Chaetonotus (Zonochaeta) bisacer Greuter, 1917 (791848-791849)	JQ798565	JQ798635	NA	Kånneby et al. 2013
Chaetonotus	JQ798549	JQ798621	JQ798687	Kånneby et al.

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

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

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

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

Figure 1 Neogosseidae
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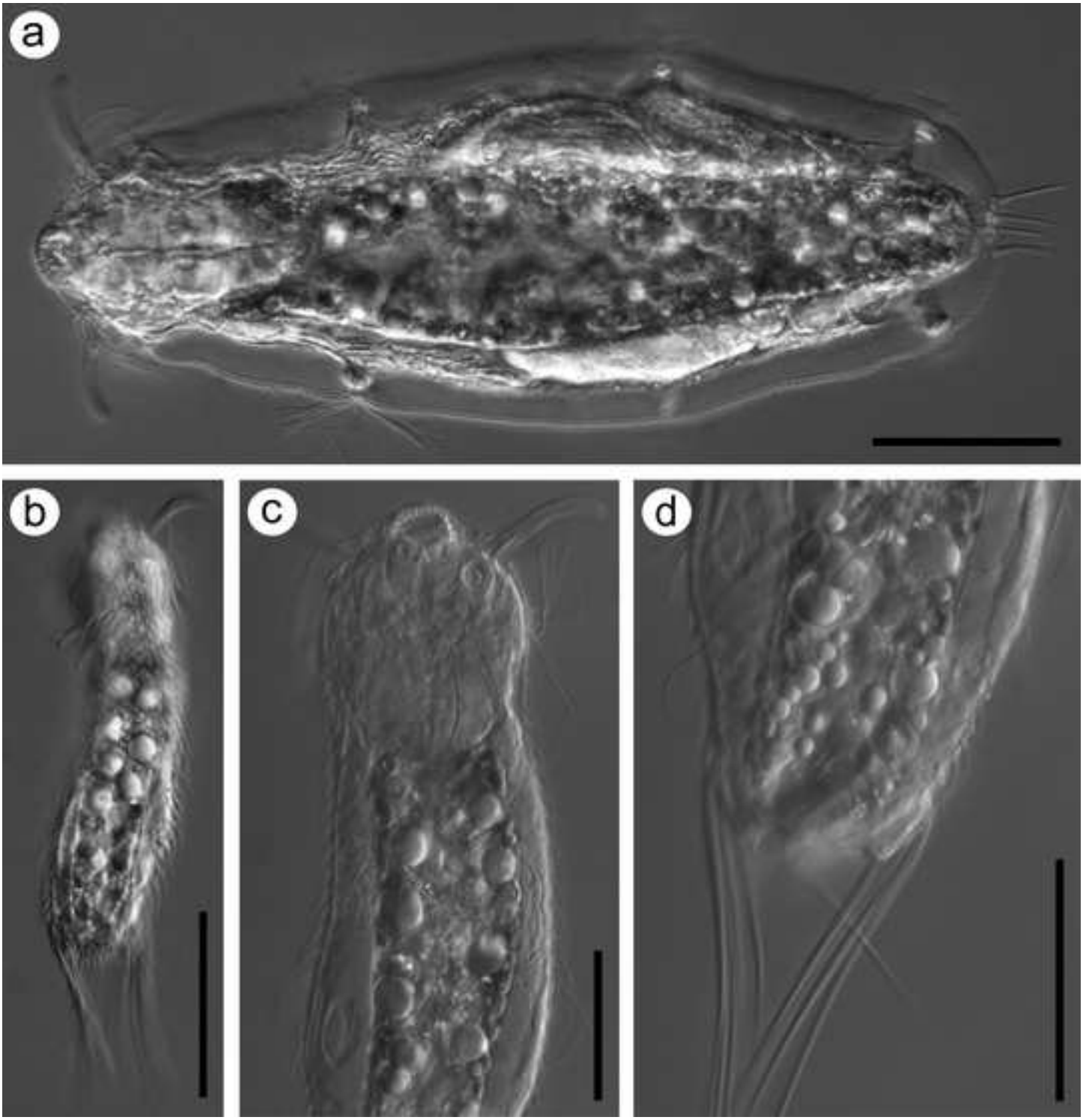

Figure 2 Phylogeny