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Pseudotachidiidae (Copepoda: Harpacticoida) from the Angola Basin and the Antarctic deep sea, with the description of a new species of *Paradanielssenia* Soyer, 1970

Elke Willen*

AG Zoosystematics and Morphology, Institute for Biology, Faculty 5, University of Oldenburg, 26111 Oldenburg, Germany

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Abstract

The species diversity of Copepoda Harpacticoida in the deep sea of the Angola Basin (DIVA I expedition) and in the Weddell Sea (ANDEEP II expedition) is investigated. In both areas, the Pseudotachidiidae Lang, 1936, together with Ameiridae Monard, 1927, Argestidae Por, 1986 and Ectinosomatidae Sars, 1903, are richest in species and numbers of individuals. From two DIVA stations and from ANDEEP station 138, all adult specimens have been determined at the level of 'working species'. Pseudomesochrinae Willen, 1996, represented mainly by the single taxon *Pseudomesochra* T. Scott, 1902 and Paranannopinae Por, 1986 turned out to be the 'dominant' taxa in terms of abundance and species number. A new species of *Paradanielssenia* Soyer, 1970 is described, which was encountered in relatively high abundances in almost every replicate sample from the DIVA stations. A key to the known species of the taxon *Paradanielssenia* is given.

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Introduction

The international deep-sea campaigns DIVA and ANDEEP are integrated into the global deep-sea biodiversity programme 'Census of the Diversity of Abyssal Marine life' (CeDAMar). CeDAMar aims to produce reliable information on deep-sea diversity and the factors regulating it in the next decades (www.cedamar.org). Eventually, the stations of the DIVA and ANDEEP expeditions will for the first time provide a sampling transect of a complete latitudinal deep-sea gradient from the tropics to the pole in the Southern

E-mail address: ewillen@gmx.de.

Atlantic. The first DIVA expedition to the Angola basin took place in July 2000. For the first time a comprehensive replicative sampling design was performed for the meiofauna (compare Rose et al. 2005). Especially the deep-sea meiofauna is still only sporadically known.

Within this framework the species diversity of Copepoda Harpacticoida in the deep sea of the Angola Basin (DIVA I) and in the Weddell Sea (ANDEEP II) has been investigated. One of the goals of the entire project is to obtain data on the presence and distribution of harpacticoid higher taxa and species. For DIVA I, all adult specimens from two sampling stations have been determined at the level of 'working' species by the cooperation of several scientists from Senckenberg's DZMB Research Institute (Deutsches Zentrum für Marine Biodiversität in Wilhelmshaven) and the

^{*}Current address: c/o Prof. H.K. Schminke, Institute for Biology, Faculty 5, University of Oldenburg, 26111 Oldenburg, Germany.

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University of Oldenburg. On the basis of the sampling design (at least five multicorer replicates at each station) this will allow the first comprehensive statistical survey with a complete quantitative data set at species level, to compare two abyssal stations on an extensive transect in a deep-sea region of equal sediment structure and depth with regard to their their species composition and diversity. First results have been published (Rose et al. 2005). In a first step, all harpacticoid species had been determined at 'core-scale' level; the resulting data set has been used to compare alpha diversity at species level.

The next step, documented in the present paper for the Pseudotachidiidae Lang, 1936, is the complete survey of species at the level of 'working species' to make a direct comparison among the stations. For the present study a third station was included in the investigation, located in the Antarctic Weddell Sea (ANDEEP II expedition, station 138, 'Weddell Sea abyssal plain') and agreeing with the other two stations in sediment structure and depth. Since the multicorer size and type used were different, direct quantitative comparison between all three stations would not be possible. However, interesting data on similar taxa composition, species overlap and thus extensive species distribution in different areas of the southern Atlantic were obtained.

From the Weddell Sea samples, the members of Pseudotachdiidae, Ameiridae Monard, 1927, Neobradiydae Olofsson, 1917 and Huntemanniidae Por, 1986 have been recorded at species level.

In the samples from the Angola Basin the Pseudotachidiidae turned out to be one of the most important taxa of Harpacticoida in terms of species and numbers of individuals, together with the Ectinosomatidae Sars, 1903, Argestidae Por, 1986 and Ameiridae. They represent a quite significant taxon within the Harpacticoida, concerning the number of species and subtaxa as well as a worldwide distribution range. Many species are known from the deep sea. Several monophyletic subgroups have already been identified (Hicks 1988; Willen 1999, 2000, 2005). Starting as a former small 'subfamily' of Thalestridae in the traditional system of Harpacticoida published by Lang (1948), the Pseudotachidiidae became a well-characterised monophyletic higher taxon within the Harpacticoida, being most successful in terms of species number and distribution (Willen 1996, 1999, 2000, 2004).

In addition, a new species of *Paradanielssenia*, *Paradanielssenia meikae* sp. n., is described. For a key to the species in that genus, see the Appendix.

Material and methods

Two out of four stations in the Angola Basin were sampled replicatively using a multicorer during the DIVA-1 campaign of the RV 'Meteor' M48/1 from 07/06/2000 to 08/08/2000. Station 325 ($19^{\circ}58.291'S$, 002°59.682'E; depth: 5494 m) was located 300 sm southwest of station 346 ($16^{\circ}17.024'S$, $005^{\circ}27.021'E$; depth: 5433 m). Seven replicates corresponding to 35 cores were taken at station 325, and eight replicates (40 cores) at station 346. ANDEEP station 138 ('Weddell Sea abyssal plain'; $62^{\circ}58,03'S$, $27^{\circ}54,08'W$; depth: 4541.3 m) was sampled on the expedition of RV Polarstern, PS 61/138-11 on 03/18/2002. At this station, nine replicates (45 cores) were taken. Treatment of the multicorer samples was described in detail by Rose et al. (2005).

Holotypes and allotypes were preserved in 5% buffered formalin and subsequently transferred to glycerine. Drawings were made with the aid of a camera lucida on a Leica Diaplan microscope equipped with UCA condenser, IC prism and $1.5 \times$ doubler. The dissected parts are mounted on several slides. The terminology is adopted from Lang (1948, 1965), except for the segmental composition of mandible and maxilliped, and the numbering of the furcal setae, which are treated after Huys and Boxshall (1991).

Abbreviations used in the text: aes = aesthetasc, benp = baseoendopodite of P5, enp = endopodite, enp1 = first segment of endopodite, exp = exopodite, Md = mandible, Mx = maxilla, Mxl = maxillula, Mxp = maxilliped, P1-P6 = swimming legs 1-6.

The term ground pattern is used in the sense of 'Grundmuster' (Ax 1984, p. 156). A map of the sampling locations is shown in Fig. 1.

Results

Paradanielssenia meikae sp. n.

(Figs. 2–12)

Etymology

The species is dedicated to my niece, Meike Willen, born 29.09.2004 in Stuttgart, Germany, who will hopefully still be able to enjoy the species diversity on our planet.

Type material

Holotype female (UNIOL 2006.001): Southern Atlantic Ocean, DIVA-1 campaign of RV 'Meteor', station 346 (16°17.024'S, 005°27.021'E; depth 5433 m); stored in UNIOL copepod collection within the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt a.M., Germany.

Paratypes. Same data as holotype, except UNIOL 2006.002 (allotype male), UNIOL 2006.003-007 (remaining paratypes).





Fig. 1. Map of sampling locations.

Diagnosis

Paranannopinae with mouthpart aesthetascs. A2 exp1 with only one seta, benp of female P5 elongate and narrow, reaching far beyond a small and rounded exp. Female antennule 5-segmented, prosomatic hyaline frill with reticular cuticula ornamentation, outer spine on male P5 exp enlarged.

Description of female (holotype)

Body length 349 µm, furcal rami length 16 µm.

Rostrum (Figs. 7B and 9C) demarcated from cephalothorax, longer than broad, rounded, with one pair of longer sensillae apically, and one pair of tiny ones subapically.

Body (Figs. 2A and 7B). Distinct separation between prosome and smaller urosome. Cephalothorax slightly broader than long, cephalic shield with sensilla and pores. Posterior margin and surface of each body somite (excluding penultimate somite) with sensilla. Urosomal somites (Figs. 2, 7 and 12A) with ventrolateral rows of large spinules on distal margins. Body dorsally without spinule ornamentation. Hyaline frills of reticulate structure; genital double-somite (free somites 5 and 6) not completely fused (Fig. 12A), genital field as in Fig. 12A; P6 with three setae. Anal somite completely divided, with two dorsal sensilla, anal operculum absent, very small peudoperculum present (Fig. 7). Furcal rami



Fig. 2. Paradanielssenia meikae sp. n. (A) Female habitus in lateral view; scale bar $a = 50 \,\mu\text{m}$. (B) Female antenna; scale bar $b = 20 \,\mu\text{m}$.

(Figs. 2, 7 and 12A) only slightly longer than broad, furcal seta I absent, II and III well developed and strong, II located subapically at outer edge, III at outer terminal edge, IV and V well developed, VI well developed, located at inner edge, VII subterminally near inner margin on dorsal surface.

Antennule (Fig. 9B). Short, with five short segments. Armature: I(1); II(8); III(8); IV(4 + aes); V(12 + aes).

Antenna (Fig. 2B). Allobasis with long abexopodal pinnate seta and two long spinules medially; exp 3-segmented, with 1-0-(1+2) setae; third segment with subapical spinule row; enp with spinule row medially on abexopodal margin; subapical armature consisting of two pinnate spines and one geniculate seta; apical armature of five setae: one pinnate spine and four geniculate setae.

Mandible (Fig. 3B). Gnathobase of rather delicate appearance, with three larger and several smaller, fine and pointed teeth, inner edge with one pinnate seta; basis with spinule row and four pinnate setae; enp consisting of short projection with large seta being modified as claviform aesthetasc, exp absent.



Fig. 3. *Paradanielssenia meikae* sp. n. (A) P1. (B) Mandible. Scale bars = $20 \,\mu$ m.

Maxillule (Fig. 4B). Arthrite of praecoxa with nine apical slender spines, two juxtaposed setae on anterior surface; coxal endite with six setae; basis with two demarcated endites, bearing four (one modified as large claviform mouthpart aesthetasc) + two setae; exp and enp demarcated, both short and rounded, with three setae each.

Maxilla (Fig. 4C). Syncoxa with three endites; proximal endite bilobed, proximal lobe with one large unilaterally pinnate seta, distal lobe with one large and one smaller pinnate setae, middle and distal endites each with three setae; basal endite with one claw fused to basis, accompanied by one slender naked seta on posterior and two setae on anterior side; enp 1-segmented, bearing four setae, one of them modified to claviform aesthetasc.

Maxilliped (Fig. 5C). Syncoxa approximately two thirds as long as basis, with several spinule rows and two pinnate setae at distal margin, one of them enlarged and almost twice as long as basis; basis bearing one very small and pinnate seta medially on inner margin as well as one spinule row on the surface; enp fused with large, slightly pinnate claw.



Fig. 4. *Paradanielssenia meikae* sp. n. (A) Female P2. (B) Maxillule. (C) Maxilla. Scale bars = $20 \,\mu$ m.

P1 (Fig. 3A). Coxa much broader than basis, with rounded outer margin, of rectangular shape, with a row of larger spinules on the anterior surface. Basis with pinnate outer and pinnate large inner spine; distal and inner margins as well as base of inner spine with spinule rows. Exp 3-segmented, outer margins fringed with spinules; exp1 and exp2 each with one outer pinnate spine, exp1 slightly longer than exp2 and exp3, exp2 with inner seta; exp3 with three outer pinnate spines, terminally with one pinnate outer spine and one long, slender and pinnate inner seta; enp 2-segmented, segments of nearly equal length, enp1 with two spinule rows along outer and distal margins, with pore on anterior surface and one long, inner, slightly pinnate and geniculate seta subdistally; enp2 with one inner plumose seta and terminally with outer pinnate seta, and two well-developed and pinnate setae.

P2–P4 (Figs. 4A; 5A, B; 6). Exps and enps 3-segmented. Coxae of almost rectangular shape, with only a few spinule rows on surface and margins. Basis



Fig. 5. *Paradanielssenia meikae* sp. n. (A) Female P3, exopod. (B) Female P3, endopod. (C) Maxilliped. Scale bars = $20 \,\mu m$.

	Exp	Enp	
P2	1-1-2, 2, 3	1-2-2, 2, 1	
P3	1-1-3, 2, 3	1-1-3, 2, 1	
P4	1-1-3 2 3	1-1-2 2 1	

 Table 1.
 Setal formulae (after Lang 1948)

with small, slender, plumose outer setae, accompanied by basal spinule rows. Endopodite shorter than exopodite on P4, of nearly equal length on P2 and P3. Enp1 inner seta on P2 and P3 almost spine like, short and only slightly pinnate, on P4 developed as long, slender, pinnate seta (Table 1).

P5 (Fig. 8A). Pair of legs not fused medially, with tiny intercoxal sclerite, basal part with slender outer seta, endopodal lobe elongate, three times as long as exp, with five pinnate setae, the innermost of them short and smaller, second innermost short and strong, pinnate only in distal half, inner and outer terminal and outer setae long and well developed; exp very small, slightly longer than broad, setation consisting of four setae/spines, innermost



Fig. 6. Paradanielssenia meikae sp. n. (A) Female P4; scale bar = $20 \,\mu\text{m}$.

seta spine like, short and pinnate at tip, inner terminal seta slender and naked, two outer terminal setae strong, long and pinnate, outer seta spine like and pinnate.

Description of male (allotype)

Body length 860 µm.

Body (Figs. 7 and 11). Slightly shorter but otherwise as in female, except for somites 5 and 6 which are completely separated, distal margin of urosomites fringed with large spinules.

Antennule (Fig. 12B). Chirocer, indistinctly 7-segmented, setal armature as follows:

I(1); II(1); III(10 + aes); IV(8 + aes); V(2);

VI(12 + aes); VII(2 + 5 + aes).

A2, mouthparts, Mxp and P1 as in female.

P2 (Fig. 8). As in female, except for short segmental outer projection on outer margin of enp2 and enp3 with outer terminal seta modified as naked apophysis fused to segment, one terminal seta shortened, one terminal seta missing, and distal inner seta enlarged relative to female.



Fig. 7. *Paradanielssenia meikae* sp. n. (A) Male habitus in lateral view. (B) Female habitus in dorsal view. Scale bars = $50 \,\mu$ m.

P3 (Fig. 10A). Enp2 with very small outer segmental projection.

P4 (Fig. 10B). As in female.

P5+P6 (Fig. 11). Pair of legs fused medially, P6 consisting of pair of small lobes with three setae each.

Systematic remarks

The new species can be assigned to a certain taxon of Paranannopinae Por, 1986. Within the latter, a lineage can be characterised clearly by the presence of mouthpart aesthetascs being derived from certain homologous setae. Since this kind of setal modification on the mouthparts is unique even within the Harpacticoida, it represents a strong autapomorphy to identify a well-defined monophylum. The taxon up to now includes 11 described species assigned to the genera *Micropsammis* Mielke, 1975, *Leptotachidia* Becker, 1974, *Paradanielssenia* Soyer, 1970, *Peltisenia* Huys & Gee, 1996, *Sentiropsis* Huys & Gee, 1996, and *Jonesiella* Brady, 1880.

Again within the Paranannopinae bearing mouthpart aesthetascs, a taxon can be characterised comprising *Micropsammis* Mielke, 1975, *Leptotachidia* Becker, 1974, and *Paradanielssenia* Soyer, 1970. Another genus,



Fig. 8. *Paradanielssenia meikae* sp. n. (A) Female P5; scale bar $a = 20 \,\mu\text{m}$. (B) Male P2; scale bar $b = 25 \,\mu\text{m}$.

Telopsammis Gee & Huys, 1991, was established to accommodate *M. secunda* Mielke, 1975, but this species was placed back in *Micropsammis* by Mielke (1997). Characters distinguishing that taxon (which for simplicity is referred to as '*Paradanielssenia* group' hereafter) and grouping the species within it were already discussed by Gee and Huys (1991, 1994) and Mielke (1997). Re-evaluating the now available data, the following picture emerges.

The '*Paradanielssenia* group' can be characterised by the following autapomorphies:

- loss of Md exp (still represented by 'inner soie fine' in *Paradanielssenia kunzi* Soyer, 1970?)
- reduced setation on Md enp; there are never more than three setae (including mouthpart aesthetasc)
- outer distal seta of male P2 enp3 fused to segment, forming a rigid apophysis (except in *Leptotachidia*)
- innermost seta of female P5 benp shortened in the ground pattern. The plesiomorphic state of this character as is assumed for the paranannopid and pseudotachidiid ground pattern (Willen 2000) is still present in the ground pattern of the Paranannopinae



Fig. 9. *Paradanielssenia meikae* sp. n. (A) Male P5; scale bar $a = 25 \,\mu\text{m}$. (B) Female antennule; scale bar $b = 20 \,\mu\text{m}$. (B) Female rostrum in dorsal view; scale bar $c = 20 \,\mu\text{m}$.

with mouthpart aesthetascs, e.g. in Sentiropsis minuta (Coull, 1969) and in both species of Jonesiella Brady, 1880 (see Huys and Gee 1992). This basic setal pattern includes an elongate innermost seta and a shortened second innermost seta (Willen 2000). By contrast, the innermost seta is also shortened in all species of Paradanielssenia. In the lineage Leptotachidia/Micropsammis (see below) only Micropsammis noodti Mielke, 1975 shows a female P5 benp (see Gee and Huys 1991), allowing the comparison of the respective setal pattern and also displaying the innermost seta shortened. However, since only four setae (of five in the plesiomorphic state in this ramus) are present in total, the homology of the respective seta in M. noodti cannot be verified for certain. The alternative possibility would be to state this character as an autapomorphy of Paradanielssenia.

Within the '*Paradanielssenia* group' the genera *Micropsammis* and *Leptotachidia* together form a taxon because of several shared advanced features, e.g. (see also Gee and Huys 1991; Mielke 1997):

• presence of a deeply incised hyaline frill ('Palisaden' in Mielke 1975) at the body somites



Fig. 10. *Paradanielssenia meikae* sp. n. (A) Male P3. (B) Male P4. Scale bars = $25 \,\mu$ m.

- fusion of both rami of P5 in both sexes
- absence of several swimming leg setae:
 - \bigcirc one outer spine at P4 exp3 missing
 - P2 enp1 asetose
 - P2 enp2 asetose
 - P2 enp3 without inner seta
 - P3 enp1 asetose
 - P3 enp3 and P4 enp3 without inner seta, inner terminal seta missing or minute
- Md basis with only one seta

The remaining taxon, *Paradanielssenia*, has retained a 'normal' frill, separate rami of male and female P5, four setae on Md basis (three in *P. kunzi*), and a basically complete swimming-leg setation (referred to the paranannopid ground pattern). The relatively primitive morphology makes it difficult to confirm the validity of the taxon. However, the following characters indicate a possible monophyly of *Paradanielssenia*:

• benp of female P5 elongate and narrow, reaching far beyond a small and rounded exp (less pronounced in *Paradanielssenia biclavata* Gee, 1988). This shape does not occur in other paranannopid taxa



Fig. 11. *Paradanielssenia meikae* sp. n. (A) Male urosome and P6. (B) Right furcal setae IV and V of A. Scale bars $= 25 \,\mu m$.

(e.g. Sentiropsis; Archisenia Huys & Gee, 1993; Jonesiella; Psammis Sars, 1910).

• A2 expl with only one seta. This feature is not very specific and is also displayed by, e.g., *Jonesiella* (see Huys and Gee 1992), but the respective seta is present in the ground pattern of the *Leptotachidia*/*Micropsammis* clade and therefore also in the one of the whole '*Paradanielssenia* group'. Since it is absent in all species of *Paradanielssenia* it can be stated as an autapomorphy for this taxon within the '*Paradanielssenia* group'. In *P. biclavata* the A2 exp is only 1-segmented, obscuring the original presence or absence of the seta.

Further characters stated by Gee and Huys (1991, 1994) are either superseded ('female A1 4-segmented' by *P. meikae* sp. n. bearing a 5-segmented antennule) or not very specific as, e.g., 'P2–P4 enp1 inner seta spine-like developed' is the case also in *Peltisenia* Huys & Gee, 1996, *Fladenia* Gee & Huys, 1990, and also outside the Paranannopinae in other Pseudotachidiidae within *Pseudomesochra* T. Scott, 1902 (see Willen 1996). The 'male sexual dimorphism of P2 endopod-2' (Gee and Huys 1994), obviously referring to the reduced



Fig. 12. *Paradanielssenia meikae* sp. n. (A) Female urosome. (B) Male antennule. Scale bars = $20 \,\mu m$.

segmental apophysis, can also be observed in *Sentiropis*, *Peltisenia* and *Leptotachidia/Micropsammis*, therefore representing at most an autapomorphy for the whole *Paradanielssenia* group.

Paradanielssenia meikae sp. n. differs from the remaining four species in the aspects summarised in Table 2. Conspicuous characters are a 5-segmented female antennule (Fig. 9B), a hyaline frill with reticular cuticula ornamentation (Figs. 2 and 7), and the enlarged outer spine on male P5 exp. The species of Paradanielssenia were previously recorded exclusively from different locations of the North Atlantic continental shelf (including the Mediterranean), in muddy sand sediments at depths from 25 to 125 m (Soyer 1970; Gee 1988; Gee and Huys 1991, 1994). Surprisingly enough, their closest relative, P. meikae sp. n., has its habitat in the Southern Atlantic deep sea at 5400 m depth. The substrate was fine sediment (although sediment structure was different at the two DIVA stations 325 and 346 (Kröncke and Türkay 2003; Rose et al. 2005)). Rather unusual for a deep-sea location is the relatively high abundance of the new species in the samples. Species of the Leptotachidia/ Micropsammis clade have been recorded from the intertidal of Sylt (Mielke 1975), the Galapagos Islands

	P. meikae sp. n.	P. biclavata	P. christinae	P. kathleenae	P. kunzi
Rostrum shape	Broad, rounded	Elongate	Elongate with hyaline margin	Nearly rectangular with hyaline margin	?
Female A1	5-segmented	4-segmented	4-segmented	4-segmented	5-segmented
A2 exp	3-segmented, 1-0-1 setae	1-segmented	3-segmented, 1-1-3 setae	3-segmented, 1-1-3 setae	3-segmented, 1-1-3 setae
Md enp	1 aesthetasc	2 aesthetascs and 1 seta	1 aesthetasc and 2 setae	1 aesthetasc and 2 setae	1 aesthetasc and 1 seta
Mxp enp	Claw	Claw+seta	Claw + 2 setae	Claw + 2 setae	?
P2–P4 enp 3	2-3-2 inner setae	2-3-? inner setae	1-1-1 inner setae	2-3-2 inner setae	2-3-2 inner setae
P2 exp 3 inner setae	2	2	2	2	3
P3 exp 3 inner setae	3	2	3	3	3
Female P5 exp	With 4 setae, innermost seta not modified; outer terminal spine elongate	With 5 setae, innermost seta modified; outer spines shortened	With 4 setae, innermost seta modified	With 4 setae, innermost seta modified	With 4 setae, innermost seta modified
Male P5 exp	With 3 setae; outermost spine enlarged	With 5 setae, innermost seta modified	With 4 setae, innermost seta modified	With 4 setae, innermost seta modified	With 4 setae, innermost seta modified

Table 2. Morphological comparison of the species of Paradanielssenia

and from 3800 m depth off the coast of Portugal (Becker 1974). Another (hitherto undescribed) specimen was collected near Papua New Guinea (Lihir Islands) at about 1400 m depth (Willen 2004). Specimens of this group were not found in the extensive material of the DIVA expedition, nor in the ANDEEP samples. The known distribution of the whole *Paradanielssenia* group reflects areas of research activity and only sporadic knowledge rather than real occurrence of species, which is most certainly more widespread.

Faunistics and ecology

Taxa of Pseudotachidiidae at the three deep-sea locations in the Angola Basin and the Antarctic Weddell Sea

(Figs. 13–15)

Fig. 13 shows the differences among the three deepsea stations in terms of species and numbers of individuals exemplary for the Pseudotachidiidae, which turned out to be the most important harpactioid taxon in the samples in those respects.

Several monophyletic subgroups have been identified (Hicks 1988; Willen 1996, 1999, 2000), i.e. the Paranannopinae Por, 1986, Pseudomesochrinae Willen, 1996, Donsiellinae Lang, 1944, and *Pseudotachidius* T. Scott, 1898 (see Hicks 1988; Willen 1996, 1999; Veit-Köhler and Willen 1999). *Idomene* Philippi, 1843 and *Dactylopodella* Sars, 1905 are not yet or only partly revised (Hicks 1989; Willen 1999). Almost all species encountered in the samples (Figs. 14 and 15)



Fig. 13. Numbers of species at the three deep-sea sampling locations exemplary for the Pseudotachidiidae.

could be placed in one of these taxa, except for a very few individuals of a hitherto unknown taxon (probably belonging to the Pseudomesochrinae). All others could be assigned to the Paranannopinae, *Pseudotachidius, Idomene* or Pseudomesochrinae. All deep-sea samples from the different locations show similar qualitative and quantitative composition of taxa (Figs. 14 and 15).

The 'dominant' taxa at all three stations are the Pseudomesochrinae and Paranannopinae, together representing about 90% of species and individuals. The former are almost excusively represented by the single genus *Pseudomesochra*, which therefore alone accounts



Fig. 14. Distribution of taxa of Pseudotachidiidae at all three sampling locations. Numbers next to pie slices stand for numbers of individuals of the respective taxa.



Fig. 15. Distribution of taxa of Pseudotachidiidae at all three sampling locations. Numbers next to pie slices stand for numbers of species of the respective taxa.

for almost half of all species and individuals of Pseudotachidiidae in the samples (Figs. 13–15).

The two stations in the Angola Basin, which were sampled with the same multicorer, differ in the number of species and individuals, which was considerably higher at the northern station 346 (Rose et al. 2005). These differences are presumably the result of differing food availability, as the southern station 325 is located in an oligotrophic area of the Angola Basin and the northern station 346 in a eutrophic one (Kröncke and Türkay 2003).

Paranannopinae

(Figs. 16–19)

The Paranannopinae are the major pseudotachidiid group in the samples. They have been thoroughly

revised in the past decade by Gee and Huys (1990, 1991, 1994) and Huys and Gee (1992, 1993, 1996a, 1996b), including redescriptions of old material, establishment of several new genera, and discussion of phylogenetic lineages within the taxon. One of these lineages, for example, comprising Leptotachidia Becker, 1974, Micropsammis Mielke, 1975, Telopsammis Gee & Huys, 1991, Paradanielssenia Soyer, 1970, Jonesiella Brady, 1880, Sentiropsis Huys & Gee, 1996, and Peltisenia Huys & Gee, 1996 (see Huys and Gee 1996b), is convincingly characterised by the presence of mouthpart aesthetascs which are always located on homologous setae on Md, Mxl and Mx. Furthermore, two major lineages, the 'danielsseniid branch' and the 'paranannopid branch' were discussed by Huys and Gee (1996a, 1996b). Up to 50 species have been described so far; 61 additional new species have been encountered at



Fig. 16. Distribution of taxa of Paranannopinae at all three sampling locations. Numbers next to pie slices stand for numbers of individuals of the respective taxa. 'Mouthpart aes' refers to taxa bearing mouthpart aesthetascs, an autapomorphic character for this monophyletic group within Paranannopinae.



Fig. 17. Distribution of taxa of Paranannopinae at all three sampling locations. Numbers next to pie slices stand for numbers of species of the respective taxa. 'Mouthpart aes' refers to taxa bearing mouthpart aesthetascs, an autapomorphic character for this monophyletic group within Paranannopinae.

the two Angola Basin stations (seven of them at both stations), 19 more at ANDEEP station 138 (+3 species overlapping with DIVA stat. 346). For the present study they have been distributed among the following groups (Figs. 16 and 17): *Paranannopus* Lang, 1936; Paranannopinae with mouthpart aesthetascs; *Cylindronannopus*

Coull, 1973; *Bathypsammis* Huys & Gee, 1993; Paranannopinae gen. (unknown taxa).

The 'dominant' groups (highest number of species and individuals) are *Paranannopus* and the species with mouthpart aesthetascs (only at station 138 a higher species number was reached by *Cylindronannopus*).



Fig. 18. Numbers of individuals and species with mouthpart aesthetascs – this group of species constituting a monophylum within the Paranannopinae – at northern station 346 and southern station 325 of the Angola Basin, specifying all replicates. 'Spec. 1' = *Paradanielssenia meikae* sp. n.



Fig. 19. Numbers of individuals and species of *Cylindronannopus* at northern station 346 and southern station 325 of the Angola Basin, specifying all replicates.

'Paranannopus' is a traditional, in all probability not monophyletic genus comprising 23 species, several of them recorded from the deep sea. However, all species in the samples which could be assigned to the current diagnosis of the genus, or by comparison related with other species presently assigned to Paranannopus, have been summarised by this label for the moment. One of these species, which is closely related to Paranannopus variabilis Schriever, 1985 recorded from the Iceland-Faroe Ridge (northern Atlantic: Schriever 1985) has been described as Paranannopus arndwilleni Willen, 2005. One male specimen has been found at each DIVA station, indicating not only local but more extensive distribution within the Angola basin. The specimens lack mouthparts, a phenomenon which occurs independently in several harpacticoid families (e.g. Argestidae, Huntemanniidae, Ectinosomatidae) and seems to be present mainly in deep-sea species. Almost half of the encountered Paranannopus specimens have been males without or with atrophic mouthparts. Within the 'variabilis' group (Willen 2005), male specimens occur with normal or atrophic or without any mouthparts. Some of the Paranannopus species have close relationships to known species recorded from the northern Atlantic; e.g. one species was closely related to Paranannopus reductus Becker, Noodt & Schriever, 1979, P. longithorax Becker, Noodt & Schriever, 1979 and P. uniarticulatus Schriever, 1985, which are characterised by a specialised shape of the female P5. 'Paranannopus' shows the highest number of species and individuals of all Paranannopinae from the DIVA stations.

Surprisingly, in terms of abundances and species numbers they are immediately followed by the taxon grouping the paranannopid species with mouthpart aesthetascs (Fig. 18). Only 11 such species have been described before, and only one, *Leptotachidia iberica* Becker, 1974, from the (Iberian) deep sea. All in all 17 unknown species were counted at the Angola Basin stations, three at the Weddell Sea station. By contrast to an often-found high 'evenness' in deep-sea samples, *Paradanielssenia meikae* sp. n. was encountered in relatively high individual numbers in nearly all replicates (Fig. 18) from the Angola Basin stations, and thus was the most abundant species of Paranannopinae. The other species of the group with mouthpart aesthetascs could not be assigned to any of the known genera.

The third prominent paranannopid group is the genus *Cylindronannopus* Coull, 1973. Only three species have been described so far, all from the north Atlantic deep sea. Nine species could be found at the Angola Basin stations (Fig. 19), seven at Weddell Sea station 138, with one species overlapping between both areas. All species seem to be new for science, but two could not be differentiated clearly from the quite insufficient descriptions of *Cylindronannopus elongatus* Becker & Schriever,

1979 and *C. bispinosus* Schriever, 1985, the latter two species having been recorded from the northern Atlantic. Species of *Cylindronannopus* have been encountered regularly in deep-sea samples from different locations (Willen 2000; P. Martínez-Arbizu pers. comm.). On present knowledge *Cylindronannopus* is a harpacticoid taxon exclusively occurring in the deep sea.

Two female specimens belonging to two species of the so far monotypic genus *Bathypsammis* Bodin, 1968 could be discovered at both sampling locations (DIVA and ANDEEP). Bodin (1968) described *Bathypsammis long-ifurca* from the Gulf of Biscayne from 3950 m depth. The new findings confirm the distribution of the taxon from the northern Atlantic down to the Weddell Sea. Its species seems to occur only sporadically, in very low abundances. A description of one of the collected specimens belonging to a new species will be published elsewhere.

Pseudomesochrinae

(Fig. 20)

The second most important group within the samples are the Pseudomesochrinae Willen, 1996, comprising the single valid and well-founded genus *Pseudomesochra* T. Scott, 1902 (see Willen 1996) and a still undescribed taxon, Pseudomesochrinae gen. spec. The latter is characterised, among other features, by a strongly modified antenna (comparable with the modified Md palp within the Stenheliinae). Species of this taxon are encountered regularly in deep-sea samples (Weddell Sea, Laptev Sea; own observations; Martínez-Arbizu pers. comm.).

Pseudomesochra alone accounts for nearly half of all species and individuals of Pseudotachidiidae at all three stations (Figs. 13–15). Sixteen species have been described from the Pacific, Atlantic and both polar regions, many of them also from the deep sea. At the Angola Basin stations alone 57 more species have been recorded, and 11 at the Weddell Sea station, indicating the major role that this taxon seems to play within the harpacticoid deep-sea fauna and the lack of knowledge on the real number of species present in this habitat. Two species overlapped between the two DIVA stations, but none with ANDEEP station 138.

Other Pseudotachidiidae

(Fig. 21)

The remaining species of Pseudotachidiidae belong to various species groups of *Pseudotachidius* T. Scott, 1897 (see Veit-Köhler and Willen 1999), *Idomene* Philippi, 1843, and to three unknown taxa which can probably be assigned near the Pseudomesochrinae.

Species of *Pseudotachidius* are regularly encountered in deep-sea samples (own observations on material from



Fig. 20. Numbers of individuals and species of Pseudomesochrinae at northern station 346 and southern station 325 of the Angola Basin, and at station 138 in the Weddell Sea.

the Weddell Sea, Laptev Sea and Lihir Islands), both hitherto known species groups (the *coronatus*- and *similis*-group) seem to occur worldwide in the deep sea with a much higher species number than indicated by the available literature. The five known species of the *P. similis* group have been recorded from the deep sea exclusively. At station 346 five more species of this group could be identified. Altogether four species of the *coronatus* group have been found, two at station 325 and one each at stations 138 and 346. Every species of *Pseudotachidius* was represented by just one specimen.

The remaining species have also been assigned to *Pseudotachidius* but could not be placed in one of the two above-discussed groups. Both specimens from the northern Angola Basin station seem to be related to *Pseudotachidius horikoshii* Itô, 1983 and *Pseudotachidius peruanus* Becker, 1974, respectively. The occurrence of *Idomene* at both deep-sea locations (Angola Basin, Weddell Sea) was quite surprising. Its species were



Fig. 21. Numbers of individuals and species of the remaining Pseudotachidiidae at northern station 346 and southern station 325 of the Angola Basin, and at station 138 in the Weddell Sea.

previously recorded from more shallow waters (mostly from the phytal) only. One species occurred in a relatively high number of individuals at the northern Angola Basin station 346.

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Appendix

Key to the species of Paradanielssenia Soyer, 1970

1.	A2 exp 1-segmented, Md enp with 2 aesthetascs, both male and female P5 exp with 5 setae, P3 exp 3 with 2 inner
	setaeP. biclavata Gee, 1988
_	A2 exp 3-segmented, Md enp with only 1 aesthetasc, both male and female P5 exp with fewer than 5 setae, P3 exp 3
	with 3 inner setae
2.	A2 exp 2 asetose, Md enp represented only by 1 claviform aesthetasc, female P5 exp with outer terminal spine
	elongate, innermost seta not modified, male exp with only 3 setae, outermost spine enlargedP. meikae sp. n.
_	A2 exp 2 with 1 seta, Md enp represented by claviform aesthetasc and additional 1 or 2 setae, female P5 with outer
	terminal spine not elongate, innermost seta modified, male exp with 4 setae, outermost spine not enlarged3
3.	P2-P4 enp 3 with only 1 inner seta eachP. christineae Gee & Huys, 1994
_	P2–P4 enp3 with 2-3-2 inner setae, respectively
4.	Female A1 4-segmented, P2 exp 3 with 2 inner setae, Md enp with 1 aesthetasc and 2 setae
	P. kathleenae Gee & Huys, 1994
—	Female A1 5-segmented, P2 exp 3 with 3 inner setae, Md enp with 1 aesthetasc and 1 seta

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