$See \ discussions, stats, and author \ profiles \ for \ this \ publication \ at: \ https://www.researchgate.net/publication/247509553$

A review of Paranannopidae (Copepoda: Harpacticoida) with claviform aesthetascs on oral appendages

Article *in* Journal of Natural History · September 1991 DOI: 10.1080/00222939100770741

citations 18 reads 113

2 authors, including:



Natural History Museum, London 218 PUBLICATIONS 3,700 CITATIONS

SEE PROFILE

Rony Huys

All content following this page was uploaded by Rony Huys on 29 January 2014.

A review of Paranannopidae (Copepoda: Harpacticoida) with claviform aesthetascs on oral appendages

J. MICHAEL GEE[†] and R. HUYS[‡]

† Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK
‡ Marine Biology Section, Zoology Institute, State University of Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium: and Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands

(Accepted 8 August 1991)

Leptotachidia iberica Becker is completely redescribed from the type material and is shown to carry claviform aesthetascs on the mouthparts. This is regarded as a character of high phylogenetic significance and, together with the loss of the mandibular exopod and the form of sexual dimorphism of the distal segment of the male P2 endopod, provides overwhelming evidence for a common ancestry for the genera Leptotachidia, Micropsammis Mielke and Paradanielssenia Soyer. Additional observations are made of the morphology of M. noodti Mielke, M. secunda Mielke and P. biclavata Gee. From a discussion of the probable relationships within this group of genera it is concluded that M. secunda is the most likely sister group of Leptotachidia and therefore must be removed to a new genus Telopsammis gen. nov. New diagnoses are given for all the genera.

KEYWORDS: Copepoda; Harpacticoida; Paranannopidae; Leptotachidia; Paradanielssenia, Micropsammis, Telopsammis, mouthparts, aesthetascs.

Introduction

Lang's composite subfamily Thompsonulinae was proposed (1944) originally to accommodate a number of 'tachidiid' genera with a distribution extending over the Arctic-Boreal region of the Atlantic Ocean and adjacent waters. The subsequent inclusion of several new species in the genera *Danielssenia* Boeck and *Psammis* Sars (see Bodin, 1988) not only extended considerably the geographical distribution of these taxa but also the ambiguities in most of the descriptions left room for various misinterpretations (Gee and Huys, 1990; Huys and Gee, 1991). The gradual widening of the generic boundaries of *Danielssenia* and *Psammis* ceased in the 1970s with the discovery of distinctive, small copepods which were placed in the genera *Paradanielssenia* Soyer, 1970, *Leptotachidia* Becker, 1974 and *Micropsammis* Mielke, 1975.

Huys and Gee (1990) removed the subfamily Thompsonulinae from the Tachidiidae (sensu Lang, 1944). They defined the family Thompsonulidae to include only the genera *Thompsonula* T. Scott, 1905 and *Caribbula* Huys and Gee, 1990, based on arguments that these genera almost certainly had completely different phylogenetic origins and relationships from the 'danielsseniid' genera listed above, which were tentatively placed in the family Paranannopidae Por. Later, Gee and Huys (1990) showed that

Danielssenia intermedia Wells, 1965, which they assigned to the genus Fladenia Gee and Huys, 1990, had characteristics intermediate between *Paranannopus* Lang, 1936 and *Danielssenia*, and this considerably strengthened the argument that the 'danielsseniid' genera should be placed in the Paranannopidae.

The detailed phylogenetic relationships among Paradanielssenia, Leptotachidia and Micropsammis are not well established. Both Becker (1974) and Mielke (1975), when proposing their respective genera, thought they bore a certain resemblance to Psammis, whilst Soyer (1970) considered Paradanielssenia merely to occupy an intermediate position between Danielssenia and Psammis. The undeniable relationships between Leptotachidia, Paradanielssenia and Micropsammis were foreshadowed by Mielke (1975), who hinted at some affinities between the latter two genera. However, it was Gee (1988) who first suggested that Leptotachidia approached these two genera in many respects. In fact, his decision not to synonymize Leptotachidia and Micropsammis was based primarily on the lack of claviform aesthetascs ('Klöppelborste', 'addendes en massue') on the oral appendages and of sexual dimorphism in the male swimming legs in Leptotachidia.

Having re-examined representatives of all three genera it has become clear that the presence and precise location of these club-shaped appendages is a character of high phylogenetic significance indicating a common ancestry. In addition, the discovery of a suite of other synapomorphic features suggests that *Paradanielssenia*, *Leptotachidia* and *Micropsammis*, despite their different habitats, are more closely related to each other than to any other member of the Paranannopidae. In this paper we completely redescribe *Leptotachidia iberica* Becker, supplement the original descriptions of *Micropsammis noodti* Mielke, *M. secunda* Mielke and *Paradanielssenia biclavata* Gee, and remove *M. secunda* to a new genus based on an analysis of the likely relationships within the group.

Methods

All drawings were prepared using a camera lucida on a Leitz Dialux-20 or Nikon Optiphot-2 interference microscope. In this paper the terminology of Lang (1948, 1965) is adopted except that (1) the terms pars incisiva, pars molaris and lacinia mobilis are omitted in the description of the mandibular gnathobase (Mielke, 1984); (2) the names of the segments of the mandible and maxilliped follow that of Boxshall (1985: 341-345); and (3) the armature of the caudal ramus follow that of Huys (1988a). Abbreviations used in the text and figures are P1–P6 for swimming legs 1–6; exopod (endopod)-1 (-2, -3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the base of the rostrum to the posterior margin of the anal somite.

Systematics

Family PARANANNOPIDAE Genus Leptotachidia Becker, 1974

Diagnosis (amended)

Paranannopidae. Body semi-cylindrical without marked distinction between prosome and urosome, devoid of spinule rows. Hyaline frill of anterior four urosomites deeply incised with minutely dentate free margin; that of penultimate somite not incised but produced posteriorly into coarsely dentate dorsal pseudoperculum. Female genital double somite completely fused. Genital field with small copulatory pore, paired seminal ducts leading to single seminal atrium and paired seminal receptacles; vestigial

P6 basal protuberance completely absent, represented by two naked setae only. Anal somite completely divided. Caudal rami slightly broader than long, tapering distally; seta I absent; seta III strongly developed, pinnate; seta VI minute. Rostrum elongate, tapering, not hyaline, with four sensilla. Female antennule 5-segmented with pinnate setae; aesthetasc on segment IV; densely opaque bulbous appendage on segment V. Antenna with well-developed coxa and allobasis; exopod with two, one, three setae on proximal to distal segments. Mandible basis with one seta; endopod 1-segmented with one lateral seta and a seta and claviform aesthetasc on distal margin; exopod absent. Maxillule basis elongate with claviform aesthetasc on distal margin; both rami with three setae. Maxilla with three endites; endopod 1-segmented bearing a claviform aesthetasc. Maxilliped prehensile; syncoxa with one large and one small spinulose seta; basis with a small pinnate seta; endopodal claw with one accessory seta. P1 nonprehensile; exopod 3-segmented with 0:1:023 setae/spines, outer spines minutely pinnate, distal outer spine of exopod-3 longer than middle outer spine, two terminal setae geniculate; endopod 2-segmented with 1:121 setae, two setae on terminal segment geniculate. P2-P4 intercoxal plate unadorned; rami 3-segmented, setal formula as follows

| | Exopod | Endopod |
|----|---------|---------|
| P2 | 1.0.123 | 0.0.021 |
| P3 | 1.0.123 | 0.0.021 |
| P4 | 1.0.022 | 0.0.011 |

exopod outer spines serrate, one geniculate terminal seta on exopod-3. Female P5 members not fused medially; baseoendopod and exopod completely fused into single plate with five serrate spines and one seta.

Male with sexual dimorphism in urosome, antennule, P3 endopod, P5 and P6. Male antennule 6-segmented, chirocerate but segment V not noticeably swollen; segment II small with one seta; segment V with a large aesthetasc; segment VI with a densely opaque bulbous appendage. P3 endopod-2 with attenuation at outer distal corner transformed into hook-shaped apophysis. P5 fused medially. P6 symmetrical, represented by two setae on each side.

Type species. Leptotachidia iberica Becker 1974 (by monotypy).

Leptotachidia iberica Becker, 1974

(Figs 1-4, 5 D, E)

Material examined

One female holotype (dissected) Zoologisches Museum der Universitat Kiel Cat. No. Cop. 1011–1012; one male paratype (dissected) ZMUK Cat. No. Cop. 1013; from 3820 m depth at 37°44'N, 10°31'W, off the Iberian peninsula: collected during the 19th *Meteor* expedition to the North African and Iberian Deep Sea and deposited by K.-H. Becker.

Description of female

Body. Length $435 \,\mu$ m, maximum width $92 \,\mu$ m (given in Becker, 1974); all somites devoid of ornamentation but probably with large pores, at least on cephalothorax (Fig. 3 E); hyaline frill of first to fourth urosomites deeply incised with minutely dentate free margin (Fig. 2 F); hyaline frill of penultimate somite not deeply incised, finely



FIG. 1. Leptotachidia iberica. Male A, segmentation of antennule; B, antennule segment III, C, antennule segment IV; D, antennule segment V, E, antennule segment VI, F, antenna ventral view; G, distal portion of antenna endopod dorsal view.



FIG. 2. Leptotachidia iberica. A, mandible; B, maxillule; C, maxilla; D, maxilliped; E, female genital complex; F, hyaline frill of urosomite-4; G, posterior border of penultimate urosomite and one half of anal somite, dorsal view.



FIG. 3. Leptotachidia iberica. A, P1; B, female P2; C, male P2 endopod; D, caudal ramus ventral view; E, rostrum and portion of anterior border of cephalothorax, dorsal view.



FIG. 4. Leptotachidia iberica. A, female P3; B, male P3 endopod; C, P4; D, female P5; E, male P5; F, male P6.

dentate laterally (Fig. 2G), coarsely dentate ventrally (Fig. 3D) and dorsally in region of pseudoperculum (Fig. 2G). Genital double-somite completely fused; genital field (Fig. 2E) with small copulatory pore at base of a depression immediately posterior to genital slit; seminal receptacles multichambered; vestigial P6 with basal protuberance completely absent, represented only by two minute naked setae. A pair of large pores posterior to genital field. Anal somite completely divided (Fig. 2G) with rows of setules on inner margins under pseudoperculum. Caudal rami (Fig. 3D) slightly longer than broad, tapering distally; seta I absent; seta III strongly developed, pinnate in distal twothirds; setae IV and V well developed, pinnate in central portion; seta VI minute; seta VII triarticulate.

Rostrum (Fig. 3 E). Not hyaline, triangular but rounded distally with four sensilla and a median pore.

Antennule (Fig. 5 D, E). Short, stout, 5-segmented; segment I with a short spinule row on distal ventral margin and one bipinnate plumose seta at anterior distal corner; segment II with nine setae, three bipinnate plumose setae on posterior ventral margin, two naked setae near ventral distal margin and four bipinnate plumose setae on anterior margin; segment III with eight setae on anterior margin, five naked and three unipinnate spinulose; segment IV with an aesthetasc, three naked setae and one unipinnate weakly spinulose seta at anterior distal corner and one unipinnate weakly spinulose seta proximally on anterior margin; segment V with a densely opaque bulbous appendage on proximal anterior margin and seven naked setae, five unipinnate weakly spinulose setae (two on distal margin fused at base) and one sagittiform unipinnate spinulose seta.

Antenna (Fig. 1 F, G). With well-developed coxa. Allobasis with row of spinules at base of abexopodal bipinnate sparsely plumose seta. Exopod 3-segmented; exopod-1 elongate, with one small naked seta and one well developed, bipinnate seta; exopod-2 small with one bipinnate seta; exopod-3 short with spinule row sub-apically and three setae, two weakly bipinnate and one unipinnate. Endopod with two rows of spinules on anterior margin and one row at posterior distal corner, in which spinules increase in length from ventral to dorsal face (Fig. 2 F, G); two minutely bipinnate spines, a geniculate seta and a small naked seta borne sub-apically on ventral face and four geniculate setae and two spinulose setae on distal margin.

Mandible (Fig. 2 A). Cutting edge of gnathobase with well-developed bicuspid and unicuspid teeth and a pinnate seta at inner distal corner. Basis slender and elongate with row of setules on both lateral margins; distal margin with one bipinnate sparsely plumose seta and a small row of spinules. Endopod short, slender, 1-segmented with one naked seta on lateral margin and a naked seta and a claviform aesthetasc on distal margin. Exopod absent.

Maxillule (Fig. 2 B). Arthrite of precoxa with two surface setae and eight elements on inner margin. Coxal endite with four naked setae. Basis elongate, with two apical setae and a claviform aesthetasc, one sub-apical and two lateral setae. Endopod with lateral row of setules and three bipinnate setae on distal margin, one densely plumose, others sparsely plumose. Exopod with three bipinnate sparsely plumose setae.

Maxilla (Fig. 2 C). Syncoxa with row of spinules on outer margin; inner margin with three endites each with two spines and a seta, spines of proximal and middle endite weakly spinulose. Allobasal endite with two spines and two setae apically and one seta sub-apically. Endopod 1-segmented with two naked setae and a claviform aesthetasc.

Maxilliped (Fig. 2D). Prehensile. Syncoxa with two lateral rows of spinules, a large seta sub-apically and a smaller apical seta, both bipinnate spinulose. Basis

elongate ovoid, with a spinule row below palmar margin and a sparsely bipinnate seta distally on palmar margin. Endopod represented by a dentate claw with one small accessory seta.

P1 (Fig. 3 A). Non-prehensile. Intercoxal plate small, rectangular, without ornamentation. Coxa with two rows of spinules near outer distal corner and on distal margin on anterior face; one row on posterior face. Basis with spinule row at base of bipinnate weakly spinulose inner spine; outer seta slender, bipinnate plumose. Exopod 3-segmented, each with spinule row on outer and distal margin; outer spines minutely spinulose, distal outer spine of exopod-3 longer than middle outer spine; terminal setae geniculate. Endopod 2-segmented, slightly longer than exopod; distal segment three times longer than broad, bipinnate plumose inner seta implanted in proximal half of segment, two setae on terminal segment geniculate.

P2-P4 (Figs 3 B, 4 A, C). Intercoxal plate square, unadorned. Precoxa with spinule row on distal margin. Coxa with spinule rows at outer margin and near distal margin on both faces. Basis with a few spinules at base of outer seta which is bipinnate weakly plumose on P2, unipinnate on P3 and naked on P4. Both rami 3-segmented. Outer spines on exopod strongly serrate; exopod-1 inner seta with pectinate tip; exopod-2 without inner setae; exopod-3 of P4 with only two outer spines. Endopod tapering distally; each segment with row of spinules on outer margin and row of setules on inner and distal margin; endopod-2 of P2 and P3 without surface pore but outer distal corner slightly attenuated; all endopod segments without inner setae; setal formula as for genus.

P5 (Fig. 4D). Members not fused medially. Baseoendopod and exopod completely fused and indistinguishable, with two pores on anterior face; distal margin with five short strongly serrate spines, middle one half length of others, outer basal seta naked.

Description of male

As in female except in following features.

Body. Length $415 \,\mu$ m, width $80 \,\mu$ m (given in Becker, 1974). Second and third urosomites not fused.

Antennule (Fig. 1 A–E). Six-segmented, chirocerate, segment V not noticeably swollen, geniculation between segments V and VI; segment I with two spinule rows on anterior margin and one naked seta at anterior distal corner; segment II small, with one bipinnate weakly plumose seta at anterior distal corner; segment III (Fig. 1 B) with five bipinnate weakly plumose and three naked setae; segment IV (Fig. 1 C) with three bipinnate sparsely plumose and three naked setae at anterior distal corner; segment V (Fig. 1 D) with two unipinnate and six naked setae and a large aesthetasc; segment VI (Fig. 1 E) with two large bipinnate basally fused setae and three naked setae on distal margin, medially with one bipinnate and four naked setae and proximally with a peculiar, densely opaque, bulbous-headed appendage.

P2 endopod (Fig. 3 C). Small hyaline flange at outer distal corner of endopod-1, otherwise as in female.

P3 endopod (Fig. 4B). Attenuation at outer distal corner of endopod-2 transformed into hook-shaped structure.

P5 (Fig. 4 E). Members fused to form a single plate, otherwise as in female.

P6 (Fig. 4 F). Basal plate completely fused to somite cuticle, limb represented by two small spinulose setae on each side of posterior border of urosomite-2.

Discussion

In his discussion of the original description of this genus, Becker (1974) recognized its affinities with *Danielssenia* and *Psammis* from the 2-segmented non-prehensile endopod of P1 in which the proximal segment was not elongated; the short, stout female antennule armed with many pinnate setae and spines and the subchirocerate male antennule (but see page 1145); the condition of the antenna with an allobasis and a 3-segmented exopod. He assigned his specimens to a separate genus, however, because of the structure of the mandibular palp (with only one basal seta and no exopod); the reduced size of the endopods of the swimming legs and reduced armature of all the rami; the lack of sexual dimorphism in the male swimming legs which he regarded as a consequence of the endopod reduction; and the complete fusion of the rami of the P5 in both sexes. In an earlier, more extensive discussion of possible phylogenetic relationships, Becker (1972) suggested that *Leptotachidia* might be most closely related to *Psammis* because of the fused condition of the female P5 and the form of the P1 endopod in which both segments are approximately the same length.

Becker (1974) was apparently unaware of the work of Soyer (1970), who described the new genus *Paradanielssenia* and assigned it to the Langian subfamily Thompsonulinae. This genus also possesses a reduced mandibular palp and has less extensive sexual dimorphism on the male P2 endopod than *Psammis*, although the armature of the swimming legs is not significantly reduced and there is no fusion of P5 exopod and baseoendopod in either sex. In addition, this genus was described as having 'addendes en massue' on the mouthparts. Mielke (1975) described similar structures ('Klöppelborste') on the mouthparts of his new genus *Micropsammis* and commented on the likely relationship between these two genera. Gee (1988) pointed out the similarity between *Leptotachidia* and *Micropsammis* in the structure of the mandibular palp, the reduction of the swimming leg armature and the fusion of the P5 rami. He even suggested that the two genera may be synonymous if the antennular appendage in *Leptotachidia* was similar to the claviform appendages in *Micropsammis*.

The present re-examination of the type material of *L. iberica* revealed that the peculiar structure on the distal antennular segment only superficially resembles the claviform aesthetascs found on the post antennular limbs of some other paranannopid genera. The appendage in *Leptotachidia* is a rigid structure consisting of a short, transparent stalk and a bulbous terminal portion filled with densely opaque material. The location of this structure on the male antennule posterior to the geniculation excludes the possibility of it being a positional homologue of an aesthetasc in other Paranannopidae because, except for the aesthetasc derived from the apical trithek, such sensory structures are never present in the part of the antennule distal to the geniculation in any extant harpacticoid.

Surprisingly, a similar structure has been found also in *Cerviniopsis obtusirostris* Brotzkaja (Cerviniidae) (Brotzkaja, 1963; Por, 1969). As to its exact segmental position there is less agreement between Por's figures 145 and 156, but his figure 180 clearly shows that the appendage arises from the posterior margin, whereas in *L. iberica* it occupies a position near the anterior margin of the antennule. Por (1969) suggested that the structure, which he named the 'Brodskaya organ', may be sensory in function because he observed '... a nerve... penetrating the organ, very much as in statocysts'. *L. iberica* and *C. obtusirostris* are in no way related morphologically or phylogenetically, but both are found only in the deep sea, suggesting that this organ may be an adaptation for a bathyal existence. On the other hand it is remarkable that this structure has not been found in any of the other 12 deep-sea species of *Cerviniopsis*.

f

ļ

:

i

1

1

More importantly, however, we have shown that claviform aesthetascs are present in *Leptotachidia* at the same loci on the mandible, maxillule and maxilla as in *Paradanielssenia* and *Micropsammis*, thus confirming that these three genera are closely related.

For the purpose of a phylogenetic analysis of this group of genera the following corrections to the description by Becker (1974) should be emphasized:

- (1) There are no rows of spinules on the posterior border of the urosomites. The deeply incised hyaline frills on these somites were mistaken for spinule rows in the original description.
- (2) The female antennule is 5-segmented rather than 4-segmented, Becker having failed to recognize that in his preparation the proximal segment was detached from the figured antennule (Becker, 1974, Fig. 5). Similarly, the male antennule is chirocerate, there being only one segment distal to the geniculation rather than two segments as stated by Becker, who erroneously suggested that the two apical seta on the distal segment acted as part of the clasping mechanism. Nevertheless, the male antennule is 6-segmented because the third segment in Becker's figure is an amalgam of segments III and IV in Fig. 1 A.
- (3) There is a lateral naked seta on the mandibular endopod (in addition to the apical seta and claviform aesthetasc) and the maxillule endopod has three setae rather than four.
- (4) The distal endopod segment of P2 and P3 bears three terminal setae rather than two, and there is sexual dimorphism on the male P3 endopod in the form of a small hooked apophysis at the outer distal corner of endopod-2.
- (5) Becker (1972) suggests that the deeply divided anal somite may be a unique character for the genus, but this is a feature found in all Paranannopidae as well as in representatives of some other harpacticoid families.

Genus Micropsammis Mielke, 1975

This genus was established by Mielke (1975) to accommodate two new species, M. noodti and M. secunda, but the author did not designate a type species. However, as M. noodti was described first and the name M. secunda implies that it is the second species, we designate M. noodti as the type species. Moreover, for reasons set out in the discussion, we assign M. secunda to a new genus. Here we rediagnose the genus Micropsammis followed by an abridged description of M. noodti giving additional information or a reinterpretation of certain features in Mielke's otherwise excellent original description and figures.

Diagnosis (amended)

Paranannopidae. Body small, semi-cylindrical without marked distinction between prosome and urosome, almost devoid of spinules. Hyaline frill of *all* urosomites deeply incised and with minutely dentate free margin. Female genital double-somite completely fused. Genital field with fused seminal receptacles; vestigial P6 with protuberance bearing two naked setae. Anal somite completely divided. Caudal rami about as long as broad; seta I minute, proximal; seta II well developed, pinnate; seta VI small. Rostrum elongate, bell-shaped, not hyaline, with four sensilla. Female antennule 6-segmented with pinnate setae; aesthetasc on segment IV. Antenna with welldeveloped coxa; allobasis with 3-segmented exopod bearing two, one, three setae on proximal to distal segment. Mandible basis with one seta; endopod 1-segmented with one lateral seta and a distal seta and claviform aesthetasc; exopod absent. Maxillule basis elongate with claviform aesthetasc on distal margin; both rami with three setae. Maxilla with three endites, endopod 1-segmented with a claviform aesthetasc. Maxilliped prehensile; syncoxa with one large and one small pinnate seta; basis with a small pinnate seta; endopodal claw with one accessory seta. P1 not prehensile; exopod 3-segmented with 0.1.023 setae/spines, outer spines spinulose, distal outer spine of exopod-3 longer than middle outer spine and terminal setae geniculate; endopod 2-segmented with 1.121 setae, one terminal seta geniculate. P2–P4 intercoxal sclerites unadorned; rami 3-segmented; exopod outer spines minutely pinnate; inner terminal seta of endopod-3 very reduced. Setal formula as follows:

| | Exopod | Endopod |
|----|---------|---------|
| P2 | 1.1.123 | 0.0.021 |
| P3 | 1.1.123 | 0.1.021 |
| P4 | 1.1.122 | 0.0.021 |

Female P5 members fused medially at base, baseoendopod and exopod fused but distinguishable, lobes with four and three setae respectively. Male with sexual dimorphism in urosome, antennule, P2, P3, P5, P6. Male antennule sub-chirocerate, 7-segmented. P2 endopod-2 outer distal corner with small apophysis; endopod-3 with outer distal seta transformed into non-articulating process. P3 endopod-2 with small hooked apophysis at outer distal corner. P5 members fused medially but distinguishable; exopod and baseoendopod fused and indistinguishable, with four setae. P6 represented by three setae.

Type species. M. noodti Mielke 1975.

Micropsammis noodti Mielke, 1975

(Figs 5 A-C, 6-8)

Material examined

One undissected adult female and one dissected adult male from the type locality, kindly placed at our disposal by Dr. W. Mielke.

Description of female

Body (Fig. 6 A–C). Small (0·39–0·44 mm, given in Mielke, 1975), semi-cylindrical, slightly tapering posteriorly, with no marked distinction between prosome and urosome. Cephalic shield rounded anteriorly, elongate, as long as succeeding four somites; with numerous pores and sensilla on dorsal surface; posterior margin irregular with four pairs of sensilla; hyaline frill entire and smooth. Free prosomites unadorned except for a few sensilla; hyaline frills entire and smooth. Urosomites unadorned except for a few pores and sensilla on anterior four somites and a row of microspinules on anterior portion of urosomite-5 (Fig. 6 B); all hyaline frills on urosome deeply incised and with minutely dentate free margin, that on penultimate somite produced into dorsal pseudoperculum. Genital double-somite completely fused. Genital field (Fig. 6 E) with copulatory pore in depression posterior to genital slit; seminal receptacles fused, anterior to copulatory pore; vestigial P6 a protuberance bearing two naked setae, inner very reduced; two large pores posterior to genital field. Anal somite completely divided medially. Caudal rami about as broad as long with a small row of spinules proximally on the inner lateral margin (Fig. 6 B) and ventrally on posterior



FIG. 5. Micropsammis noodti. Female. A, antennule; B, maxilliped; C, P1. Leptotachidia iberica female. D, antennule; E, antennule segment IV.



FIG. 6. *Micropsammis noodti*. Female. A, body dorsal view; B, urosomites-4-6 and caudal ramus dorsal view; C, caudal ramus lateral view; D, antenna allobasis and exopod; E, genital complex.



FIG. 7. Micropsammis noodti. Female. A, cephalothorax lateral view; B, rostrum dorsal view; C, P2 endopod; D, P3 endopod; E, P4 endopod, arrow indicates minute inner terminal seta; F, P5.



FIG. 8. Micropsammis noodti. Male. A, antennule (setation of proximal and middle segments omitted); B, P2 endopod; C, P3 endopod; D, P5 (secretory pores arrowed); E, P6.

margin (Fig. 6 C); seta I minute, proximally on lateral margin; seta II well developed, pectinate in distal portion; seta III slender; seta IV and V strongly developed, spinulose in distal half; seta VI small and seta VII triarticulate.

Rostrum (Fig. 7 B). Articulating with cephalothorax; not hyaline, elongate bellshaped with four sensilla and a median pore.

Antennule (Fig. 5 A). Short, stout, 6-segmented. Segment I with two spinule rows on dorsal surface and one bipinnate seta at anterior distal corner. Segment II with three bipinnate setae on posterior margin and five pinnate and two naked setae on anterior margin; Segment III with five pinnate and three naked setae on anterior margin. Segment IV with an aesthetasc fused at base to a large naked seta, five other setae on anterior margin. Segment V with two naked setae on posterior margin and three spinulose and two naked setae on anterior margin. Segment VI with five naked setae on posterior margin and two large bipinnate setae fused at base on distal margin. Antenna (Fig. 6 D). With well-developed coxa. Allobasis with row of spinules proximally and group of setules near base of abexopodal bipinnate seta. Proximal segment of 3-segmented exopod with one small naked seta and one large pinnate seta; middle segment with one seta; distal segment with three setae, two pinnate and one pectinate-tipped.

Mandible, maxillule, maxilla. Each with a claviform aesthetasc (Fig. 7 A) and as described by Mielke (1975).

Maxilliped (Fig. 5 B). Endopodal claw with one short accessory seta, otherwise as described by Mielke (1975).

P1 (Fig. 5 C). Precoxa unadorned; coxa with two rows of spinules medially on distal margin; basis with a row of setules on inner margin, a row of minute spinules medially on distal margin and a group of spinules at base of inner bipinnate spine. Rami as described by Mielke (1975) except that two terminal setae of exopod-3 and outer terminal seta of endopod-2 geniculate.

P2-P4 (Fig. 7 C-E). As described by Mielke except that a minute inner terminal seta present on endopod-3 of each leg (arrowed in Fig. 7). Setal formula therefore as for genus.

P5 (Fig. 7 F). As described by Mielke (1975) except that members fused medially at base and outer basal seta naked and as long as inner spine of exopodal lobe.

Description of male

As in female except for following features.

Antennule (Fig. 8 A). Seven-segmented, sub-chirocerate; segment V slightly swollen with large aesthetasc.

P2 endopod (Fig. 8 B). Endopod-2 with small apophysis at outer distal corner; endopod-3 with outer seta transformed into non-articulating process, outer terminal seta reduced, inner terminal seta enlarged compared to female.

P3 endopod (Fig. 8 C). Endopod-2 with small hooked apophysis on anterior distal margin.

P5 (Fig. 8D). Members fused medially; baseoendopod and exopod fused and indistinguishable with four bipinnate spines and two pores on distal margin.

P6 (Fig. 8 E). A single plate, fused to somite, with two bipinnate and one naked setae on each side.

Discussion

Mielke (1975) described *Micropsammis noodti* and *M. secunda* from a single locality in eulittoral beach sands on the island of Sylt in the southern North Sea. He placed them in the same genus on the basis of the structural similarities in the body ornamentation, reduced seta and spine formula of the swimming legs and the fusion of the rami of the P5 in both sexes. At the time of writing, Mielke was obviously unaware of the existence of *Leptotachidia iberica* described by Becker in the previous year, which also displayed the characteristics mentioned above for *Micropsammis*. The close affinity between these two genera is now beyond doubt with the discovery that *Leptotachidia* bears claviform aesthetascs on mouthparts whose general structure is also identical in both genera.

From the detailed reappraisal of both genera, and using the genus *Paradanielssenia* as the outgroup (see page 1160), we have been able to define a suite of synapomorphies

supporting the monophyletic status of the clade comprising *Micropsammis* (as defined by Mielke) and *Leptotachidia*.

- (1) The reduction of body ornamentation. The plesiomorphic condition in the outgroup is the presence of rows of spinules on the dorsal and ventral posterior border of the urosomites.
- (2) The complete fusion of the genital double-somite in the female. In all other Paranannopidae a subcuticular ridge is present at least laterally on the genital double-somite.
- (3) The presence of a deeply incised hyaline frill (described as 'palisadenartiger' by Mielke, 1975) around the posterior margin of at least the first to fourth urosomites (see Figs 2 F, 6, 9). Although the dorsal hyaline frill of urosomite-1 (fifth pedigerous somite) in *Danielssenia typica* Boeck approaches this structure, the plesiomorphic condition of all urosomal hyaline frills in the Paranannopidae is plain, albeit with a minutely dentate posterior margin which is still retained by *Micropsammis* and *Leptotachidia*.
- (4) An elongate mandibular basis bearing only one seta. The usual condition within the family is for the basis of the mandible to be almost as broad as long and to bear three or four setae. Huys and Gee (1991) have shown that although the mandibular basis of *Sentirenia* (a new genus erected to accommodate *Danielssenia perezi* Monard and *D. eastwardae* Coull) is also more elongate than usual, it still carries three setae.
- (5) The presence of terminal geniculate setae on both rami of P1. The plesiomorphic non-geniculate form of these setae is found in all other Paranannopidae but in Mielke's two species of *Micropsammis* and in *L. iberica* both terminal setae on P1 exopod-3 and at least one seta on P1 endopod-2 are of the geniculate type.
- (6) The presence of only two outer spines on exopod-3 of P4 rather than the usual three spines.
- (7) The fusion of the P5 exopod and baseoendopod in both sexes. This feature is known to have arisen more than once in the Paranannopidae, probably as a result of parallelism but the primitive condition, also found in *Paradanielssenia* is for the exopod and baseoendopod to be clearly separate.

The foregoing combination of synapomorphies leaves little doubt about the common ancestry of M. noodti, M. secunda and L. iberica, however, the relationships within this clade are less well established. Close scrutiny of the genus *Micropsammis* has led us to hypothesize that the latter is a paraphyletic assemblage and that M. secunda is the most likely sister group of L. iberica.

We can identify the following synapomorphies which would support this hypothesis:

(1) The complete loss of the sexually dimorphic apophysis on P2 endopod-2 in the male. In all other genera and species in the Paranannopidae with a 3-segmented P2 endopod in the male, the outer distal corner of endopod-2 is more or less attenuated into an apophysis. It attains its maximum development in the genus Danielssenia Boeck (sensu Gee and Huys, 1990) where it reaches far beyond the distal margin of P2 endopod-3. In Micropsammis noodti there is a small but distinct apophysis (Fig. 8 B) which is absent in M. secunda (Fig. 11 D) and Leptotachidia (Fig. 3 C).

- (2) The transformation of both terminal setae on P1 endopod-2 into geniculate setae. In *M. noodti* only one terminal seta on this limb is geniculate.
- (3) The absence of an inner seta on P3 endopod-2.
- (4) The absence of an inner seta on P4 exopod-3.
- (5) The complete reduction and fusion of the baseoendopodal and exopodal lobes in the female P5 so that they become indistinguishable. Throughout the family there is a range of degree of fusion of the P5 rami from completely separate to completely fused, but in all other species, except in the genera *Paranannopus* and *Cylindronannopus*, the two rami are distinguishable as separate lobes as is the case in *M. noodti* (Fig. 7 F).
- (6) The female P5 bears only five setae (excluding the outer basal seta which is still identifiable). The primitive condition within the family is probably 10 setae on the female P5 and *M. noodti* still retains seven setae on this limb.
- (7) The male P6 bears only two setae. *M. noodti* has three setae on this limb which is the plesiomorphic condition in the family.

The alternative hypothesis is that the genus Micropsammis is monophyletic and that M. noodti is the sister group of M. secunda. Only the following synapomorphies can be found which support this view:

- (1) The reduction to a minute seta (which Mielke, 1975 interpreted as a setule) of the normally robust inner terminal seta of endopod-3 on P2.
- (2) The presence of only four setae (excluding the outer basal seta) on the male P5. The primitive condition in the family is probably seven setae on this limb and *L. iberica* still retains five setae.

The corollary to adopting either of these hypotheses is that the characters listed under the alternative hypothesis must have arisen twice within these closely related species. This is not unknown within the family, and in a forthcoming full phylogenetic analysis of the Paranannopidae we will show that such characters as reductions in setae and fusion of the P5 rami have occurred a number of times. We attach higher significance to apomorphies in sexually dimorphic characters and further, by invoking the principle of parsimony, we conclude that the first hypothesis which makes M. secunda the sister group of L. iberica is the most likely solution on phylogenetic grounds.

It follows, therefore, that M. secunda should be removed from the genus *Micropsammis*. It cannot be included in *Leptotachidia* because this genus can be clearly defined by the following autapomorphies: (1) the presence of 'Brodskaya's organ' on the distal segment of the antennule (see page 1144 and Figs 1 A and 5 D); (2) the 5-segmented condition of the female antennule; (3) the loss of sexual dimorphism in the male P2 endopod-3 as well as endopod-2; (4) the absence of an inner seta on exopod-2 of P2–P4.

Micropsammis secunda must therefore be placed in a new monotypic genus, Telopsammis gen. nov. which, from the description given below, can be identified by the following autapomorphies: (1) the proximal segment on the antenna exopod bears only one seta; (2) the syncoxa of the maxilliped bears only one seta (the long seta present in all other Paranannopidae has been lost); (3) the loss of an inner seta on exopod-3 of P2-P3; (4) the loss of the inner terminal seta of endopod-3 on P3-P4.

The genus *Micropsammis* s.st. can thus be identified by the following autapomorphies: (1) the penultimate urosomite with a deeply divided hyaline frill and pseudoperculum; (2) the reduction of the inner terminal seta of P3–P4 endopod-3; (3) the medial fusion of the members of the female P5; (4) the presence of a single-chambered, dumbbell-shaped seminal receptacle. This character has arisen more than once in the Paranannopidae as it is also present in the genus *Fladenia*, but the ancentral condition of a multi-chambered seminal receptable (see Gee and Huys, 1990, fig. 12) is retained in *Leptotachidia* (Fig. 2E) and *Telopsammis* (Fig. 12C).

Genus Telopsammis gen. nov.

Synonym. Micropsammis Mielke 1975 (part.).

Diagnosis

Paranannopidae. Body small, semi-cylindrical without marked distinction between prosome and urosome. Hyaline frill of first to fourth urosomites deeply incised, that of penultimate somite entire, all with minutely dentate free margin. Female genital double-somite completely fused. Genital field with multi-chambered seminal receptacles; vestigial P6 a protuberance with two naked setae. Anal somite completely divided. Caudal rami about as broad as long; seta I minute, seta II well developed; seta VI small. Rostrum elongate, bell-shaped, not hyaline, with four sensilla. Female antennule 6-segmented with pinnate setae; aesthetasc on segment IV. Antenna with well-developed coxa; allobasis with 3-segmented exopod bearing one, one, three setae on proximal to distal segment. Mandible basis elongate, with one seta; endopod 1segmented with two setae and a claviform aesthetasc; exopod absent. Maxillule basis elongate with claviform aesthetasc on distal margin; both rami with three setae. Maxilla with three endites, endopod 1-segmented with a claviform aesthetasc. Maxilliped prehensile; syncoxa with only one small pinnate seta; basis with a small pinnate seta. P1 not prehensile; exopod 3-segmented with 0.1.023 setae/spines, distal outer spine of exopod-3 longer than middle outer spine and terminal setae geniculate; endopod 2-segmented with 1.121 setae, endopod-2 with two geniculate terminal setae and inner seta implanted very close to base of segment. P2-P4 intercoxal sclerites unadorned; rami 3-segmented; exopod outer spines minutely pinnate; inner terminal seta on P2 endopod-3 minute. Setal formula as follows

| | Exopod | Endopod |
|----|---------|---------|
| P2 | 1.1.023 | 0.1.021 |
| P3 | 1.1.022 | 0.0.011 |
| P4 | 1.1.022 | 0.0.011 |

Female P5 members not fused medially at base, baseoendopod and exopod completely fused and indistinguishable, with five setae (excluding outer basal seta).

Male with sexual dimorphism on urosome, antennule, P2, P3, P5 and P6. Male antennule chirocerate, 6-segmented. P2 endopod-2 without apophysis, endopod-3 with outer terminal seta transformed into non-articulating process. P3 endopod-2 with small hooked apophysis at outer distal corner. P5 members fused medially but distinguishable; exopod and baseoendopod fused and indistinguishable, with four setae. P6 represented by two bipinnate setae.

Etymology. The name derives from the Greek *telos*, end and *psammis*, sand, and refers to the fact that this genus represents the final stage in a gradual reduction in body size and ornamentation as an adaptation to an interstitial existence. Gender feminine.

Type species. Telopsammis secunda (Mielke, 1975) by monotypy.

Telopsammis secunda (Mielke, 1975)

(Figs 9–12)

Material examined. Two undissected adult females and one dissected adult male from the type locality, kindly loaned to us by Dr Wolfgang Mielke.

Description of female

Abbreviated, giving additional information or a reinterpretation of certain features in Mielke's original description and figures.

Body (Figs 9, 10 D, 12 C, D). Small (0·33–0·38 mm, given in Mielke, 1975) semicylindrical, without marked distinction between prosome and urosome. Cephalic shield rounded anteriorly, as long as following four somites; prosome unadorned except for a few pores on dorsal surface (Fig. 9). Urosome with two small groups of spinules on ventral posterior margin of urosomites (Fig. 12 D); hyaline frill of anterior three urosomites deeply divided with minutely dentate free margin; that of penultimate somite (Figs 10 D, 12 D) denticulate but not divided, extended dorsally into pseudoperculum. Genital double-somite completely fused; genital field (Fig. 12 C) with relatively large copulatory pore posterior to genital slit, seminal receptacles convoluted, vestigial P6 a small protuberance with two minute setae. Anal somite completely divided. Caudal rami slightly longer than broad with a ventrolateral row of spinules at inner distal margin; seta I minute, proximal on lateral margin; seta II strongly developed, smooth; seta-III slender, seta IV, V strongly developed, latter spinulose on central portion; seta VI small; seta VII triarticulate.

Rostrum (Fig. 9). Elongate, tapering anteriorly, not hyaline.

Antennule (Fig. 9). Six-segmented, aesthetasc on segment IV.

Antenna (Fig. 9 B). Exopod 3-segmented, with one, one, three setae on proximal to distal segments.

Mandible, Maxillule, Maxilla (Fig. 10 A). As in M. noodti.

Maxilliped (Fig. 10 C). Syncoxa with two rows of spinules and one small bipinnate seta at distal margin. Basis ovoid, with row of fine spinules and a short pinnate seta on palmar margin. Endopodal claw finely denticulate on distal inner margin.

P1 (Fig. 11 A). Intercoxal plate without ornamentation. Precoxa unadorned. Coxa with two spinule rows on anterior face and one on posterior face near distal and outer margin. Basis with rows of spinules on inner margin, at base of inner spine and on distal margin. Rami and setation as in generic diagnosis.

P2-P4 (Figs 11 B, C, 12 A). Intercoxal plates unadorned. Precoxa with row of spinules. Coxa with row of spinules at inner distal margin of anterior face and two rows distally on posterior face. Basis with row of spines at base of outer seta and on distal margin. Inner seta on P2 endopod-2 and inner distal seta on P2 endopod-3 (arrowed in Fig. 11 B) minute. Setal arrangement as in generic diagnosis.

P5 (Fig. 12 B). Members not fused medially; baseoendopod and exopod fused and indistinguishable, with five setae (excluding seta homologous with basal outer seta).

Description of male

As in female except for following.

Body. Smaller (0.3-0.33 mm, given in Mielke, 1975). Third urosomite with median ventral row of small spinules near anterior margin. Third to fifth urosomites with row of spinules medially on ventral margin.

Antennule (Fig. 10 B). Chirocerate, 6-segmented with large aesthetasc on slightly swollen segment-V.



FIG. 9. Telopsammis secunda. Female. A, Habitus dorsal view; B, habitus lateral view.



FIG. 10. *Telopsammis secunda*. A, Relative position of cephalic appendages, ventral. Insertion of antenna stipled; B, Male rostrum and antennule (setation omitted); C, maxilliped; D, female urosome, dorsal view of distal half.



FIG. 11. Telopsammis secunda. Female A, P1; B, P2; C, P3. Male D, P2 endopod; E, P3 endopod.

1158



FIG. 12. Telopsammis secunda. Female A, P4; B, P5; C, genital area, ventral; D, urosome excluding urosomite-1, ventral. Male E, P5, P6 and urosomite-3, ventral.

P2 (Fig. 11 D). Endopod-2 without apophysis. Endopod-3 with outer spine transformed into non-articulating process; outer distal spine very reduced and inner distal spine enlarged compared to female.

P3 (Fig. 11 E). Endopod-2 with small process at outer distal corner.

P5 (Fig. 12 E). Members fused medially at base but distinct. Baseoendopod and exopod fused and indistinguishable with four bipinnate setae on distal margin (excluding seta homologous to basal seta).

P6 (Fig. 12 E). Represented by two bipinnate setae on each side.

Genus Paradanielssenia Soyer, 1970

This genus was established by Soyer (1970) to accommodate the new species *P. kunzi* found occasionally at a large number of sites in the region of Banyuls-sur-Mer. One further species, *P. biclavata* Gee from the southern Celtic Sea, has since been added to the genus and we have re-examined the type material of this species. Here we give a full diagnosis of genus followed by additional information or a reinterpretation of certain features in the original description of *P. biclavata* by Gee (1988).

Diagnosis (amended)

Paranannopidae. Body small, slightly dorso-ventrally flattened, widest at posterior margin of cephalothorax, tapering posteriorly with clear distinction between prosome and urosome. Prosome unornamented; urosome with spinule rows on posterior border of somites; hyaline frills not incised but with minutely dentate free margin. Female genital double-somite with lateral internal cuticular ridge. Female genital field with copulatory pore immediately posterior to genital slit; seminal receptacles anterior to copulatory pore; vestigial P6 with basal protuberance bearing one seta. Anal somite deeply divided. Caudal rami about as long as broad, seta I minute, seta III and VI well developed. Rostrum elongate, triangular, not hyaline with four sensilla. Female antennule 4-segmented with pinnate spines on distal segment; aesthetasc on segment III. Antenna with well-developed coxa, allobasis with unsegmented or 3-segmented exopod with one, one, three setae on proximal to distal segments. Mandible basis robust with four setae on distal margin; endopod 1-segmented with two setae and a claviform aesthetasc; exopod absent. Maxillule basis elongate with claviform aesthetasc, endopod with two or three setae, exopod with three setae. Maxilla with three endites; endopod 1-segmented with claviform aesthetasc. Maxilliped prehensile; syncoxa with one large and one small pinnate seta; basis with a small pinnate seta; endopodal claw with one accessory seta. P1 non-prehensile; exopod 3-segmented with 0.1.023 setae/spines, distal outer spine of exopod-3 as long as middle outer spine, terminal setae not geniculate; endopod 2-segmented with 1.121 setae, endopod-2 inner seta implanted proximally, terminal setae not geniculate. P2 intercoxal sclerite with two rows of small spinules. P2-P4 rami 3-segmented. P2-P3 endopod longer than exopod, endopod-1 inner element is a dentate, pinnate spine. Female P5 elements of each side not fused medially; baseoendopod and exopod separate, endopodal lobe large with five setae, exopod with four or five setae.

Male with sexual dimorphism in urosome, antennule, P2, P3, P5, and P6. Male antennule 6-segmented, chirocerate; segment V slightly swollen with large aesthetasc. P2 endopod-2 with small apophysis at outer distal corner; endopod-3 outer seta on distal margin transformed into rigid process, terminal two setae reduced and distal inner seta enlarged compared to female. P3 endopod-2 with hooked apophysis at outer distal corner. P5 elements fused medially; baseoendopod and exopod separate; endopodal lobe reduced, with two setae of which outer is minute; exopod with four or five setae. P6 a single plate with three setae on each side.

Paradanielssenia biclavata Gee, 1988

(Figs 13–16)

Material examined

Type material as listed in Gee (1988).

Description of female

As in Gee (1988) except for the following:

Body. Hyaline frills of urosomites not incised but with minutely dentate free margin; frill of penultimate urosomite expanded dorsally into pseudoperculum (Fig. 14 E); operculum absent. Caudal rami seta I ventro-lateral and minute (arrowed in Fig. 14 A), setae II, III and VI normal, setae IV and V strongly developed and spinulose, seta VII triarticulate..

Rostrum (Fig. 15 C). Not hyaline, elongate, bluntly triangular with four sensilla. Antenna (Fig. 15 D, E). With well-developed coxa and allobasis. Endopod with two pectinate spines and a geniculate seta subterminally; a pectinate spine, three geniculate setae and two small naked setae on distal margin; outer geniculate seta pinnate medially and basally fused to outer naked seta. As stated by Gee (1988) exopod of holotype (Fig. 15 E) aberrant, probably as a result of damage during development. Exopod of paratype appears normal but is unique within the Paranannopidae in that it is 1-segmented (obviously as a result of fusion of the 3-segmented condition) with two lateral setae (only one of which is minutely unipinnate) and two naked terminal setae (one of which is minute).

Mandible (Fig. 14B). Structurally as described in Gee (1988) but should be reinterpreted as: basis broad with numerous surface rows of spinules and four setae on distal margin, three normal pinnate setae set close together and a bipinnate specialized appendage; endopod 1-segmented with a claviform aesthetasc and two spatulate seta; exopod absent.

Maxillule (Fig. 14 C). As in Gee (1988) except basis with one subterminal seta and three setae and a claviform aesthetasc on distal margin.

Maxilla (Fig. 14D). Syncoxa with three endites, each with three elements; allobasis with three setae, one articulating spine and one fused spine on distal margin. Endopod 1-segmented with two setae and two claviform aesthetascs.

Maxilliped (Fig. 9 A). Syncoxa with three rows of spinules on inner margin, a small bipinnate seta on distal margin and a large bipinnate seta on posterior face; basis oval moderately elongate, with a group of setules on outer and distal inner margin, a row of spinules on anterior face near inner margin which also bears a small blunt pinnate seta; endopod represented by a dentate claw with one long accessory seta.

P1 (Fig. 16 B). As in generic diagnosis and Gee (1988).

P2-P4 (Fig. 15 A, 16 C). As in generic diagnosis and Gee (1988). P5 (Fig. 13 F). As in Gee (1988).



FIG. 13. Paradanielssenia biclavata. A, female antennule; B male antennule (setation of segment III and V omitted); C, male third antennular segment; D, male fifth antennular segment; E, female genital area; F, female P5.

1162



FIG. 14. Paradanielssenia biclavata. A, male urosome, ventral (seta I of caudal ramus arrowed);
 B, mandible; C, maxillule; D, maxilla; E, pseudoperculum and anal somite, left half omitted.



FIG. 15. *Paradanielssenia biclavata*. A, female P3 protopod and endopod; B, male P3 endopod; C, rostrum; D, antenna of male paratype; E, antenna allobasis and exopod of female holotype.



FIG, 16. Paradanielssenia biclavata. A, maxilliped; B, P1 exopod; C, female P2; D, male P2 endopod; E, distal portion of endopod-3 of male P2.

Description of male

As in Gee (1988) except that.

Antennule (Fig. 13 B–D). Six-segmented, chirocerate, with major geniculation between fifth and distal segment; fifth segment only slightly swollen; two setae on distal margin of terminal segment fused at base.

P2 (Fig. 16 D-E). Endopod with small apophysis at outer distal corner of endopod-2; endopod-3 not reduced but outer distal spine completely fused to segment and outer terminal seta minute (Fig. 16 E), inner terminal seta smaller and distal inner seta much larger than in female (Fig. 16 D).

P3 (Fig. 15B). Endopod-2 with small hooked apophysis at outer distal corner.

Discussion

We have been unable to examine specimens of P. kunzi, and therefore have relied on the original description and drawings in Soyer (1970) when constructing the generic diagnosis. However, the caudal setae arrangement described by Soyer (eight setae) must be erroneous because seven is the maximum number of setae found in Harpacticoida (see Huys, 1988a). He was obviously mistaking for setae some of the slender spinules at the inner distal margin of the caudal ramus, and the true setal arrangement is almost certainly as in P. biclavata, which is normal for the family. The antennal exopod of P. biclavata is unique within the family and that described by Soyer (1970) for P. kunzi is more usual, i.e. 3-segmented with one, one, three setae on the proximal to distal segments. The plesiomorphic condition of the antenna exopod in the Paranannopidae is almost certainly 3-segmented with two, one, three setae on the proximal to distal segment. Soyer (1970) also states that the mandibular basis of P. kunzi bears only three setae on the distal margin whereas P. biclavata has four. As far as we are aware, the number of setae on this segment is constant in each genus in the Paranannopidae and it is possible that there are four setae in both species of Paradanielssenia because the configuration of the distal border of the basis in Soyer's Fig. 4 C suggests that one of the three closely set setae found in P. biclavata is missing in his figured specimen of P. kunzi.

It was suggested in the introduction to this paper that the presence of a peculiar claviform aesthetasc on the mandible, maxillule and maxilla of Leptotachidia, Micropsammis, (Telopsammis) and Paradanielssenia is an apomorphy of high phylogenetic significance indicating that these four genera are all very closely related. Oral aesthetascs of any sort are very rare within the Harpacticoida although, as shown from our re-examination of the type material of Leptotachidia, they may have been overlooked by previous workers because they are unexpected features and/or are difficult to see without interference phase contrast illumination. So far, oral aesthetascs have been reported in only one other harpacticoid family. Huys (1988b) found a slender aesthetasc on the endopod of the maxilla of Rotundiclipeus canariensis, a small species from an anchihaline cave in the Canary Islands belonging to the family Rotundiclipeidae in the superfamily Cervinioidea to which the Paranannopidae are in no way related. Even in other orders of copepod the presence of aesthetascs on oral appendages is very unusual. Ho (1984) reported a large aesthetasc on the basal segment of the maxilla of Asterocheres aesthetes Ho (Siphonostomatoida) and a survey of other genera revealed that this character is quite common among the Asterocheridae (Boxshall, personal communication). Calanoids belonging to the Scolecithricidae have very delicate sensory filaments on the endopod of the maxilla (Arashkevich, 1969).

Within the Paranannopidae the absence of oral aesthetascs is almost certainly the plesiomorphic condition exhibited by most of the constituent genera. However, in a recent revision of three species of the genus Danielssenia (D. perezi, D. paraperezi and D. eastwardae), Huys and Gee (1991) found a sensory aesthetasc on the endopod of the mandible, the basis of the maxillule and the endoped of the maxilla, and used this and other features to remove these species to a new genus Sentirenia. Similar aesthetascs are also known to be present on the mouthparts of another species at present in the genus Danielssenia (D. minuta Coull, 1969). There is little doubt that the oral aesthetascs in these paranannopid genera are homologous, as they are found in the same position on the same limbs and appear to have arisen from the same setae. Evidence that the claviform appendages are derived from simple setae is found in Sentirenia and D. minuta which both show the initial stage of modification. In these taxa the oral appendages are equipped with slender, slightly swollen aesthetascs which have retained a more or less setiform appearance and are finer that the aesthetascs found on the antennule of most harpacticoids. They are typically tipped with a flagellum which presumably represents the tip of their setal precursors. The specialized type derived from the former condition is found in the advanced genera dealt with in this paper. Here the aesthetascs are distinctly claviform (club-shaped), having a definite shaft region and a swollen tip. Their in situ arrangement as shown in Fig. 7 A indicates that they are the mouthpart structures which first come into contact with the sediment, leading us to suspect that they may be used to sense the presence of food in dark or low-light-intensity habitats. This is further reinforced by the fact that they are present in the copepodite V stage (observations on P. biclavata) which probably would not be the case if they had a reproductive function. It is interesting to note that Boxshall and Iliffe (1986) found conspicuous, strap-like aesthetascs hanging down from the anteroventral surface of the antennules in the cave inhabiting misophrioid Speleophria bivexilla. They suggested that these aesthetascs come into contact with the substratum as the copepod approaches it, and might provide chemosensory information of use in food location.

Thus we suggest that the presence of claviform aesthetascs is a synapomorphy for the clade comprising *Paradanielssenia*, *Micropsammis*, *Leptotachidia* and *Telopsammis*, and that its closest relative is probably the genus *Sentirenia* and/or *Danielssenia minuta*. Further synapomorphies which define this clade are as follows: (1) the loss of the exopod on the mandible which is present in all other Paranannopidae; (2) the form of the sexual dimorphism on P2 endopod-3 in the male in which the outer distal seta is fused to the segment to form a rigid apophysis. In other Paranannopidae this seta remains an articulating element although it may be altered in form compared to the female.

Paradanielssenia can be defined by the following autapomorphies: (1) a 4-segmented female antennule and (2) the proximal segment of the antenna exopod with only one seta.

The four genera examined in this study have been recorded only from western Europe. Paradanielssenia is found in muddy sand sediments on the continental shelf with one species, P. kunzi, being found at 25–60 m on the Mediterranean shelf off Banyules (Soyer, 1970) and the other, P. biclavata, being known from four specimens from 100 m on the Atlantic shelf off southwest Ireland (Gee, 1988). However, Micropsammis and Telopsammis have been found only in intertidal sandy sediments on the island of Sylt in the southern North Sea (Mielke, 1975) whilst Leptotachidia is a bathyal genus known only from two specimens recovered from 3800 m off the coast of Portugal. It is interesting to note that the closest living relative of the deep sea genus Leptotachidia, undoubtedly the most advanced known genus within the Paranannopidae, is to be found in the intertidal. A similar phenomenon is known from some marine canthocamptid genera. Huys and Thistle (1989) described *Bathycamptus* eckmani from bathyal muds (1218–1223 m) in San Diego Trough, California, and its closest relative turned out to be *Psammocamptus axi* Mielke, also described from the intertidal of Sylt. These observations lend further credence to the hypothesis that the modern deep-sea fauna had its origins in shallow water (Stock, 1986).

Acknowledgements

For the loan of valuable material, the authors wish to thank Dr W. Mielke, University of Göttingen; Dr M. E. Christiansen, Curator of the Zoologisk Museum, Oslo; and the Curator of the Zoologisches Museum, Universität Kiel. For the senior author this work forms part of the Community Ecology programme of the Plymouth Marine Laboratory, a component body of the Natural Environment Research Council. The junior author acknowledges an EC Science Grant ST2*0443. This is contribution no. 498 of the Delta Institute for Hydrobiological Research, Yerseke.

References

- ARASHKEVICH, E. G., 1969, Kharakter pitaniya kopepod severo-zapadnoi chasti Tikhogo okeana, [The character of feeding of copepods in the northwestern Pacific], Okeanologiya, 9, 857–872 [in Russian].
- BECKER, K.-H., 1972, Eidonomie und Taxonomie abyssaler Harpacticoidea (Crustacea, Copepoda), Inaugural dissertation, Christian-Albrechts Universität, Kiel, 163 pp.
- BECKER, K.-H., 1974, Eidonomie und Taxonomie abyssaler Harpacticoidea (Crustacea, Copepoda) Teil I. Cerviniidae-Ameridae, 'Meteor' Forschungs-Ergebnisse Reihe D, 18, 1-28.
- BODIN, PH., 1988, Catalogue des nouveaux Copépodes Harpacticoïdes marins (Edition 1988) (Brest: Université de Bretagne Occidentale, Laboratoire d'Océanographie Biologique), 288 pp.
- BOXSHALL, G. A., 1985, The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding mormonilloid, *Philosophical Transactions of the Royal Society*, *London*, *B*, **311** (1150), 303–377.
- BOXSHALL, G. A. and ILIFFE, T. M., 1986, New cave-dwelling misophrioids (Crustacea: Copepoda) from Bermuda, Sarsia, 71, 55–64.
- BROTZKAJA, V. A., 1963, Obzor semeistva Cerviniidae (Crustacea, Copepoda), [A survey of the family Cerviniidae (Crustacea, Copepoda)], Zoologicheskij Zhurnal, 42, 1785–1803 [in Russian].
- COULL, B. C., 1971, Meiobenthic Harpacticoida (Crustacea, Copepoda) from the North Carolina continental shelf, *Cahiers de Biologie marine*, **12**, 195–237.
- GEE, J. M., 1988, Some harpacticoid copepods (Crustacea) of the family Tachidiidae from sublittoral soft sediments in Norway, the Celtic Sea and Gulf of Mexico, Zoologica Scripta, 17, 181–194.
- GEE, J. M. and HUYS, R., 1990, The rediscovery of *Danielssenia intermedia* Wells 1965 (Copepoda, Harpacticoida): a missing link between the 'danielsseniid' genera and *Paranannopus* Lang 1936 (Paranannopidae), *Journal of Natural History*, **24**, 1549–1571.
- Ho, J.-s., 1984, Copepoda associated with sponges, cnidarians and tunicates of the Sea of Japan, Report of the Sado Marine Biological Station, Niigata University, 14, 23-61.
- Huys, R., 1988a, A redescription of the presumed associated Caligopsyllus primus Kunz 1975 (Harpacticoida: Paramesochridae) with emphasis on its phylogenetic affinities with Apodopsyllus Kunz 1962, Hydrobiologia, **62**, 3–19.
- Huys, R., 1988b, Stygofauna of the Canary Islands, 10. Rotundiclipeidae fam. nov. (Copepoda, Harpacticoida) from an anchihaline cave on Tenerife, Canary Islands, Stygologia, 4, 42-63.
- Huys, R. and GEE, J. M., 1990, A revision of Thompsonulidae Lang, 1944 (Copepoda: Harpacticoida), Zoological Journal of the Linnean Society of London, 99, 1–49.

- Huys, R. and GEE, J. M., 1991, A revision of Danielssenia perezi Monard, D. paraperezi Soyer, D. eastwardae Coull (Harpacticoida; Paranannopidae) and their removal to a new genus, Zoological Journal of the Linnean Society of London (In press).
- HUYS, R. and THISTLE, D., 1989, *Bathycamptus eckmani* gen. et spec. nov. (Copepoda, Harpacticoida) with a review of the taxonomic status of certain other deepwater harpacticoids, *Hydrobiologia*, **185**, 101–126.
- LANG, K., 1944, Monographie der Harpacticiden (Vorläufige Mitteilung), (Uppsala: Almqvist & Wiksell), 39 pp.
- LANG, K., 1948, Monographie der Harpacticiden, 2 volumes (Lund: Håkan Ohlsson), 1682 pp.
- LANG, K., 1965, Copepoda Harpacticoidea from the California Pacific coast, Kungliga Svenska VetenskapsAkademiens handlingar, 10 (2), 1–560.
- MIELKE, W., 1975, Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt, Microfauna Meeresbodens, 52, 1–134.
- MIELKE, W., 1984, Some remarks on the mandible of the Harpacticoida (Copepoda), Crustaceana, 46, 257-260.
- POR, F. D., 1969, Deep-sea Cerviniidae (Copepoda: Harpacticoida) from the western Indian Ocean, collected with R/V Anton Bruun in 1964, Smithsonian Contributions to Zoology, 29, 1-60.
- SOYER, J., 1970, Contribution a l'étude des Copépodes Harpacticoïdes de Méditerranée Occidentale 2. Tachidiidae Sars, Lang, Vie et Milieu, 21 (2A), 261–277.
- STOCK, J. H., 1986, Deep sea origin of cave faunas; an unlikely supposition, Stygologia, 2, 105-111.