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Paranannopidae (Copepoda: Harpacticoida) from sublittoral soft sediments in Spitsbergen

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Based on specimens of Paranannopidae collected from 30 to 123 m depth in Sassenfjord, Spitsbergen, two species of *Paradanielssenia* Soyer, 1970 (*P. christineae* sp. nov. and *P. kathleenae* sp. nov.) are described. These can be distinguished from known species by differences in the number of claviform aesthetascs on the mouthparts and in the arrangement or form of setae on the legs. A key to species of *Paradanielssenia* is provided. *Mucrosenia* gen. nov. (type species *M. kendalli* sp. nov.) is established on the basis of a single female and can be distinguished from all known paranannopid genera by the structure of the caudal ramus and the P2 endopod-2 which has no inner seta and a large mucroniform process at the outer distal corner. *Psammis kliei* Smirnov, 1946 is assigned to this genus as species *incertae sedis*. *Danielssenia quadriseta* Gee, 1988 is recorded for the first time outside its type locality in Oslofjord. *Danielssenia spitsbergensis* sp. nov. is described from a single male specimen and can easily be distinguished from other known species by the presence of only two outer spines on exopod-3 of P3–4. However, because of differences in the structure of the P2 endopod and P5, the species is placed *incertae sedis* within *Danielssenia* pending the discovery of the female.

KEYWORDS: Copepoda, Harpacticoida, Paranannopidae, *Danielssenia*, *Paradanielssenia*, *Mucrosenia* gen. nov.

Introduction

During the course of an ecological study of latitudinal gradients in the structure of shallow sub-littoral benthic communities, a set of macrofauna and meiofauna samples was obtained from 30 to 123 m depth in Sassenfjord, Spitsbergen, well within the Arctic Circle. The meiofauna samples yielded 267 harpacticoid copepods, belonging to 49 species or putative species mostly in the families Ectinosomatidae, Diosaccidae, and Cletodidae *sensu* Por, 1984, Twelve individuals however, belonged to the Paranannopidae and all had affinities to the 'danielsseniid' genera moved to this family from the Langian sub-family Thompsonulinae by Huys and Gee (1990) although most could not be assigned to known species. There are only two previous records of Paranannopidae from Spitsbergen. The first is that of Scott and Scott (1901) who found *Danielssenia typica* Boeck, 1872 (syn. *Jonesiella spinulosa* (Brady

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and Robertson, 1875)) in some material dredged from 120 m depth southeast of Spitsbergen (76°17′N, 21°36′E). The other is that of Lang (1936) who recorded the same species (as *D. fusiformis* (Brady, 1880)) from among *Laminaria* at a depth of 30 m off the northwest tip of Vest Spitsbergen (Fig. 1).

In a recent series of papers (Gee and Huys, 1990, 1991; Huys and Gee, 1992, 1993) the pre-1980s concept of the genera *Danielssenia* Boeck, 1872 and *Psammis* Sars, 1910 has been challenged. It was shown that careful assessment of the structure of the mouthparts and sexual dimorphism of the swimming legs held the key to understanding the phylogenetic relationships within the group, resulting in the creation of a number of new genera. Until now the genus *Psammis* had five constituent species: *P. longisetosa* Sars, 1910 (type species); *P. borealis* Klie, 1939; *P. kliei* Smirnov, 1946; *P. longifurca* Bodin, 1968; and *P. longipes* Becker, 1974. After a re-examination of original specimens, Huys and Gee (1993) removed *P. longifurca* to a new genus *Bathypsammis* (based mainly on the structure of the mouthparts and the female swimming legs). They also concluded that *P. borealis* could not be included in the genus *Psammis* because of the lack of sexual dimorphism in the swimming legs but maintained it as *species incertae sedis* within the Paranannopidae. Although unable to examine the original material of *P. kliei*, they suggested that it had certain affinities with one of the Spitsbergen specimens which also could not be included in *Psammis*. As a result of these considerations they redefined the genus *Psammis* to include only the type species and *P. longipes*.

In this paper on the Spitsbergen material we record the presence of *Danielssenia quadriseta* Gee 1988, describe a new species which we place *incertae sedis* in this genus, describe two new species of *Paradanielssenia* Soyer, 1970, and erect a new genus *Mucrosenia* to accommodate *Mucrosenia kendalli* sp. nov. and consider *Psammis kliei* as *incertae sedis* within this genus.

Materials and methods

Samples were collected by M. A. Kendall in July 1990 at five stations near Gipsvika, a bay of Sassenfjord, Spitsbergen (78°23′N, 16°30′E) (Fig. 1). The area is under the influence of the northward-flowing West Spitsbergen current and had a bottom salinity of 34 ppt and a temperature of 0·5°C at 50 m depth in August 1989 (Weslawski *et al.*, 1990). Bottom depth ranged from 30 to 123 m and the bottom sediment at all sites was between 87 and 95% silt/clay but at the 30–35 m sites substantial quantities of hydroid debris were incorporated into the surface sediment. At each station a Jonnasson and Olausson box core was taken from which four subcores were obtained using a sawn-off 50 ml syringe. These were preserved in 10% formalin for transport to the laboratory where the meiofauna was extracted by sieving and differential flotation using Ludox® made up to a specific gravity of 1·15.

Before dissection, the habitus was drawn and body length measurements made from whole specimens mounted in lactophenol. Specimens were then dissected in lactophenol and the parts mounted in polyvinyl lactophenol. Drawings were prepared using a camera lucida on a Nikon Optiphot-2 or Leitz Diaplan microscope with differential interference contrast illumination. The terminology for body and appendage morphology follows Huys and Boxshall (1991). Abbreviations used in the text and figures are P1–6 for legs 1–6; exopod(endopod)-1 (-2, -3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the anterior border of the cephalothorax to the posterior margin of the anal somite. All material is deposited in The Natural History Museum, London.

FIG. 1. Map of Spitsbergen showing location of sample site.

Systematics

Family **PARANANNOPIDAE** Por, 1984

Genus ***Paradanielssenia*** Soyer, 1970

The genus was established by Souer (1970) to accommodate a new species *P. kunzi* from the region of Banyuls-sur-Mer. One further species, *P. biclavata* Gee 1988, is known from three specimens collected in the southern Celtic Sea (Gee, 1988b). An amended diagnosis of the genus and some observations on its phylogenetic relationships within the family Paranannopidae have been given by Gee and Huys (1991). The following descriptions should be read in conjunction with the generic diagnosis.

Paradanielssenia christineae sp. nov.

(Figs 2–8)

Material examined

HOLOTYPE 1 adult ♀ (dissected onto three slides) BMNH Reg. No. 1993.415; from a mud bottom at 30 m depth in Sassenfjord, Spitsbergen. PARATYPES 1 ♂ (dissected onto two slides) 35 m depth and 2 ♀ (one partly dissected) from 35 and 123 m depths in the same locality BMNH Reg. No. 1993.416-418. Collected by M. A. Kendall, July 1990.

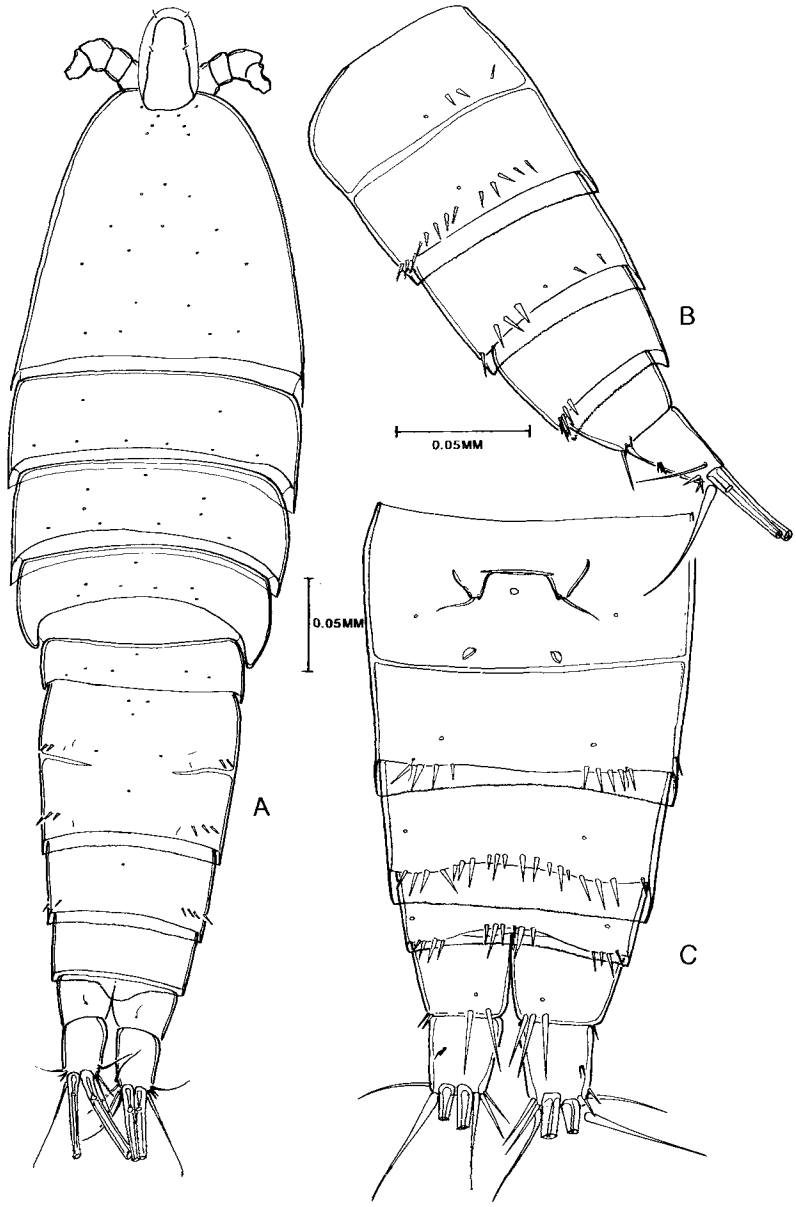

FIG.2. *Paradanielssenia christineae.* Female: (A) dorsal view of habitus. Urosome excluding urosomite-1: (B) lateral; (C) ventral.

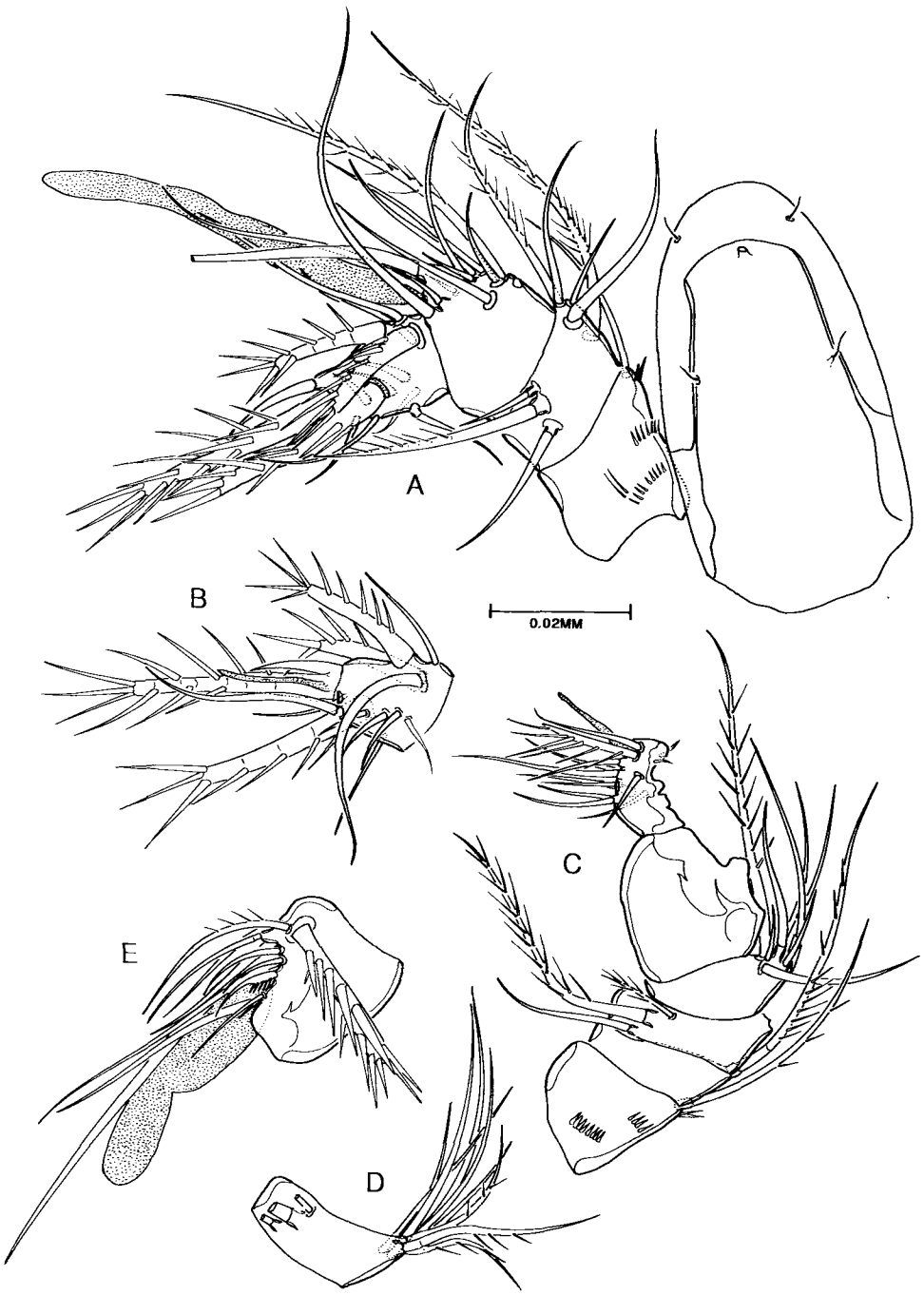

FIG. 3. *Paradanielssenia christineae.* Female antennule: (A) with rostrum; (B) ventral view of segment-4. Male antennule: (C) segmentation and setae of segment-1, -2, -4 and -6; (D) segment-3; (E) segment-5.

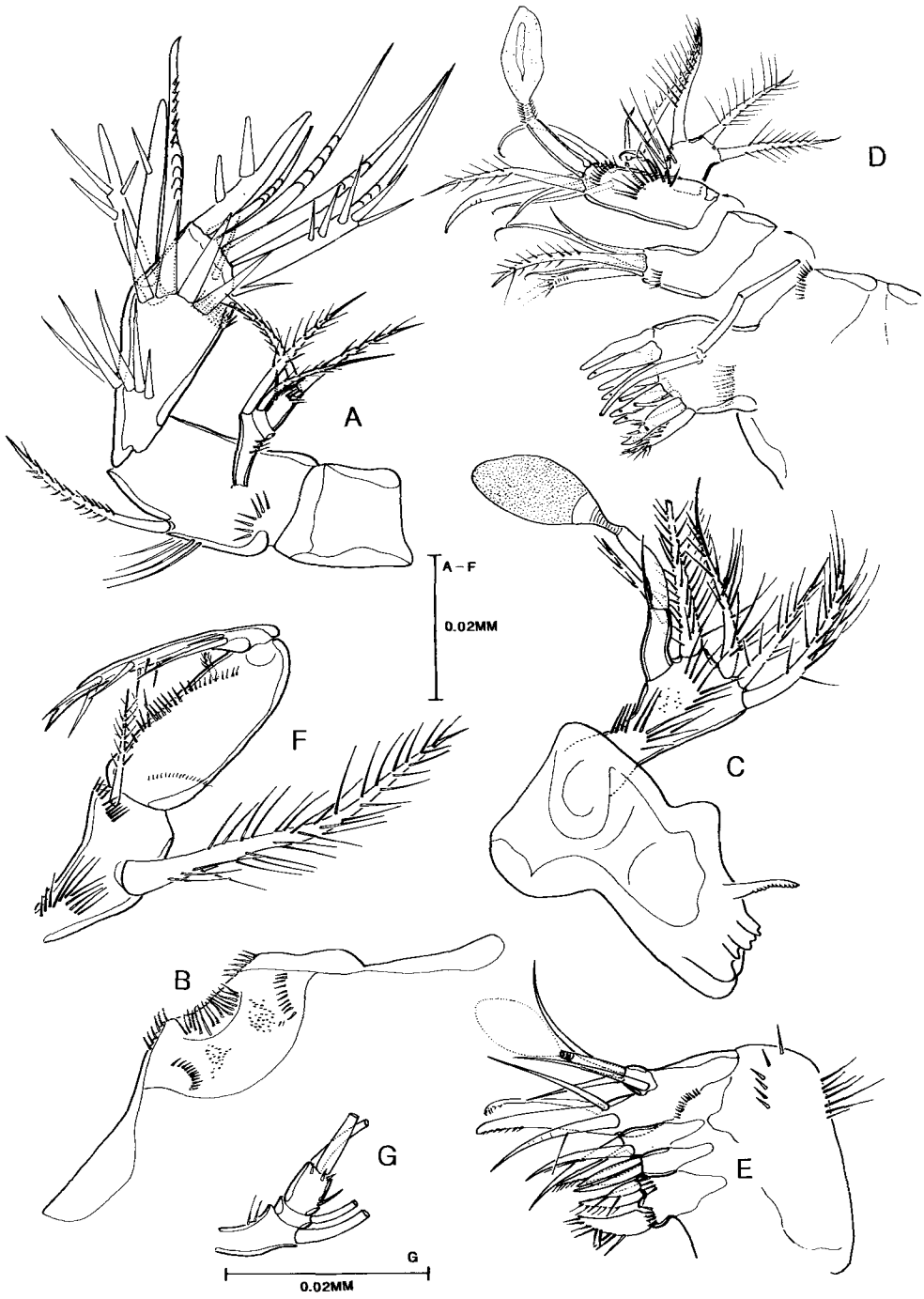

FIG. 4. *Paradanielssenia christineae.* Female: (A) antenna; (B) labrum; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped. Male: (G) exopod of antenna.

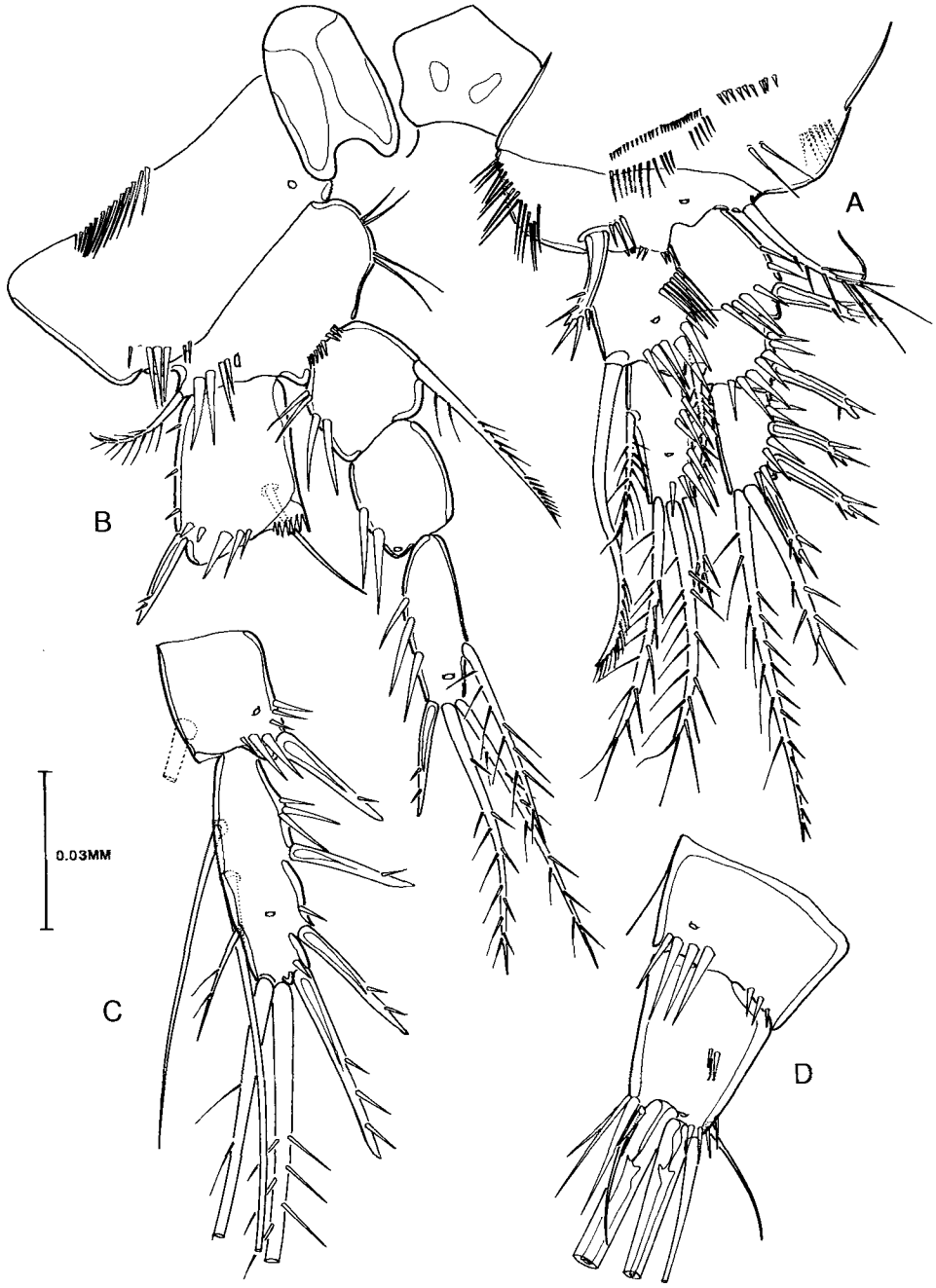

FIG. 5. *Paradanielssenia christineae.* Female: (A) P1; (B) P4 exopod-1 and endopod; (C) P4 exopod-2–3. Male: (D) ventral view of caudal ramus.

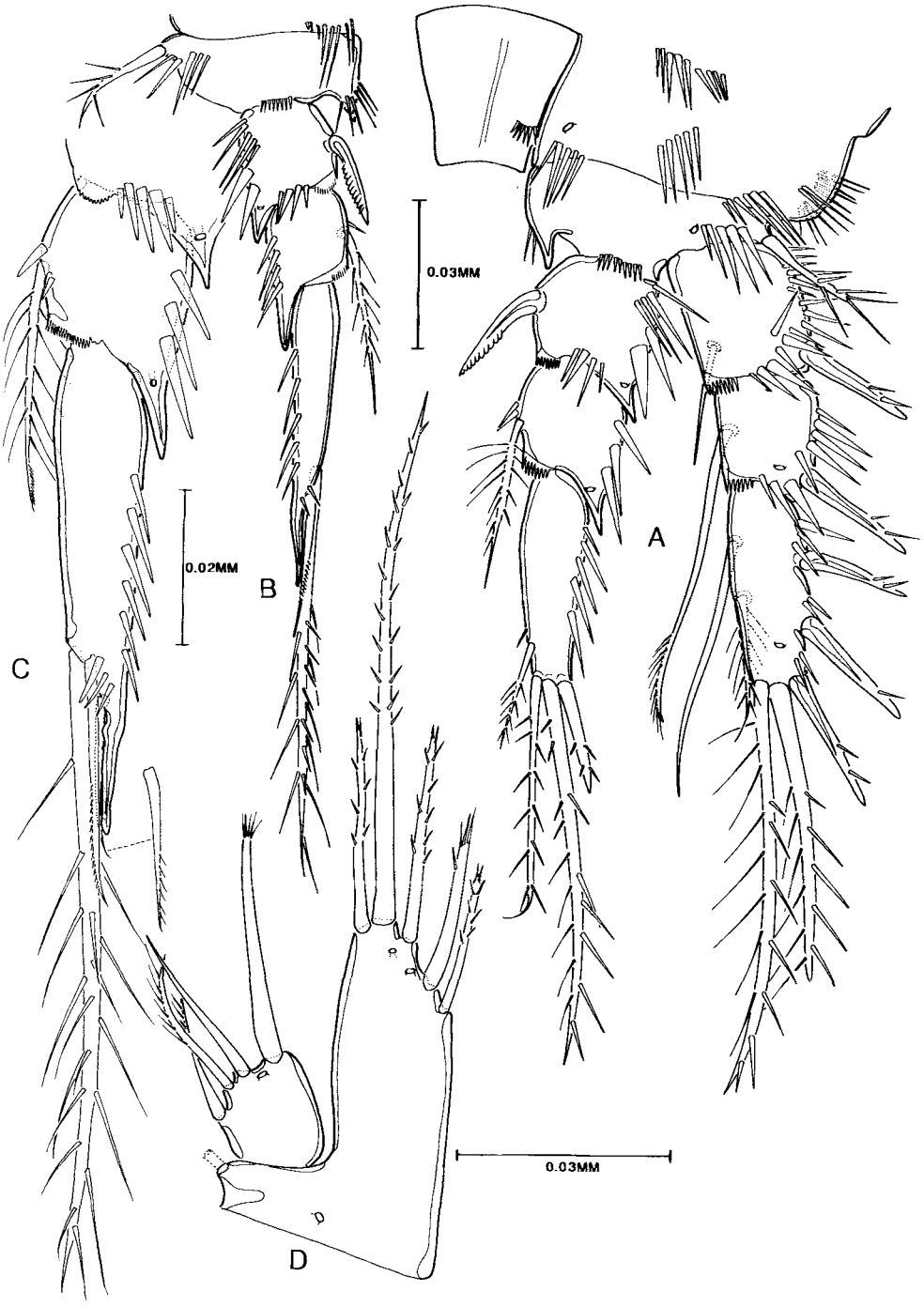

FIG. 6. *Paradanielssenia christineae.* (A) Female P2; (B) and (C) male P2; (D) female P5.

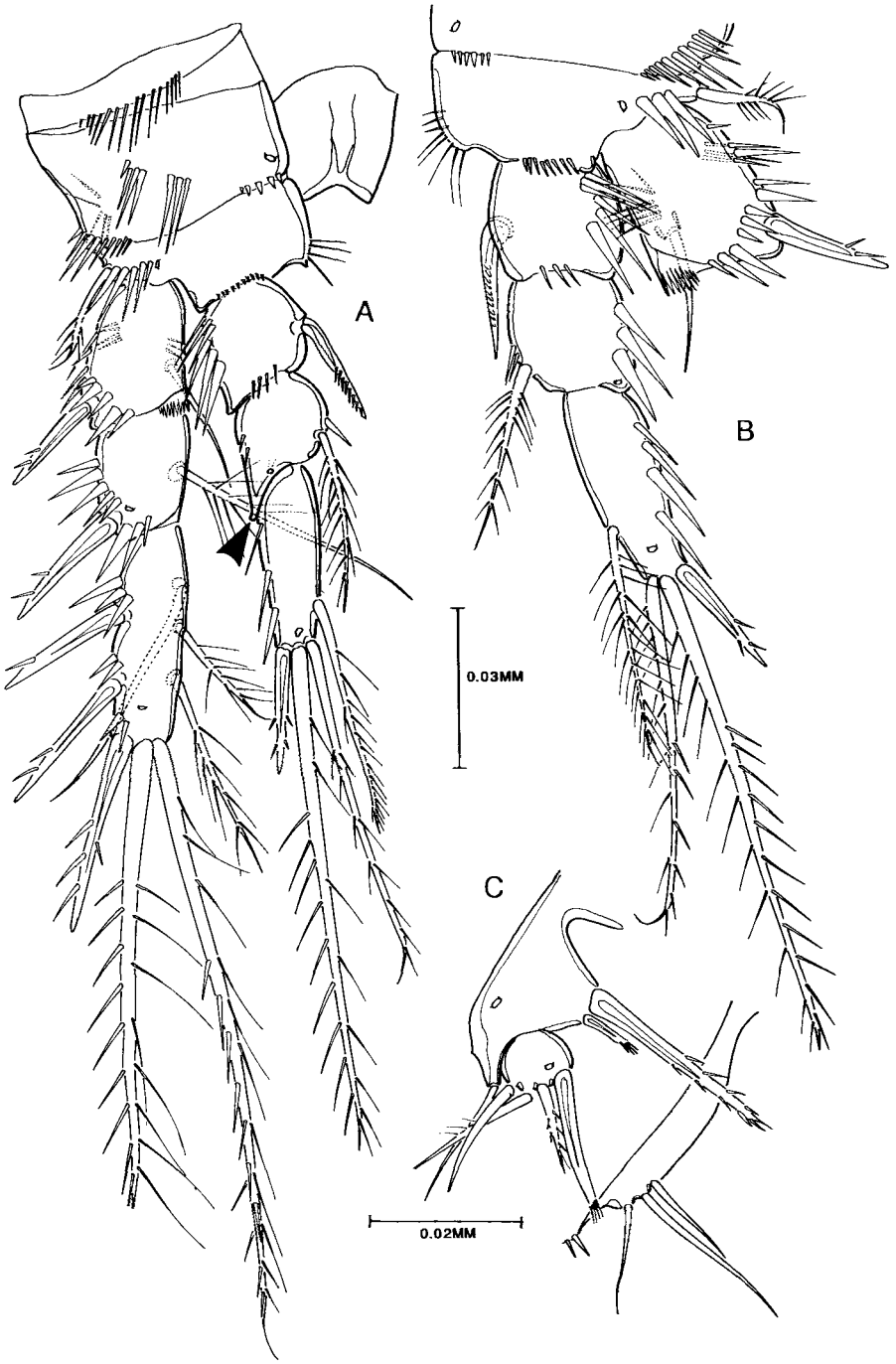

FIG. 7. *Paradanielssenia christineae.* (A) Male P3; (B) female P3 endopod; (C) male P5 and P6.

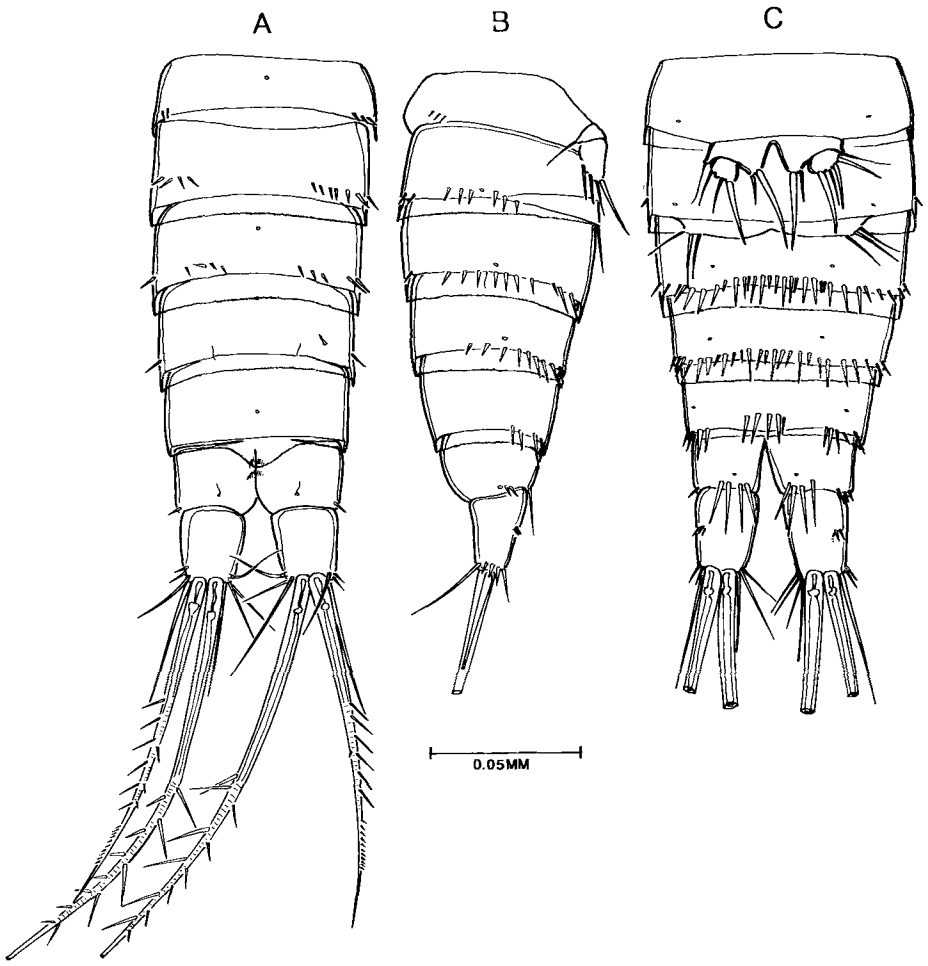

FIG. 8. *Paradanielssenia christineae.* Male urosome: (A) dorsal; (B) lateral; (C) ventral.

Description of female

Body (Fig. 2). Length 0·4–0·5 mm, slightly fusiform, widest at posterior margin of first free prosomite, not noticeably dorso-ventrally flattened. Prosome and urosomite-1 without spinule rows but with many pores. Genital double-somite with lateral and ventral internal cuticular ridge, a small group of spinules dorsolaterally anterior to ridge and a dorsolateral, lateral and ventrolateral group of spinules on posterior margin. Antepenultimate urosomite with lateral and ventral spinule row at posterior margin and penultimate urosomite with three groups of spinules on ventral posterior margin. Anal somite and caudal rami (Figs 2 and 5D) with long spinules medially and at inner distal corner respectively and with short spinules at outer, distal corner. Genital field (Fig. 2C) and caudal rami as for genus, seta IV and V on latter strongly pinnate (as in male, Fig. 8A).

Rostrum (Fig. 3A). Elongate, rounded anteriorly with hyaline margin, a central pore and four sensilla.

Antennule (Fig. 3A, B). As for genus, segment-1 with three rows of spinules on anterior face and one seta; segment-2 with eight setae; segment-3 with 12 setae and a large aesthetasc (Fig. 3A); segment-4 with four pectinate spines, ten setae and a small terminal aesthetasc.

Antenna (Fig. 4A, G). As for genus. Exopod 3-segmented with 1.1.3 setae on proximal to distal segments; inner seta of distal segment minute. Endopod with two rows of heavy spinules, two pectinate spines and a geniculate seta on outer margin; terminal margin with a pectinate spine, four geniculate setae and two small naked setae.

Labrum. Ornamented as in Fig. 4B.

Mandible (Fig. 4C). As for genus; gnathobase with blunt teeth, endopod with one claviform aesthetasc and two setae, exopod absent.

Maxillule (Fig. 4D). As for genus. Coxal endite with two pinnate and three naked setae; basis with five setae and one claviform aesthetasc; endopod with one pinnate and two minute naked setae; exopod with three pinnate setae.

Maxilla (Fig. 4E). As for genus. Syncoxal endites each with three elements, allobasal endite with a non-articulating claw and three setae; endopod with three setae and a claviform aesthetasc.

Maxilliped (Fig. 4F). As for genus. Seta on palmar margin of basis very small; endopodal claw with well developed spinules and two accessory setae (one very small).

P1 (Fig. 5A). As for genus. Inner spine on basis stout, outer seta bi-pinnate.

P2–4 (Figs 5B, C, 6A, 7B). As for genus except P2–3 endopods only as long as exopod. P3–4 intercoxal sclerites without spinules. P2 endopod-1 and endopod-2 with outer distal corner somewhat attenuated. Ornamentation of protopods as in figures. Setal formula as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.1.121
P3	1.1.323	1.1.121
P4	1.1.323	1.0.121

P5 (Fig. 6D). As for genus. Without ornamentation. Second outer seta of endopodal lobe over twice as long as others which are almost equal in length. Exopod almost square, inner seta with tuft of setules at tip, second inner seta smooth, two outer setae pinnate and almost equal in length.

Description of male

As for female except as detailed below.

Body (Fig. 8). Length 0·35 mm, urosomites-2-3 not fused. Urosomite-1 with a few spinules dorso-laterally. Urosomite-3-4 with complete ventral row of spinules.

Antennule (Fig. 3C–E). As for genus. Segment-1 with three rows of spinules and one seta; segment-2 with one seta; segment-3 with 12 setae; segment-4 with 8 setae; segment-5 slightly swollen, with a pinnate spine, 12 setae and a large aesthetasc; segment-6 with 11 setae and a small aesthetasc.

P2 endopod (Fig. 6B, C). As for genus, endopod-2 with small apophysis at outer distal corner only slightly larger than in female. Endopod-3 with outer distal spine transformed into a rigid process, terminal two setae reduced and inner seta very enlarged compared to female.

P3 endopod (Fig. 7A). As for genus, endopod-2 with hooked apophysis at outer distal corner (arrow).

P5 and P6 (Fig. 7C). As for genus. P5 exopod almost circular with four setae.

Etymology

This species is named to honour the wife of the first author.

Paradanielssenia kathleenae sp. nov.
(Figs 9–14)

Material examined

HOLOTYPE 1 adult ♀ (dissected onto two slides) BMNH Reg. No. 1993.419 from a mud bottom at 30–35 m depth in Sassenfjord, Spitsbergen. PARATYPE 1 adult ♂ (dissected onto two slides) BMNH Reg. No. 1993.420 from the same locality. Collected by M. A. Kendall, July 1990.

Description of female

Body (Fig. 9A–C). As for genus. Length 0·84 mm, slightly dorsoventrally flattened. Prosome and urosomite-1 without spinule rows. Genital double-somite with lateral and ventral internal cuticular ridge, bearing a lateral row of spinules anterior to the ridge and a row of spinules all round the posterior margin except middorsally and midventrally. Antepenultimate somite with a lateral and ventral row of spinules on posterior margin. Penultimate somite with a median and lateral spinule row on the ventral posterior margin. Anal somite and caudal rami with spinules as in *P. christineae*. Genital field (Fig. 9D) as for genus, vestigial P6 with one pinnate seta and a non-articulating process. Caudal rami as for genus, setae IV and V spinulose (Fig. 9A).

Rostrum (Fig. 9E). Almost rectangular, rounded anteriorly with hyaline margin, a pore and four sensilla.

Antennule (Fig. 9E). As for genus, setation as in *P. christineae* except that segment-2 with nine setae and segment-3 with 13 setae.

Antenna (Fig. 10A). As for genus. Exopod 3-segmented, inner seta on distal segment slender and smooth. Endopod as in *P. christineae*.

Mandible. As for genus, identical to *P. christineae*.

Maxillule. As for genus. Basal endite with five setae and a claviform aesthetasc, endopod with two setae.

Maxilla. As for genus, identical to *P. christineae*.

Maxilliped (Fig. 10B). As for genus. Seta on palmar margin of basis larger than in *P. christineae* and with long pinnules. Endopodal claw with small spinules and two accessory setae.

P1. As for genus except that middle outer spine (arrowed in Fig. 11A) of exopod-3 slightly longer than distal outer spine.

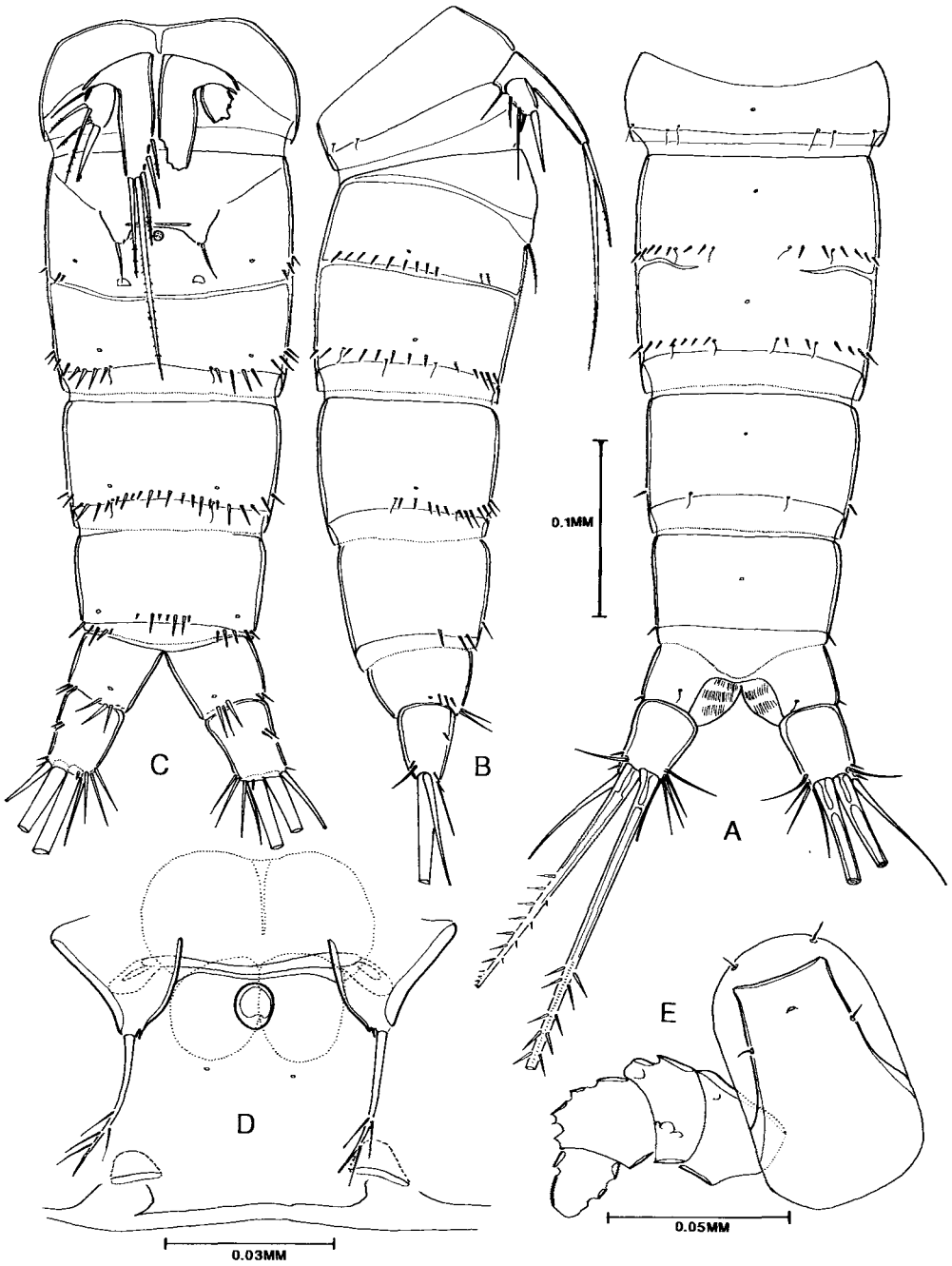

FIG. 9. *Paradanielssenia kathleenae*. Female urosome: (A) dorsal; (B) lateral; (C) ventral. Female: (D) genital field; (E) rostrum and antennule segmentation.

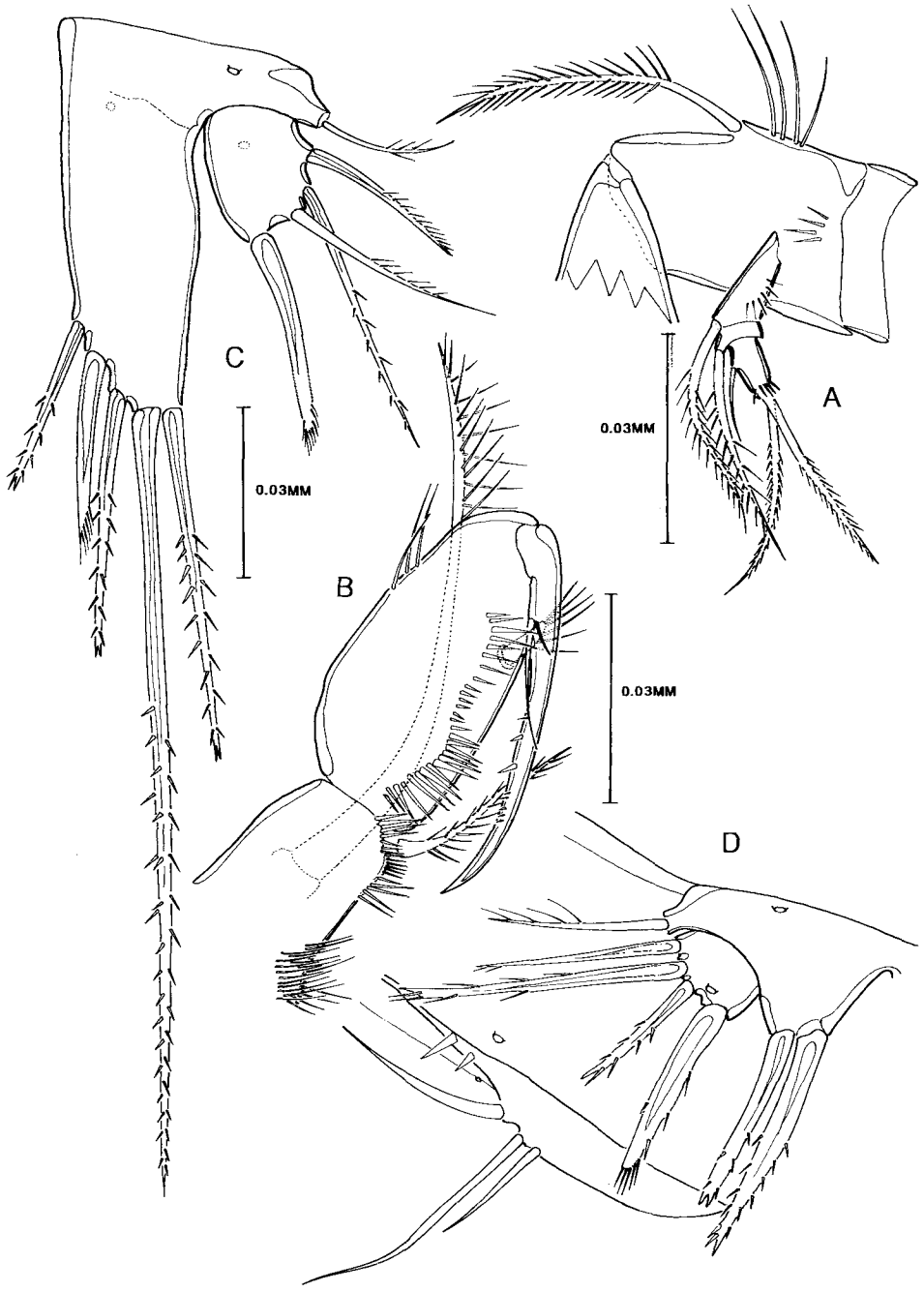

FIG. 10. *Paradanielssenia kathleenae.* (A) Allobasis and exopod of antenna; (B) maxilliped; (C) female P5; (D) male P5 and P6.

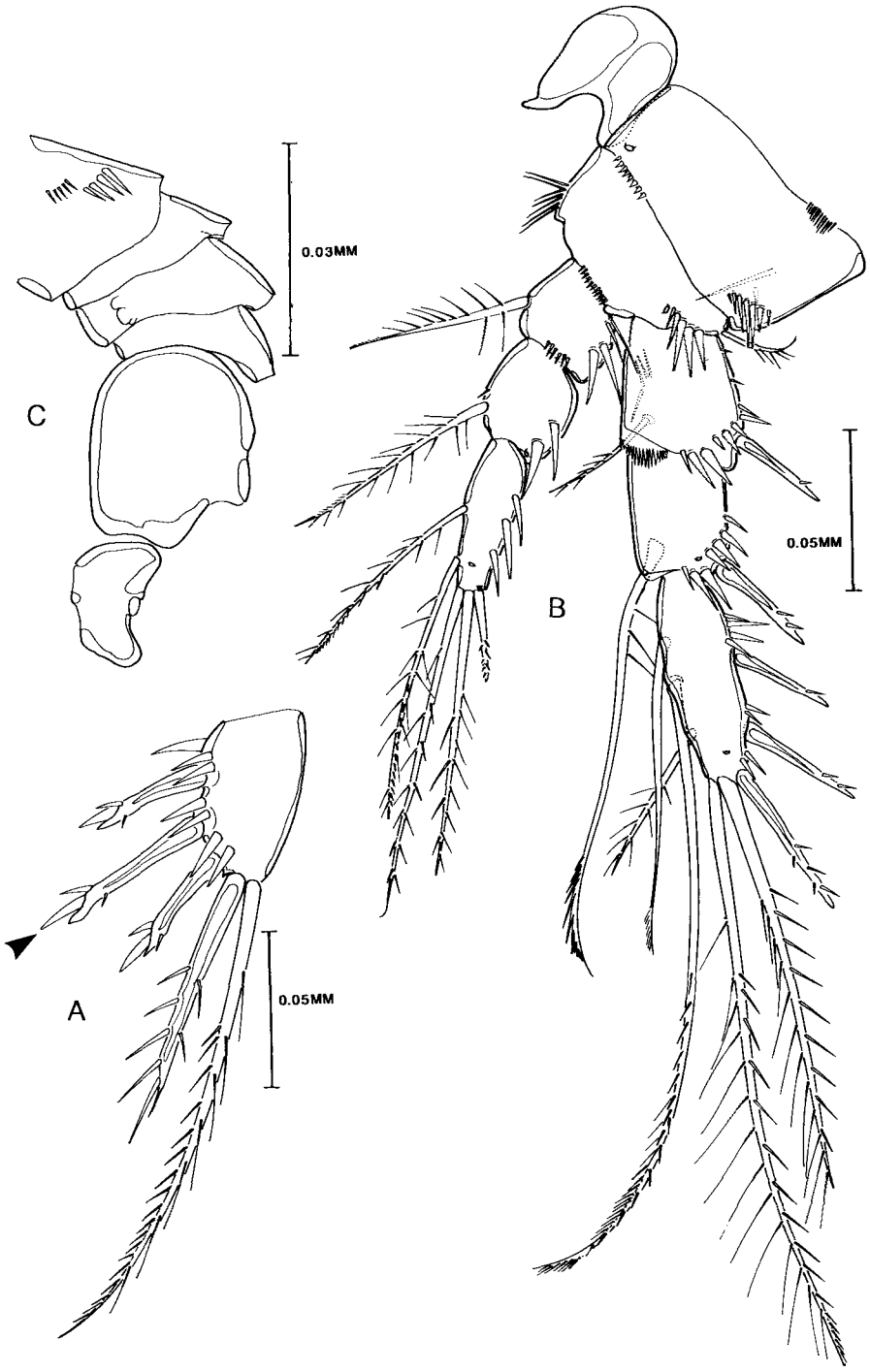

FIG. 11. *Paradanielssenia kathleenae.* (A) P1 exopod-3; (B) female P4; (C) male antennule segmentation.

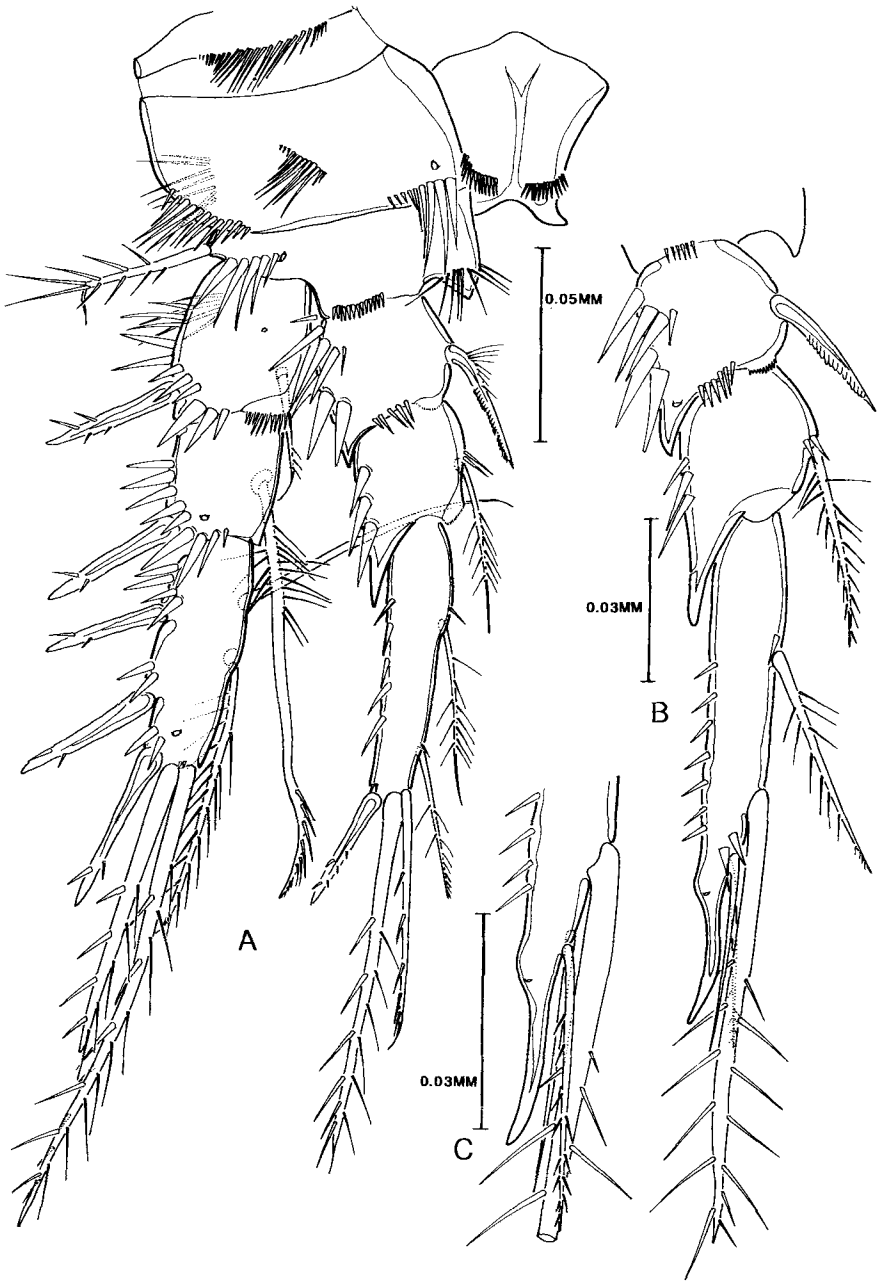

FIG. 12. *Paradanielssenia kathleenae.* P2: (A) female; (B) male endopod anterior; (C) male endopod-3 posterior.

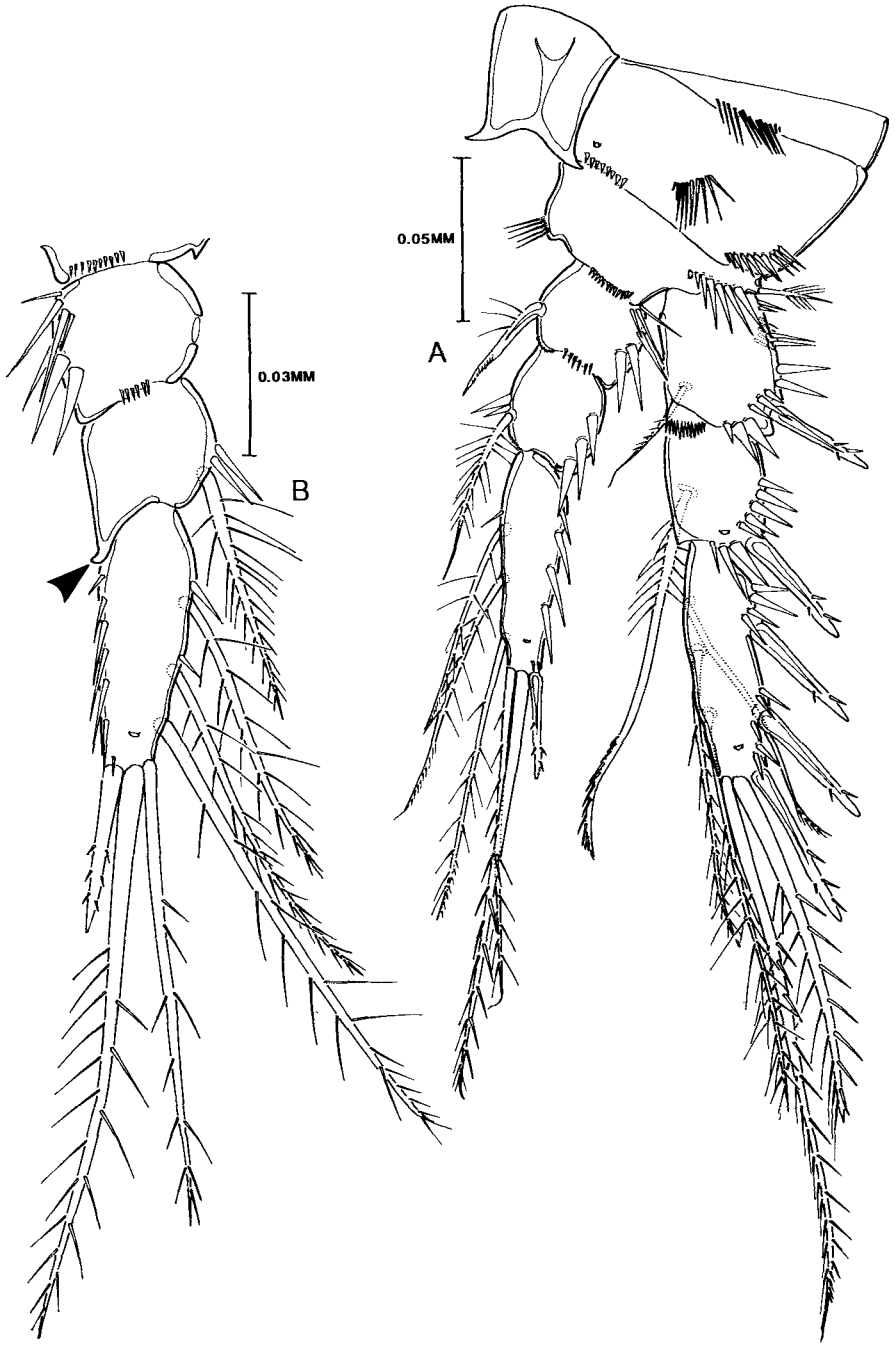

FIG. 13. *Paradanielssenia kathleenae*. P3: (A) female; (B) male endopod.

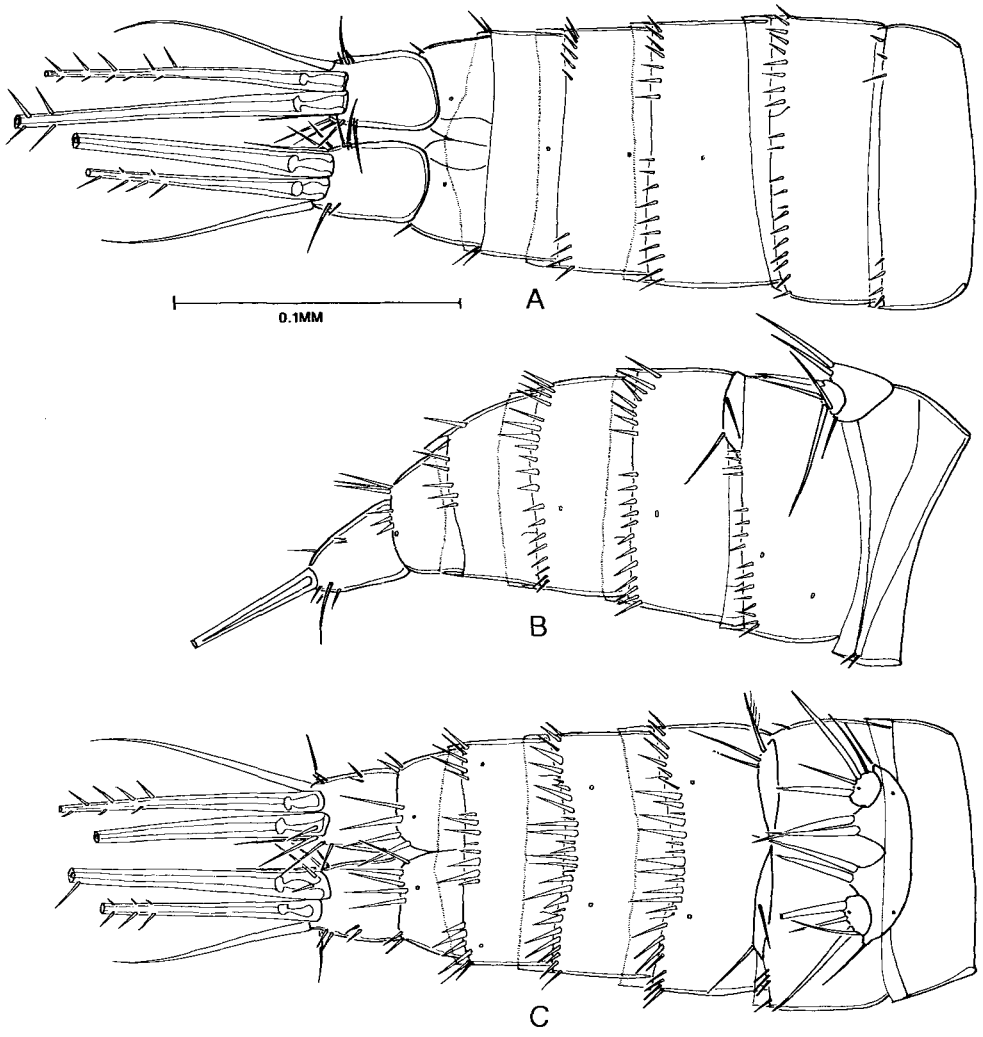

FIG. 14. *Paradanielssenia kathleenae.* Male urosome: (A) dorsal; (B) lateral; (C) ventral.

P2–4 (Figs 11B, 12A, 13A). As for genus except P3 endopod slightly shorter than exopod. P3–4 intercoxal sclerites without spinules. P2 endopod-1 and endopod-2 with outer distal corner somewhat attenuated. Setal formula as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.1.221
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

P5 (Fig. 10C). As for genus. Inner seta on endopodal lobe of baseoendopod as long as second inner; second outer seta more than twice as long as outer seta. Exopod slightly longer than wide with four setae, outer seta well developed, pinnate, almost as long as inner seta which is stout with a plumose tip.

Description of male

As in female except for following characters.

Body (Fig. 14). Smaller than female and urosomites-2-3 not fused. Urosomite-2 with dorsal and lateral row of spinules on posterior border. Urosomite-3 with row of spinules all round posterior margin. Spinules generally larger than in female.

Antennule (Fig. 11C). As for genus. Setation as in *P. christineae* (Fig. 3C–E).

P2 endopod (Fig. 12B, C). As for genus. Apophysis at outer distal corner of endopod-2 short but more strongly developed than in female. Endopod-3 with outer seta of distal margin transformed into a rigid process, two terminal setae reduced and distal seta of inner margin much more strongly developed than in female.

P3 endopod (Fig. 13B). As for genus. Endopod-2 with a hooked apophysis on outer distal margin (arrowed in Fig. 13B).

P5 and P6 (Fig. 10D). As for genus except that outer seta on endopodal lobe almost as long as inner seta. Exopod much broader than long with four setae.

Etymology

The specific name is in honour of the wife of the second author.

Discussion

There is no doubt that these two species can be assigned to the genus *Paradanielssenia* based on (1) the detailed structure of the mouthparts and the presence of claviform aesthetascs on the endopod of the mandible and maxilla and the basis of the maxillule, (2) the structure of the female genital field, (3) male sexual dimorphism of P2 endopod-2, and (4) the distinctive features of the P5 in both sexes. Both species depart from the generic diagnosis given in Gee and Huys (1991) only in (*a*) the rostrum which is ovoid (rather than triangular) with a lateral and anterior hyaline margin and (*b*) the relative length of the endopod of P2 and P3 which is, respectively, as long as and slightly shorter than the exopod. On the other hand, the setal arrangement of the caudal ramus and the presence of four setae on the basis of the mandible in these two species confirms the generic diagnosis in these respects.

Within the genus *Paradanielssenia*, both new species are more closely related to *P. kunzi* than to *P. biclavata* in that they have a 3-segmented exopod on the antenna, only one claviform aesthetasc on the post-antennary mouthparts (both almost certainly plesiomorphic conditions for this genus) and four setae on the exopod of the P5 in both sexes. *Paradanielssenia christineae* is clearly differentiated from the other species on the basis of the reduced setation on the endopod of P2–4 but the specimens we have allocated to *P. kathleenae* are very similar to the description and figures of *P. kunzi* given in Soyer (1970). However, we have assigned them to a new species on the basis of the following characters: (1) length of the female P2 endopod which in *P. kathleenae* is only as long as the exopod (Fig. 12A) whereas in *P. kunzi* it is clearly much longer than the exopod (Soyer, 1970: Fig. 3B): (2) the relative lengths of setae on the P5 of both sexes; in female *P. kathleenae* the inner seta on the endopodal lobe and the outer seta on the exopod and in the male the outer seta on the endopodal lobe are almost as long as the adjacent seta (Fig. 10C, D) whereas in *P. kunzi* they are extremely reduced (Soyer, 1970: Fig. 3D, G). Such differences in proportional lengths of setae could be a result of within species variability but, at present, we have no knowledge of the range of variation which might be exhibited by species in this genus as only *P. kunzi* is known from more than four specimens (49♀, 7♂). We have been unable to examine the material of *P. kunzi* but Soyer (1970) does not indicate that there is any variability in his material. Further, in the other Paranannopidae which we

have studied there is little evidence of significant variability in the size of armature elements. Although *Danielssenia typica* does exhibit variation in body size and number of setae on male P5 baseoendopod both within and between localities there are no significant differences in rami and setal proportions (Gee, 1988a). Similarly, Huys and Gee (1992) found only slight differences in proportional length of some mouthpart rami and a seta on the male P5 baseoendopod in *Sentirenia perezi* (Monard) from the Scilly Isles and Mediterranean (now a junior synonym of *Jonesiella fusiformis* Brady, 1880 according to Huys and Gee, 1993). On this basis, we believe that the differences between *P. kunzi* and our specimens, coupled with the disparate localities of origin (Spitsbergen in the Arctic Circle and the Mediterranean off Banyuls) are sufficient to assign our specimens to a new species.

Key to species of *Paradanielssenia*

1 Antenna exopod 3-segmented; P5 exopod of both sexes with four setae/spines . . 2
– Antenna exopod 1-segmented; P5 exopod of both sexes with five setae/spines
P. biclavata Gee, 1988

2 P2–4 endopod-3 with 5:6:5 setae/spines; P4 endopod-2 with an inner seta . . . 3
– P2–4 endopod-3 with 4:4:4 setae/spines; P4 endopod-2 without an inner setae
P. christineae sp. nov.

3 P2 endopod much longer than exopod; P5 inner seta of endopodal lobe and outer seta of exopod in female or outer seta of endopodal lobe in male at most 0·25 times length of adjacent seta . . . . . *P. kunzi* Soyer, 1970
– P2 endopod about as long as exopod: P5 inner seta of endopodal lobe and outer seta of exopod in female or outer seta of endopodal lobe in male nearly as long as adjacent seta . . . . . *P. kathleenae* sp. nov.

Genus ***Mucrosenia*** gen. nov.

Diagnosis

(Based on female only.) Paranannopidae. Body small, not dorsoventrally flattened. Rostrum large, hyaline with four sensilla. Genital double-somite with almost continuous subcuticular ridge. Genital field with copulatory pore immediately posterior to genital slit; paired copulatory ducts leading to transverse seminal receptacle anterior to genital slit; P6 with outer plumose seta and inner smooth seta. Caudal rami as long as broad with group of long setules at inner distal margin; seta II implanted near dorsal posterior margin. Antennule 4-segmented with pinnate setae and pectinate spines, aesthetasc on segments III and IV. Antennal exopod 3-segmented with 1.1.3 setae on proximal to distal segments. Mandibular gnathobase with bluntly rounded bicuspid teeth and one seta at dorsal distal corner; basis with three setae; endopod 1-segmented; exopod 2-segmented. Maxillule rami with three setae. Maxilla syncoxal endites with three elements, endopod with four setae. Maxilliped syncoxa with two setae, basis with a small naked seta, endopodal claw with one accessory seta. P1 exopod 3-segmented; outer elements on proximal two segments seta-like; distal outer spine on exopod-3 longer than middle outer spine. P1 endopod longer than exopod, 2-segmented; endopod-2 twice as long as endopod-1, inner seta implanted in distal half. P2–4 rami 3-segmented, endopod shorter than exopod; intercoxal sclerites unadorned; exopod-1 without inner seta. P2 endopod-2 without inner seta; formed into a mucroniform process reaching almost to the end of endopod-3. P5 exopod separate from baseoendopod on anterior face only, with four setae, inner seta implanted at a distance from other three; endopodal lobe well developed, rounded anteriorly with five setae.

Type species. *Mucrosenia kendalli* sp. nov. (by monotypy).

Etymology

Derived from the Latin *mucro* meaning a point and referring to the pointed projection on the P2 endopod-2 of the female.

Gender. Feminine.

Mucrosenia kendalli sp. nov.
(Figs 15–20)

Material examined

HOLOTYPE 1 egg-bearing ♀ (dissected onto three slides) BMNH Reg. No. 1993.421 from 95 m depth in Sassenfjord, Spitsbergen. Collected by M. A. Kendall, July 1990.

Description of female

Body. (Figs 15, 16A). Length 0·38 mm, more or less cylindrical with clear distinction between prosome and urosome. Free prosomites with plain hyaline frill and with row of spinules near posterior dorsal margin. Genital double-somite with transverse subcuticular ridge complete except middorsally. Urosome unadorned dorsally, each somite with a short lateral spinule row. Posterior part of genital double-somite with a midventral row of short spinules and a row of spinules on posterior ventral margin. Antipenultimate somite with row of spinules on posterior ventral margin. Penultimate somite with three groups of spinules on posterior ventral margin. Genital field (Fig. 16C) with small ovoid copulatory pore immediately posterior to genital slit, a dumb-bell shaped seminal receptacle located anterior to genital slit, vestigial P6 with an outer pinnate seta and a smooth inner seta. Anal somite deeply divided. Pseudoperculum not prominent. Caudal rami (Fig. 16B) about as long as broad with a ventral and lateral group of long spinules at the outer distal margin and a ventrolateral group of long fine setules at the inner distal margin. Seta I minute, midlateral; seta II well developed inserted near dorsal distal margin; setae III and VI normal; seta IV and V minutely pinnate; seta VII triarticulate, dorso-lateral on median inner margin.

Rostrum (Fig. 17A). Large, ovoid, completely hyaline with central pore and four sensilla.

Antennule (Fig. 17A–D). 4-segmented with pinnate or pectinate setae on all segments. Segment-1 with two rows of spinules and one seta on anterior margin; segment-2 with eight setae; segment-3 with 13 setae and a large aesthetasc; segment-4 with five pectinate spines, eight setae and an aesthetasc.

Antenna (Fig. 18A). With well-developed coxa. Allobasis with a row of setules and a pinnate seta on abexopodal margin. Exopod 3-segmented with 1:1:3 pinnate setae on proximal to distal segments. Endopod with two rows of large spinules on anterior margin and bearing two pectinate spines, a geniculate seta and a small smooth seta subdistally and a pectinate spine, four geniculate setae and a small smooth seta terminally.

Mandible (Fig. 17E). Coxa robust, gnathobase with well developed bluntly rounded bicuspid teeth and one seta at distal dorsal corner. Basis with whorl of long spinules on anterior face and three pinnate setae, two subdistally (one missing in Fig. 17E but insertion site arrowed) and one on distal margin. Endopod short, 1-segmented with three lateral and six terminal setae. Exopod 2-segmented, proximal segment with a row of spinules and two lateral seta, distal segment with three terminal setae.

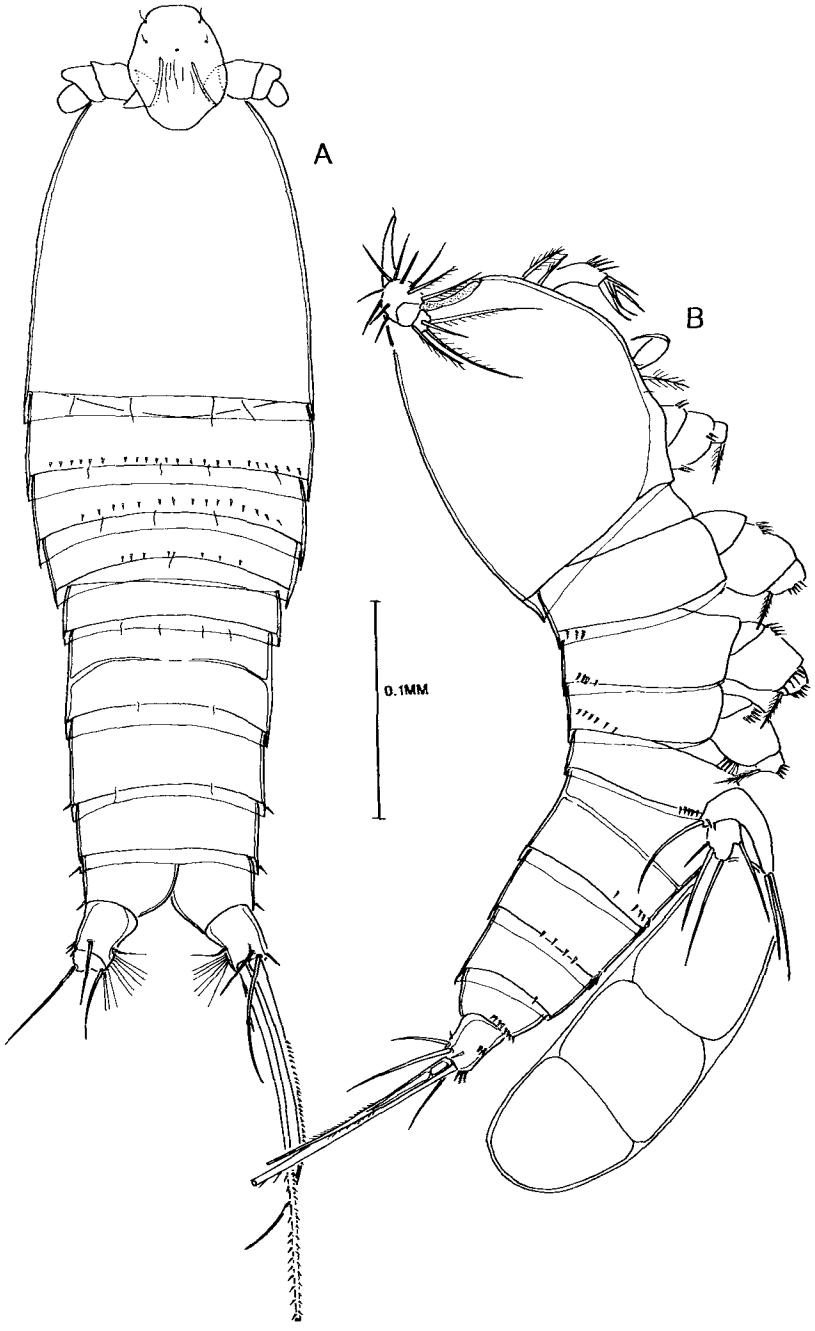

FIG. 15. *Mucrosenia kendalli.* Female habitus: (A) dorsal; (B) lateral.

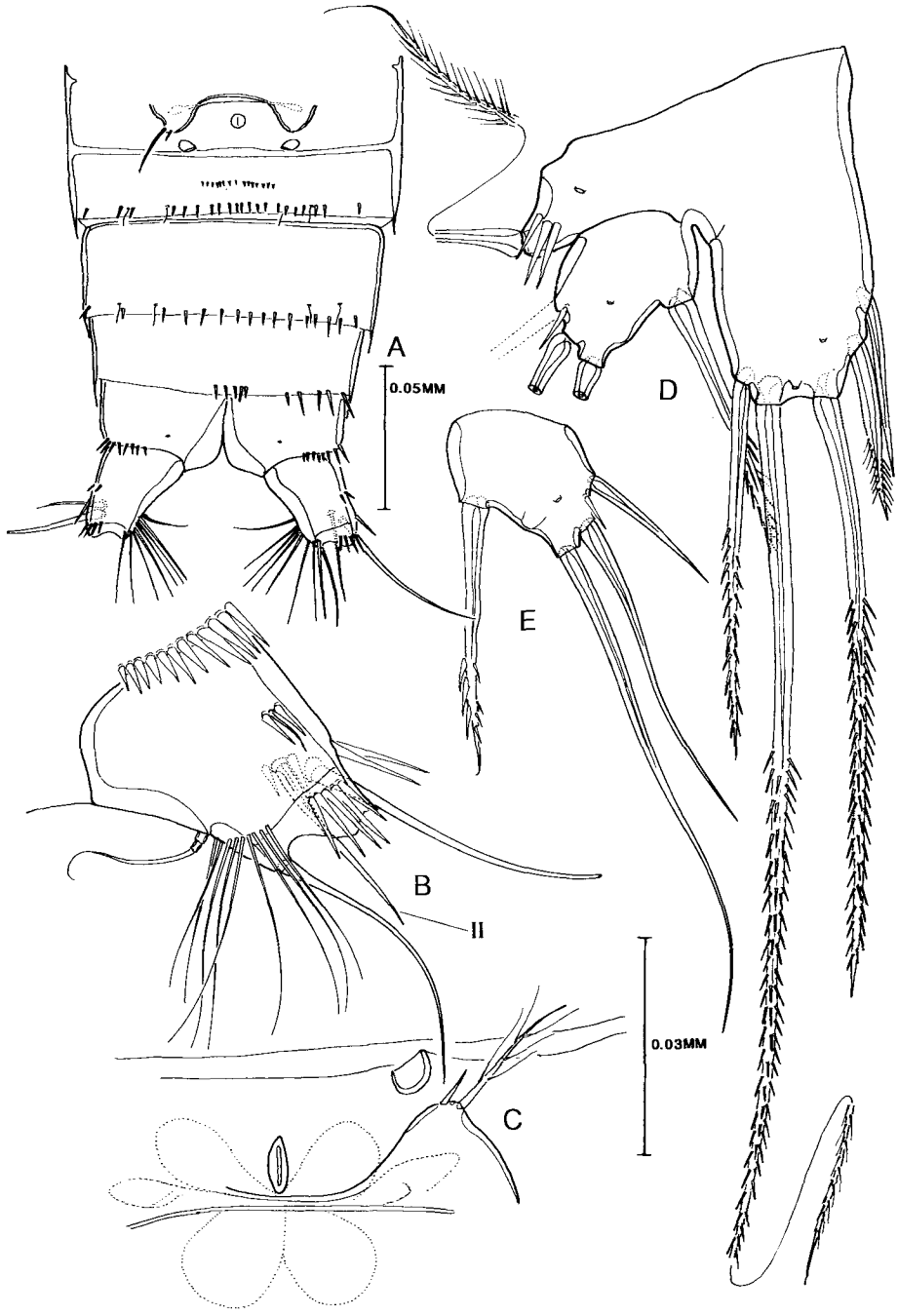

FIG. 16. *Mucrosenia kendalli.* Female: (A) ventral urosome, excluding urosomite-1; (B) caudal ramus, ventral; (C) genital field; (D) P5; (E) exopod of P5 detached.

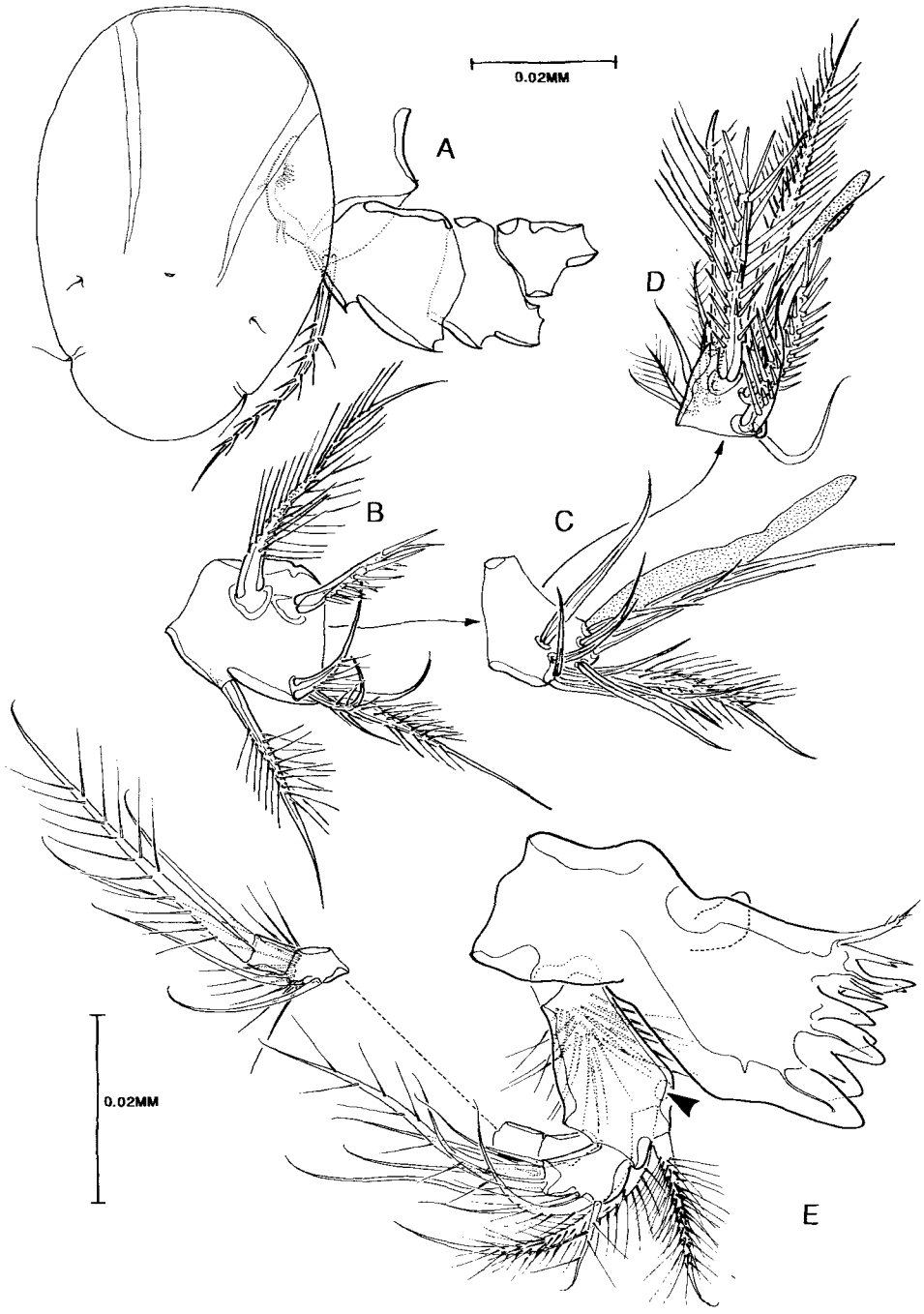

FIG. 17. *Mucrosenia kendalli.* Female: (A) rostrum and segmentation of antennule; (B) antennule segment-2; (C) antennule segment-3; (D) antennule segment-4; (E) mandible.

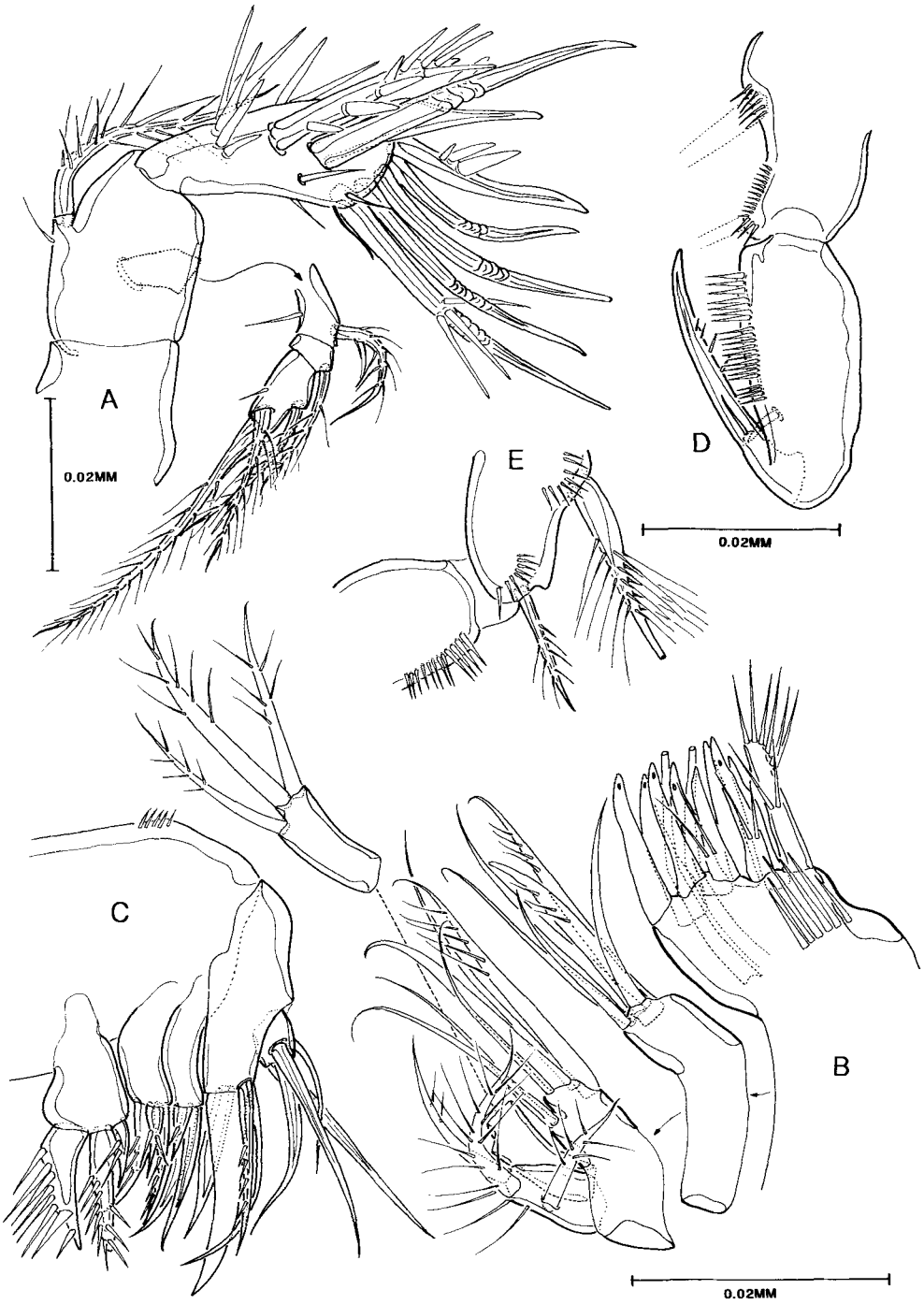

FIG. 18. *Mucrosenia kendalli.* Female: (A) antenna; (B) maxillule; (C) maxilla; (D) maxilliped; (E) syncoxa of maxilliped.

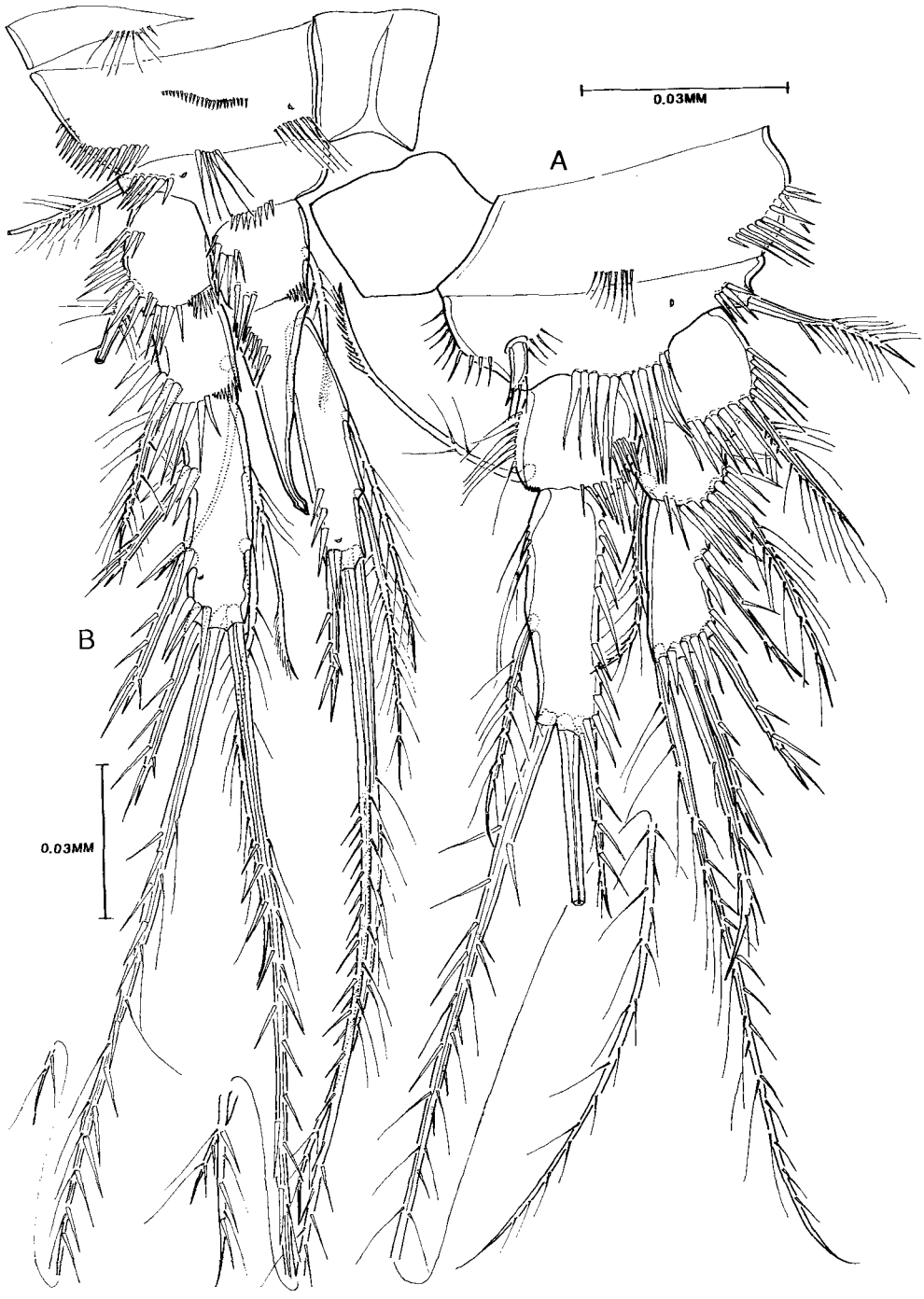

FIG. 19. *Mucrosenia kendalli.* Female: (A) P1; (B) P2.

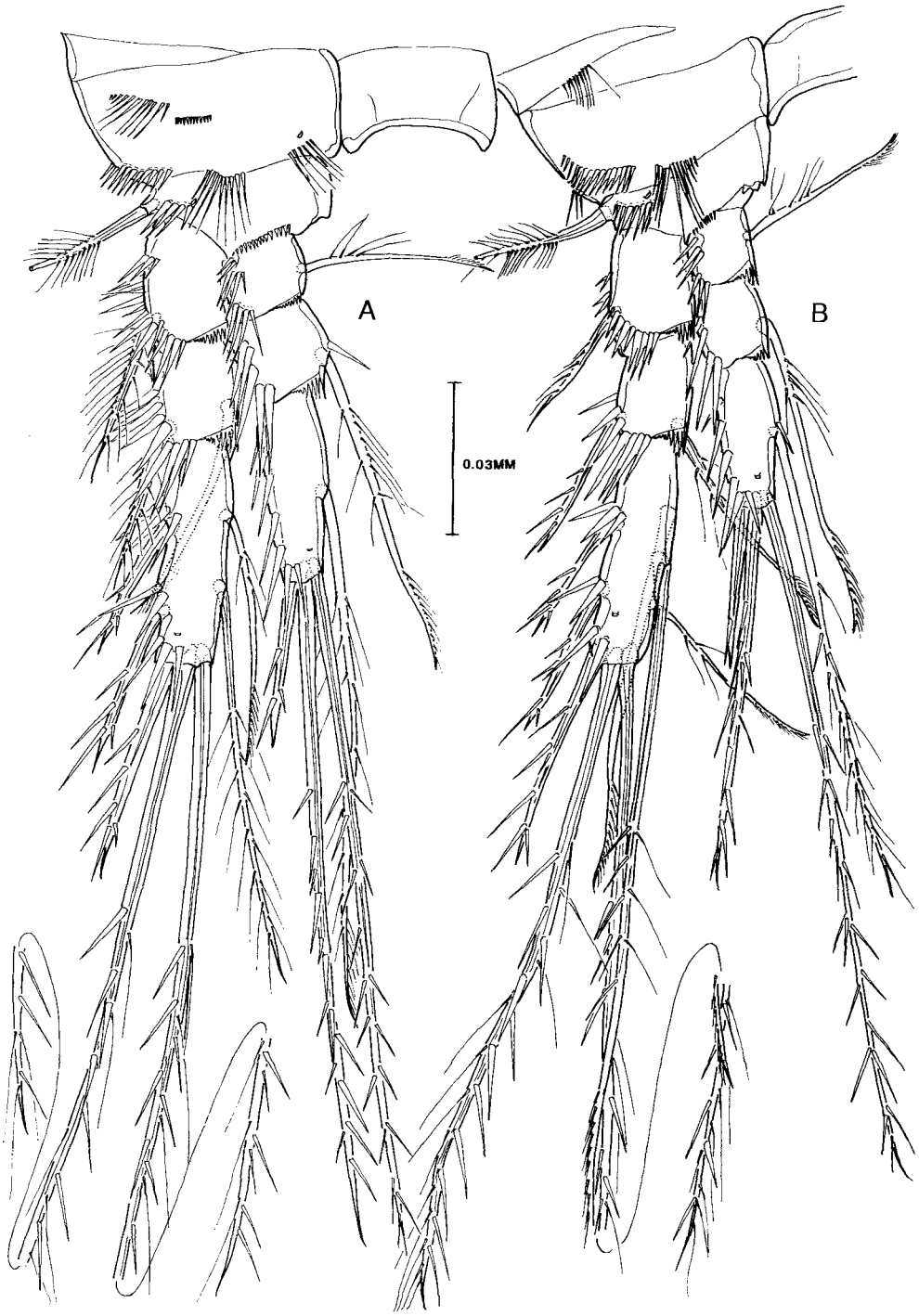

FIG. 20. *Mucrosenia kendalli.* Female: (A) P3; (B) P4.

Maxillule (Fig. 18B). Coxal and basal endites each with six setae; basal endites each with six setae; endopod pointing inwards; both rami with three setae.

Maxilla (Fig. 18C). Praecoxal and inner coxal endites with three pectinate spines, outer coxal endite with a small spine and two setae. Allobasal endite with two articulating spines and two setae. Endopod with four setae.

Maxilliped (Fig. 18D, E). Syncoxa with a smaller distal and a larger subdistal pinnate seta each with row of spinules at base. Basis ovoid with row of spinules on palmar margin and a small peg-like unadorned seta. Endopodal claw with a few spinules and one small accessory seta.

P1 (Fig. 19A). Coxa with row of spinules at outer margin and row of setules in middle of distal margin on anterior face. Basis with row of spinules on inner margin and medially on distal margin; inner spine very short, pinnate; outer seta bipinnate reaching just past exopod-1. Outer elements on proximal and middle segments of exopod slender, finely pinnate; exopod-3 distal outer spine longer than middle outer spine. Endopod longer than exopod, endopod-2 twice as long as endopod-1; endopod-2 with a group of long setules on inner proximal margin, inner seta implanted in distal half.

P2 (Fig. 19B). Intercoxal sclerite almost square, unadorned. Coxa with row of small spinules in centre of anterior face and three rows of spinules around distal margin. Basis with a row of spinules at base of rami, outer seta multipinnate. Rami 3-segmented, terminal setae on distal segments long. Exopod-1 without inner seta. Endopod slightly shorter than exopod; endopod-1 outer margin not attenuated, inner seta not spiniform; endopod-2 without inner seta, modified into a slightly recurved mucroniform process with a sagittiform tip not reaching distal margin of endopod-3.

P3–4 (Fig. 20). Intercoxal sclerites rectangular, unadorned. Protopod ornamentation similar to P2. Rami 3-segmented with long terminal setae on distal segments, endopod shorter than exopod. Exopod-1 without inner seta. Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	0.1.223	1.0.221
P3	0.1.223	1.1.121
P4	0.1.323	1.1.121

P5 (Fig. 16D, E). Elements of each side not fused medially. Exopod partially fused to baseoendopod, clear demarcation line visible on anterior face only. Baseoendopod with a few spinules on peduncle of outer seta; endopodal lobe well developed, rounded distally with five setae, middle seta over half as long as second outer seta, others shorter, inner seta smooth. Exopod semi-ovoid, a pinnate seta implanted in proximal half of inner margin and three naked setae on distal and outer margin.

Etymology

This species is named in honour of M. A. Kendall of the Plymouth Marine Laboratory who collected the type specimen.

Discussion

Autapomorphies of Mucrosenia

After having made only a preliminary examination of the material described above, Huys and Gee (1993) thought that it might be synonymous with *Psammis kliei*. This species they excluded from the genus *Psammis* because it did not possess any of the setal apomorphies evident in the female by which they defined the genus *Psammis*. After more detailed examination it is clear that the present material does not exhibit any of the definitive characters of *Psammis* or the character combination of any other genus of Paranannopidae and so we have placed it in a separate genus, *Mucrosenia*. This can be defined by the following autapomorphies: (1) P2 endopod-2 with a mucroniform process reaching almost to the end of endopod-3 in the female. This is a sexually dimorphic character in the males of most 'danielsseniid' genera but it not present in the female of any species. The outer distal corner is slightly attenuated on P2 endopod-1 in female *Psammis* and on P2 endopod-2 in female *Archisenia* Huys and Gee, 1993 (and some species of *Paradanielssenia*; Figs 6A and 12A above) but in no case is this similar to the degree of prolongation found in the male. Further, our specimen does not appear to be an intersex specimen (such as that reported for *Archisenia sibirica* (Sars, 1898) by Huys and Gee, 1993) as in every other respect it is a viable (egg-bearing) mature female and we must therefore regard this character as genuine. (2) P2 endopod-2 without inner seta(e). This is unique in females of the 'danielsseniid' genera without claviform aesthetascs on the mouthparts but in the males of *Archisenia* and *Afrosenia* Huys and Gee (in preparation) its absence is a sexually dimorphic character.

Other apomorphies of phylogenetic significance by which *Mucrosenia* may be characterized are: (1) The posterior displacement of seta II on the caudal ramus (Fig. 16B); (2) the presence of a bunch of long setules at the inner distal corner of the caudal ramus. The only other paranannopid with a similar group of long setules in this position is *Bathypsammis longifurca*, first described by Bodin (1968) from a depth of 4000 m in the southern Bay of Biscay. This species also shows displacement of a seta to near the distal margin but in this case it is seta VII which has moved from the inner median lateral margin. (3) The P2 endopod shorter than the exopod. In all primitive 'danielsseniid' genera without claviform aesthetascs on the mouthparts, the P2 endopod is at least as long as to much longer than the exopod. (4) The absence of an inner seta on exopod-1 of P2–4. This is not the usual condition in the Paranannopidae and is found only in *Danielssenia* as defined by Huys and Gee (1993) and *Sentiropsis* Huys and Gee (in preparation).

Status of Psammis kliei

Psammis kliei was very briefly described by Smirnov (1946) from a single female taken in 60 m of water around Henrietta Island, one of the New Siberia Islands in the East Siberian Sea, and the description is accompanied by very small, poor quality illustrations of only the anal somite and caudal rami. P1, P4 and P5. However, from this description it would appear that *P. kliei* is similar to *M. kendalli* in the following features: (1) The caudal ramus. This is unusual in that in both species seta II (which is median lateral on the outer margin in most other genera) is displaced to near the posterior margin. Also unusual is the group of very long, fine setules at the inner distal margin of both species. (2) The form and setation of P2–4. In both species the P2 endopod is shorter than the exopod; there is no inner seta on exopod-1 of P2–4 and

endopod-3 has 5.4.4 setae/spines respectively, a setal count otherwise found only in *Danielssenia quadriseta* and *D. spitsbergensis* sp. nov. (see below) within the 'danielsseniid' genera. (3) Shape and setation of P5. The general shape of the limb and the relative lengths of all the setae except the inner seta of the exopod are very similar in both species as far as can be ascertained from Smirnov's drawing (Smirnov, 1946 fig 25.4).

Nevertheless, there are a number of apparent differences between *P. kliei* and *M. kendalli.* (1) Smirnov states that in *P. kliei* 'the anal plate is broad, feebly prominent, devoid of armature' (from the English summary) and illustrates it (fig 25.1) as projecting half way up the caudal rami from an anal somite which is not divided. In all Paranannopidae the anal somite is deeply divided and an operculum is absent. A pseudoperculum (an extension of the hyaline frill of the penultimate somite) is usually present but in *M. kendalli* even this is very reduced. As Smirnov states that in general body facies his specimen is similar to *Psammis longisetosa* it could be assumed that his illustration of the anal somite is not strictly accurate. (2) Smirnov draws (fig. 25.3) the P1 endopod only as long as the exopod but describes it as slightly longer, whereas in *M. kendalli* it is distinctly longer. (3) Smirnov illustrates (fig. 25.1) seta V of the caudal ramus as over three times as long as seta IV although he describes it as twice as long which is the case in *M. kendalli.* (4) Smirnov states that the P5 exopod of *P. kliei* is fused to the baseoendopod whereas in *M. kendalli* the exopod has a distinct suture on the dorsal face and can become detached undamaged from the baseoendopod during dissection (Fig. 16E). Further, in Smirnov's drawing of the P5 (fig. 25.4), the inner seta of the exopod is shorter and implanted much nearer the next inner seta than is the case in *M. kendalli.* (5) Most importantly, although Smirnov makes a brief mention (in the Russian text) of the setation of endopod-3 of P2–4 in *P. kliei* he makes no mention of the mucroniform process on P2 endopod-2 which is a prominent feature even in a lateral view of the whole specimen of *M. kendalli* where it projects somewhat ventrally. Therefore, it is a matter of conjecture as to whether this process is present or absent in *P. kliei* especially as all Smirnov's material is generally regarded as being either lost or unavailable for re-examination.

On the basis of the foregoing evidence it seems unlikely that *Psammis kliei* and *M. kendalli* are synonymous. However, even from Smirnov's brief description it is clear that *P. kliei* definitely displays four of the six apomorphies which we have used to erect the genus *Mucrosenia.* We propose therefore, that *P. kliei* should be removed from the genus *Psammis* and be placed as species *incertae sedis* in *Mucrosenia.*

Phylogenetic relationships

Within the phylogenetic scheme for the 'danielsseniid' grouping outlined in Huys and Gee (1993), it is clear that *Mucrosenia* is most closely related to the primitive genera, *viz. Fladenia* Gee and Huys, 1990, *Archisenia*, *Danielssenia*, *Psammis* and *Bathypsammis*, which lack sensory aesthetascs on the mouthparts, the presence of which is a powerful synapomorphy for the more advanced genera *Jonesiella* Brady, 1880 (cf. Huys and Gee 1992, 1993), *Paradanielssenia*, *Micropsammis* Mielke, 1975, *Telopsammis* Gee and Huys, 1991 and *Leptotachidia* Becker, 1974 (cf. Gee and Huys, 1991), *Sentiropsis* and *Peltisenia* Huys and Gee (in preparation). Within the group of primitive genera, *Mucrosenia* appears most closely allied to the *Danielssenia–Psammis–Bathypsammis* group of genera as it possesses the synapomorphies evident in the female which distinguish this particular lineage, *viz.* a 4-segmented antennule, and a reduced setation on P4 endopod-3.

Detailed consideration of the relationships within this group however, are severely hampered by the absence of information on the male condition in both *Mucrosenia* and *Bathypsammis*. These two genera share unique characteristics of the caudal ramus with a cluster of long setules at the inner distal corner and the posterior displacement of a seta. However, as pointed out earlier it is a different seta which is displaced in each genus and these characters therefore may be the result of convergence. *Mucrosenia* has none of the mouthpart specializations exhibited by *Psammis* such as the sharply pointed, widely separate multicuspid teeth of the mandibular gnathobase, the comb-like spines on the coxa of the maxillule and the large pinnate seta on the basis of the maxilliped. Further *Mucrosenia* does not have the more primitive setal characteristics of *Psammis* and in this respect appears to be most closely related to *Danielssenia* by the following shared apomorphies, *viz.* loss of a seta on exopod-1 of the antenna, the basis of the mandible, exopod-1 of P2–4 and endopod-2 of P2. *Mucrosenia* is distinguished from *Danielssenia* in that the mandibular exopod is 2-segmented with five setae, there is a mucroniform process and no seta on P2 endopod-2, it does not have a deeply incised dorsal hyaline frill on the P5-bearing somite or an elongate anterior extension of the seminal receptacle.

Genus ***Danielssenia*** Boeck, 1872

Danielssenia quadriseta Gee, 1988

Material examined

1 ♀ (dissected on one slide) from 35 m depth in Sassenfjord, Spitzbergen; 1 ♂ (in alcohol) from 123 m depth in the same locality BMNH Reg. No. 1993.422. Collected by M. A. Kendall, July 1990.

Structurally the Spitsbergen specimens agreed with the original description based on material from 35 m depth at Bjornehodebukta in Oslofjord (Gee, 1988a) and have the same body ornamentation pattern. The dorsal, deeply incised hyaline frill on urosomite-1 described for *D. typica* Boeck, 1872 is also present in this species and supports the contention of Huys and Gee (1993) that this feature represents a diagnostic apomorphy for this genus. This is the first confirmed record of this species outside the type locality.

Danielssenia spitsbergensis sp. nov.

(Figs 21–26)

Material examined

HOLOTYPE 1 adult ♂ (dissected onto three slides) BMNH Reg. No. 1993.423 from a mud bottom at 30 m depth in Sassenfjord, Spitsbergen. Collected by M. A. Kendall, July 1990.

Description of male

Body (Fig. 21). Length 0·34 mm, more or less cylindrical with clear distinction between prosome and urosome. Cephalothorax and prosome unadorned. Urosomites-1–4 with row of spinules on dorsal and lateral posterior margin; urosomites-3–6 with row of long spinules on ventral posterior margin. Hyaline frill on P5-bearing somite deeply incised forming rectangular lappets, but minutely dentate on other urosomites. Pseudoperculum formed by deeply incised posterior extension of hyaline frill of penultimate somite. Anal somite deeply divided. Caudal rami about as long as broad ventrally with row of spinules on ventral posterior margin; seta I minute, seta IV and V minutely pinnate; seta V long, equal to total body length.

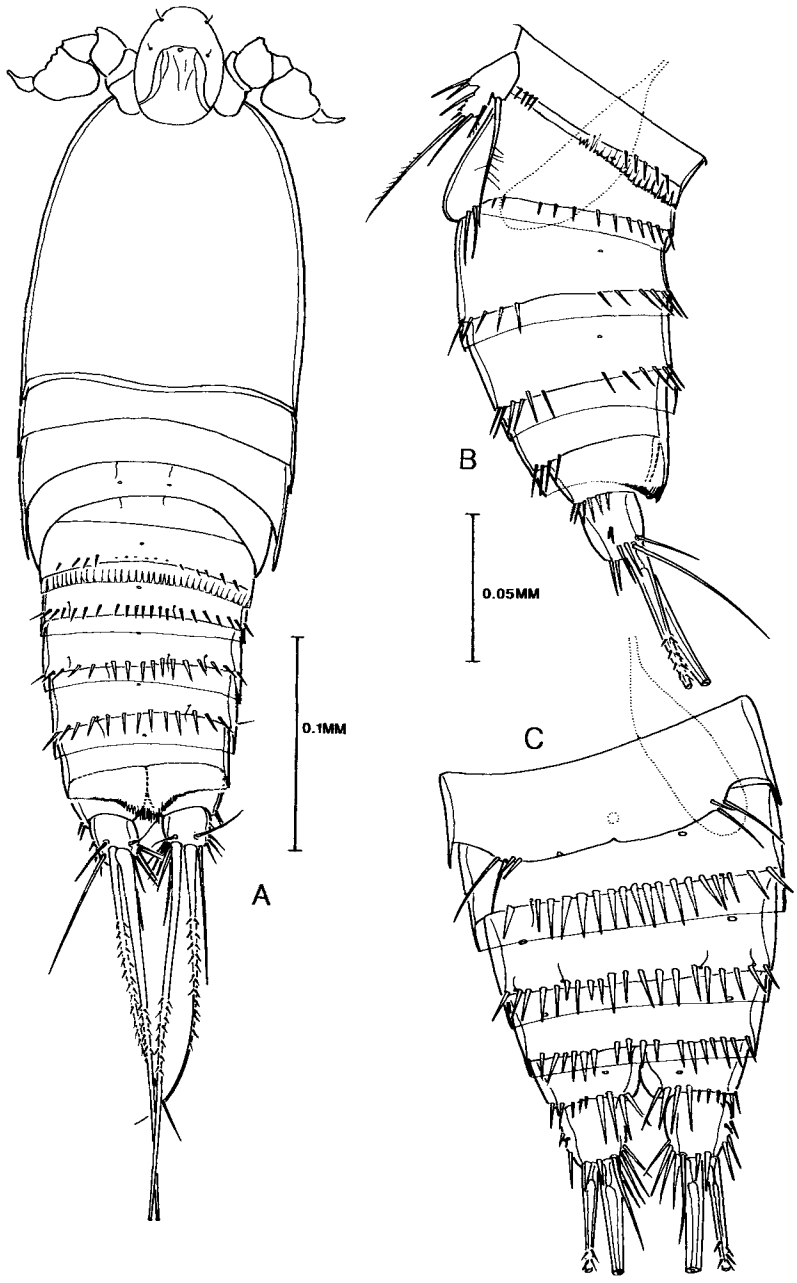

FIG. 21. *Danielssenia spitsbergensis*. Male: (A) habitus, dorsal; (B) urosome, lateral; (C) urosome, ventral excluding urosomite-1.

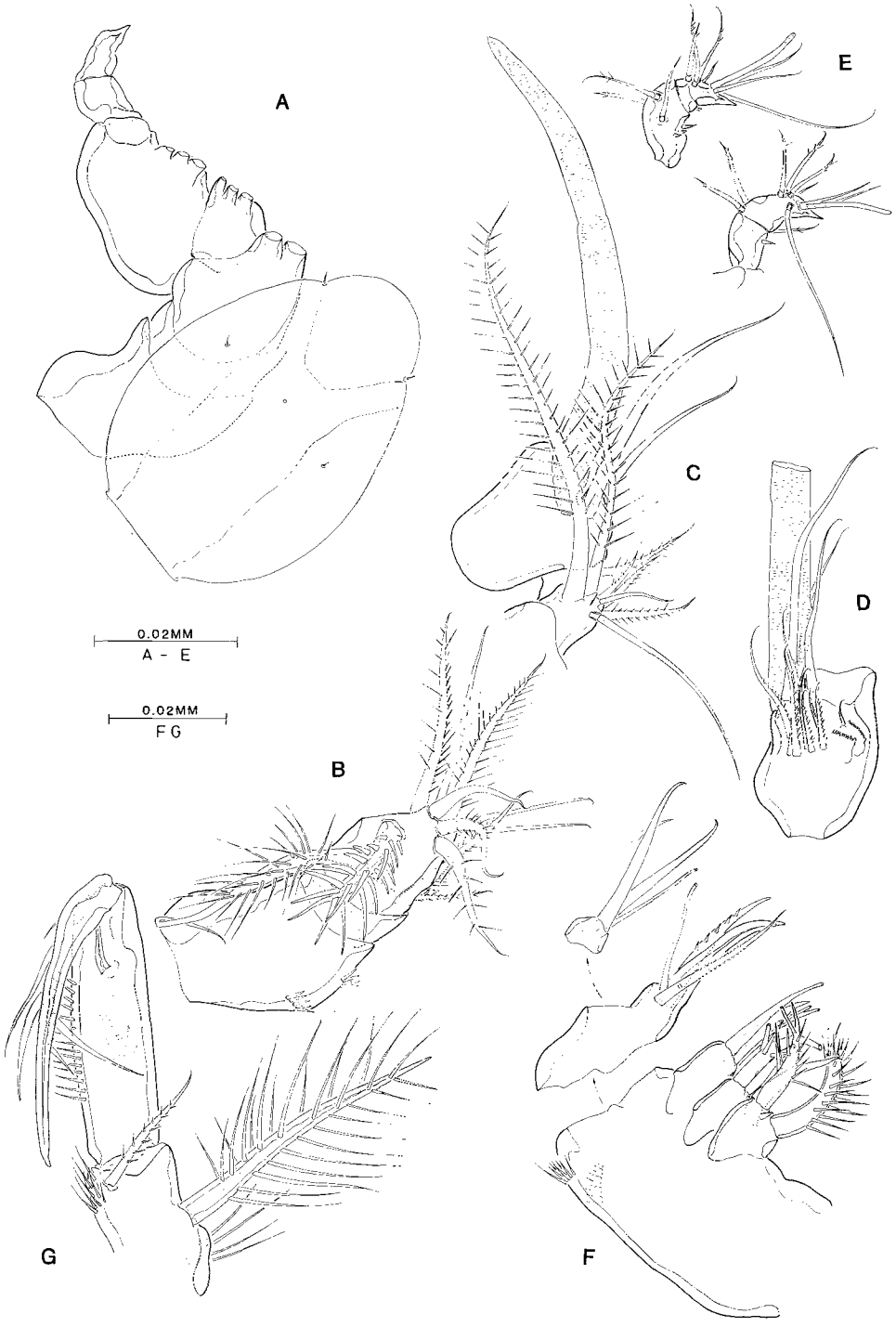

FIG. 22. *Danielssenia spitsbergensis.* Male: (A) rostrum and segmentation of antennule. Antennule: (B) segments-1–3; (C) segment-4; (D) segment-5; (E) segment-6 anterior and posterior view. (F) maxilla; (G) maxilliped.

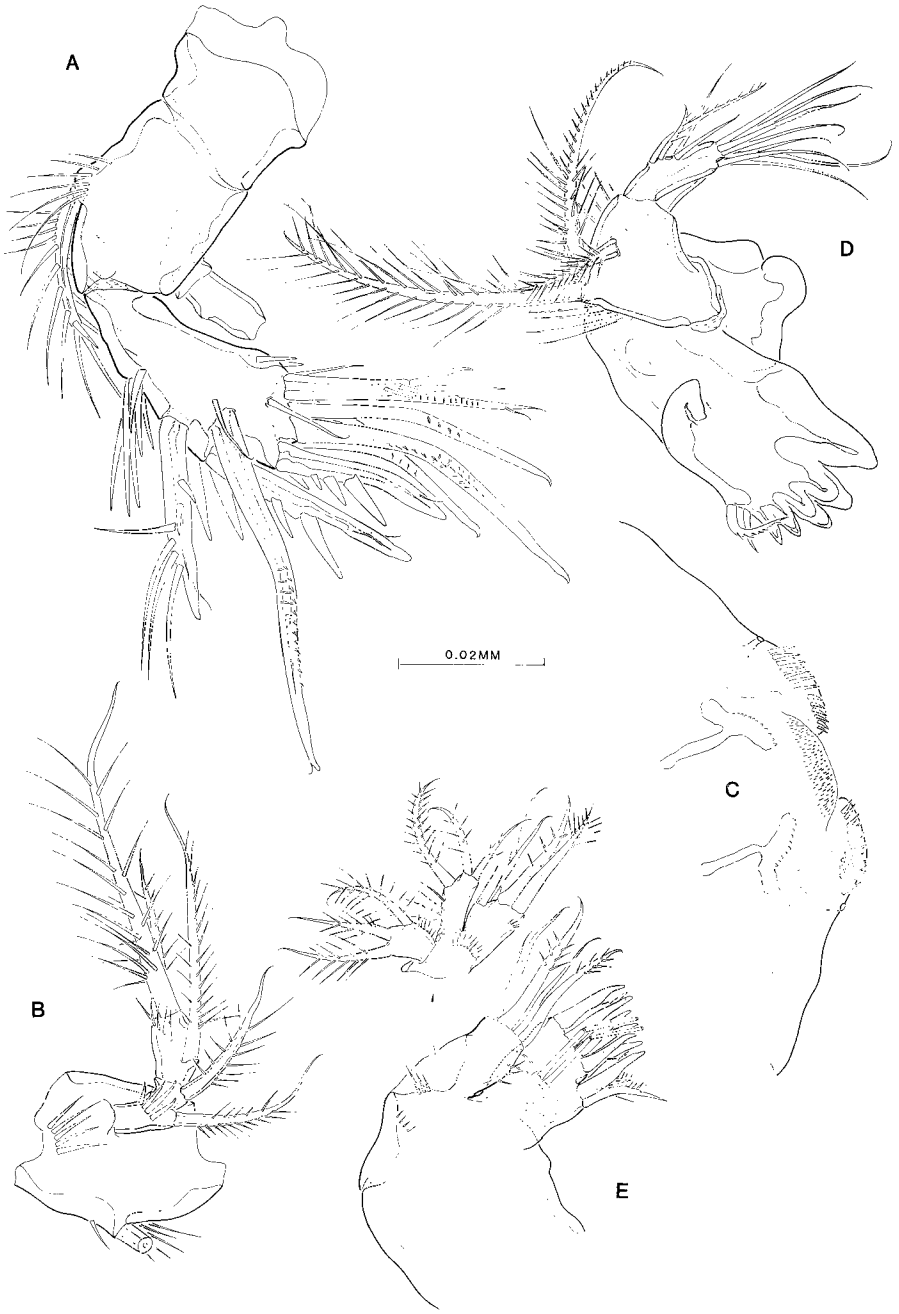

FIG. 23. *Danielssenia spitsbergensis.* Male: (A) antenna; (B) exopod of antenna; (C) labrum; (D) mandible; (E) maxillule.

FIG. 24. *Danielssenia spitsbergensis.* Male: (A) P1; (B) P4.

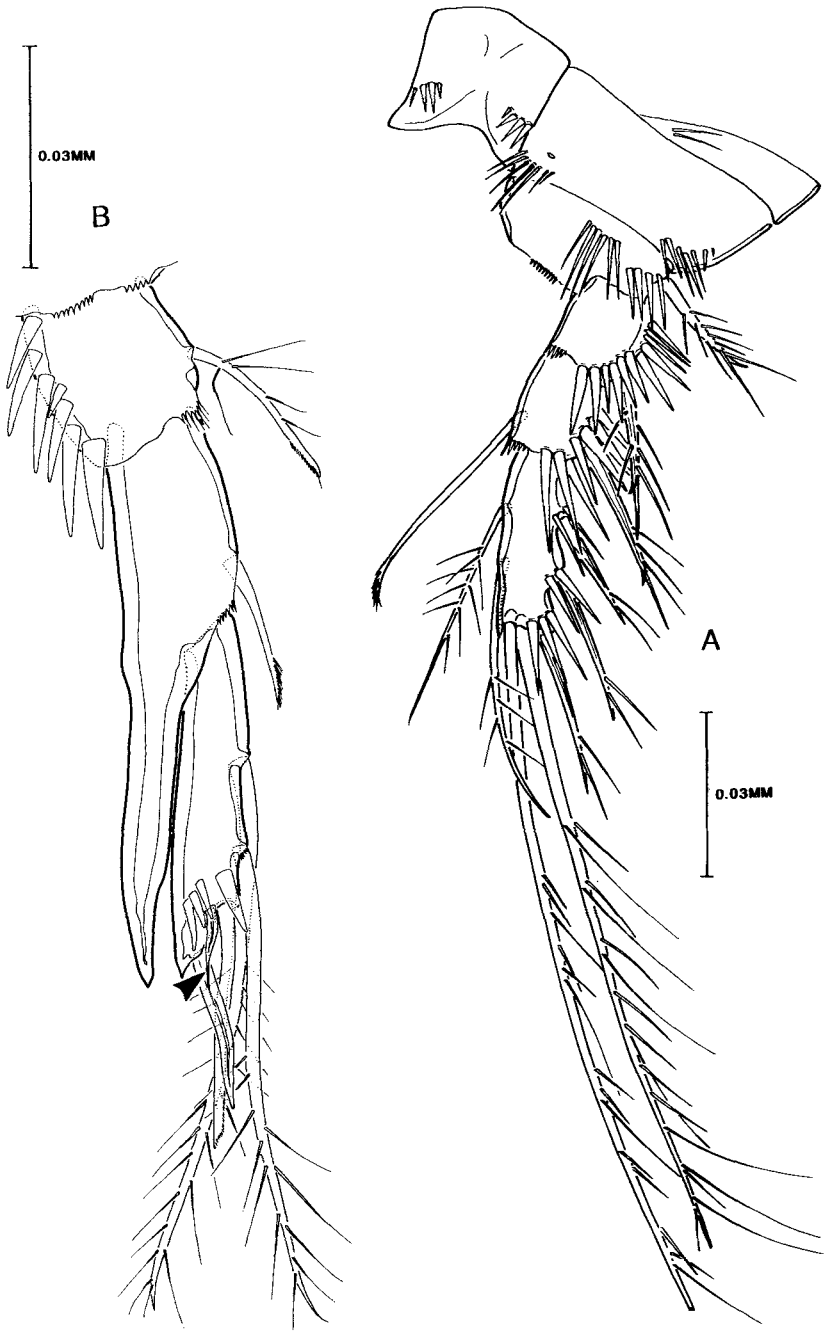

FIG. 25. *Danielssenia spitsbergensis.* Male P2: (A) protopod and exopod; (B) endopod.

FIG. 26. *Danielssenia spitsbergensis*. Male: (A) P3; (B) P3 endopod-2; (C) P5.

Rostrum (Fig. 22A). Large, oval, semi-hyaline, with a median pore and four sensilla.

Antennule (Fig. 22A–E). Chirocerate, 6-segmented with segment-5 moderately swollen. Segment-1 with two rows of spinules on anterior margin and a seta at anterior distal corner; segment-2 with one seta; segment-3 with 10 setae (six pinnate); segment-4 with 8 setae (six pinnate); segment-5 with 11 setae and an aesthetasc; segment-6 partially divided with 10 setae (six pinnate), a small aesthetasc and two setules and three spinules which are all modified setae.

Antenna (Fig. 23A, B). With well developed coxa. Allobasis with pinnate seta and row of spinules on abexopodal margin; spinule row at base of 3-segmented exopod (Fig. 23B) which bears 1-1-3 setae on proximal to distal segments respectively. Endopod with rows of spinules medially on anterior margin and subterminally on ventral surface; bearing two pectinate spines, a geniculate seta and a small naked seta sub-terminally and on distal margin a pectinate spine, four geniculate setae and two naked setae.

Labrum. Ornamented as in Fig. 23C.

Mandible (Fig. 23D). Coxa robust, gnathobase with well developed, bluntly rounded bicuspid teeth and a seta at distal dorsal corner. Basis with whorl of spinules on anterior face and two long and one short pinnate setae on distal margin. Endopod 1-segmented with three lateral and six terminal setae. Exopod 1-segmented with one lateral and two terminal setae.

Maxillule (Fig. 23E). Praecoxal arthrite with nine spines and one tubular seta on distal margin, two tube setae on anterior face and a row of spinules on posterior face; coxal endite with two pinnate setae, one naked seta and two tubular setae; basal endite with two pinnate and three naked setae. Rami 1-segmented each with three pinnate setae.

Maxilla (Fig. 22F). Praecoxal endite with two pinnate spines and one basally fused spine with a tubular extension; coxal endites with one spine and two tubular setae each; allobasis with two articulating spines, a pinnate seta and a tubular seta. Endopod 1-segmented with four setae.

Maxilliped (Fig. 22G). Syncoxa with small distal and large subdistal pinnate seta each with row of spinules at base. Basis with group of spinules on outer margin and a row of spinules and a small naked seta on palmar margin. Endopod represented by a spinulose claw bearing two accessory setae.

P1 (Fig. 24A). Intercoxal sclerite rectangular. Praecoxa with central row of spinules. Coxa with one row of large and four rows of small spinules on anterior face. Basis with row of spinules at base of inner and outer elements and centrally on distal margin; inner basal spine short, pectinate; outer basal seta well developed, pinnate. Exopod 3-segmented, outer spines with long pinnules; exopod-3 distal outer spine shorter than middle outer spine. Endopod 2-segmented, as long as exopod; endopod-2 not quite twice as long as endopod-1, with group of long strong spinules proximally on inner margin, inner seta implanted medially.

P2 (Fig. 25). Intercoxal sclerite almost square, ornamented with two rows of spinules. Praecoxa with central row of spinules. Coxa with spinule row at inner and outer distal corner. Basis with row of spinules at base of outer pinnate seta, centrally on anterior face and on median distal margin. Exopod-1 without inner seta. Endopod modified (Fig. 25B). Endopod-2 with a mucroniform process at outer distal corner reaching to the end of endopod-3; with one inner seta. Endopod-3 with distal inner seta not noticeably larger than proximal seta; two terminal setae reduced, smooth, inner one

with spatulate, dentate, tip, outer one minute (arrowed in Fig. 25B); distal outer spine recurved, articulating with segment.

P3–4 (Figs 24B, 26A, B). Intercoxal plate and protopod ornamented as for P2. Exopod-1 without inner seta; exopod-3 with only two outer spines. P3 endopod-2 with hooked apophysis at outer distal corner. Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	0.1.223	1.1.221
P3	0.1.222	1.1.121
P4	0.1.322	1.1.121

P5 (Fig. 26C). Elements fused medially, exopod fused to baseoendopod but distinguishable with faint suture line on posterior face. Baseoendopod outer seta relatively large, pinnate; endopodal lobe reduced, bearing two setae equal in length; exopodal lobe reduced with four setae, inner one short, spinous and inserted at a distance from outer three.

P6 (Fig. 21C). A single plate fused to somite bearing two setae and one or two spinules on each side.

Etymology

The specific name refers to the island containing the type locality.

Discussion

A single female with only two outer spines on P3–4 exopod-3 was also found in the same sample as this male but was lost after preliminary sorting. This is unfortunate as without the female it is very difficult to determine the exact taxonomic status of this species.

Danielssenia spitsbergensis exhibits almost all diagnostic features of the genus *Danielssenia* (as defined by Huys and Gee, 1993) which can be seen in the male, *viz.* a deeply divided dorsal hyaline frill on urosomite-1; the dentate border of the pseudoperculum; the structure of all the mouthparts; the absence of an inner seta on exopod-1 of P2–4; the detailed sexually dimorphic arrangement and modification of setae on endopod-3 of the male P2; and the presence of only two setae on the male P6. On the other hand, *D. spitsbergensis* does differ from the generic diagnosis of Huys and Gee (1993) in three respects (1) the mucroniform process on endopod-2 of the male P2 only reaches to the distal margin of endopod-3 whereas in all other species it reaches far beyond the distal margin; (2) the exopod of the male P5 is fused to the baseoendopod whereas in other species it articulates with the baseoendopod; (3) there are only two outer spines on exopod-3 of P3–4 whilst all other species have three outer spines on this segment. In other genera in the 'danielsseniid group' these features are almost always constant in the constituent species. None of them are unique however, and can be found in various combinations in a number of genera. For instance, in *Psammis* the mucroniform process on P2 endopod-2 only reaches the end of endopod-3 and the exopod of the male P5 is either fused or separate; and in *Telopsammis* the P5 exopod is fused and there are only two outer spines on exopod-3 of P3–4. Further, none of these features involve structural innovation but can be

derived merely as a result of reduction from the character state found in other species of *Danielssenia.*

For these reasons and because we have been unable to identify any autapomorphies on which a new genus could be erected, we have placed this species as *incertae sedis* within *Danielssenia* pending the discovery of the female. The segmentation of the female antennule and the detailed structure of the genital field, particularly the seminal receptacle, might provide definitive evidence as to the true taxonomic position of the species.

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