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Prionos gen. nov. from the Meiofauna of a Malaysian Mangrove Forest and the Status of *Psammis borealis* (Copepoda, Harpacticoida, Paranannopidae)

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Abstract: A new genus and species, *Prionos ornata*, is described from a Malaysian mangrove forest, representing the first member of the Paranannopidae recorded from the mangrove habitat. On the basis of female antennulary segmentation patterns *Prionos* gen. nov. is tentatively assigned to a clade grouping *Psammis*, *Danielssenia* and *Mucrosenia*, yet a full assessment of the phylogenetic relationships will have to await the discovery of the male. The type material of *Psammis borealis*, formerly placed *species incertae sedis* in the Paranannopidae, is re-examined. The unique sexual dimorphism has provided supporting evidence for its removal to a new genus *Anapophysia* together with a second closely related species *A. segonzaci* sp. nov. described from the deep sea off La Réunion. The detailed armature of the antennary endopod is used to place *Bathypsammis*, *Anapophysia* and *Fladenia* in a lineage leading to the deepwater genera *Paranannopus* and *Cylindronannopus*. The possible sistergroup relationship between *Bathypsammis* and *Anapophysia* is discussed.

Résumé : *Prionos gen. nov. de la méiofaune d'une forêt de mangrove de Malaisie et le statut de Psammis borealis (Copepoda, Harpacticoida, Paranannopidae).*
Une nouvelle espèce appartenant à un nouveau genre, *Prionos ornata*, est décrite de la forêt d'une mangrove de Malaisie et représente le premier membre de Paranannopidae signalé dans la mangrove. Le modèle de segmentation de l'antennule de la femelle nous permet de proposer le regroupement de *Prionos* gen. nov. dans un clade comprenant *Psammis*, *Danielssenia* et *Mucrosenia*, bien que l'étude des mâles soit nécessaire à l'établissement définitif de ces relations phylogénétiques. Le matériel type de *Psammis borealis*, primitivement placé comme espèce *incertae sedis* dans les Paranannopidae, est réexaminé. Le dimorphisme sexuel unique a conduit à la création d'un nouveau genre *Anapophysia*, comportant une seconde espèce très proche de *A. borealis*, *A. segonzaci* sp. nov., décrite des fonds océaniques au large de l'île de La Réunion. Les détails de l'endopodite de l'antenne sont utilisés pour placer *Bathypsammis*, *Anapophysia* et *Fladenia* dans une lignée conduisant aux genres *Paranannopus* et *Cylindronannopus* vivant dans les eaux profondes. Les éventuelles relations de parenté entre *Bathypsammis* et *Anapophysia* sont discutées.

Keywords : Copepoda, Harpacticoida, *Prionos* gen. nov., *Anapophysia* gen. nov., systematics.

Introduction

Paranannopidae are ubiquitous in the marine environment, occurring from tidal rock pools and sandy beaches to the abyssal zone. Surprisingly, the vast majority of the 49 valid species have been described from the North Atlantic and Mediterranean basin exclusively. Notable exceptions are *Archisenia sibirica* (Sars, 1898) which is essentially circumpolar (Huys & Gee, 1993), *Danielssenia typica* Boeck, 1872 whose distribution includes outliers in

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the Arctic, and three species described from abyssal muds in the Peru Trench: *Psammis longipes* Becker, 1974; *Paranannopus truncatus* Becker, 1979 and *P. longithorax* Becker, 1979. Apart from Becker's (1974, 1979) deep-sea species, there are only two other records from the Indo-Pacific: *Danielssenia spinipes* Wells, 1967 described from Inhaca Island (Mozambique) and recently transferred to a new genus *Afrosenia* (Huys & Gee, 1996), and *D. typica*, recorded from off Yentai (Chefoo) in the Yellow Sea by Shen & Bai (1956). An ecological study of meiofaunal diversity in Malaysian mangrove forests undertaken by one of us (JMG), resulted in the discovery of a new species of Paranannopidae to be described below. The Malaysian species is the first paranannopid to be recorded from the mangrove habitat and with the interstitial species *Micropsammis noodti* Mielke, 1975 and *Telopsammis secunda* (Mielke, 1975) only the third from the tidal zone.

In their review of the genus *Psammis* Sars, Huys & Gee (1993) made some brief comments on the validity and status of *P. borealis* Klie, 1939. A cursory examination based on Klie's type material from Iceland revealed no justification for maintaining *P. borealis* in *Psammis* nor for accommodating it in any of the existing genera and, consequently, the authors proposed to rank the species *incertae sedis* in the Paranannopidae. In this paper we have attempted to place *P. borealis* more confidently based on new observations of the type slides and additional information of a new, closely related species from the deep sea off La Réunion.

Methods

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Zeiss Axioskop microscope equipped with differential interference contrast.

The descriptive terminology applied to segmentation and setation of body appendages is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1 - P6, first to sixth thoracopods; exp, exopod; enp, endopod; exp(enp)-1(-2, -3), to denote the proximal (middle, distal) segment of a ramus.

Systematics

Family PARANANNOPIDAE Por, 1986

Prionos gen. nov.

Diagnosis. Paranannopidae. Body relatively small, dorsoventrally depressed, robust; with prosome distinctly wider than urosome. Rostrum large, elongate, defined at base; rounded anteriorly and tapering distally, not hyaline; with 1 pair of large frontal and 1 pair of small lateral sensilla. Pleural area of cephalothorax and pleurotergites of thoracic somites bearing P2-P4 strongly developed. Somatic hyaline frills well developed; deeply serrate on cephalothorax and somites bearing P2-P3, smooth on somites bearing P4-P5, dentate ventrally and serrate dorsally on genital double-somite and remaining urosomites. Female genital and first abdominal somites completely fused forming genital double-somite; original segmentation marked by dorsolateral and ventral subcuticular transverse ridges. Pseudoperculum hyaline with irregularly serrate margin. Caudal rami wider than long; with 7 setae: seta I vestigial, setae II-III and VI naked, setae IV-V well developed, presumably spinulose or pinnate; seta VII triarticulate at base. Sexual dimorphism unknown.

Female antennule short, indistinctly 5-segmented with segments 4 and 5 partly fused along anterior margin, distal segments very short; large aesthetasc on segment 3; segment 4 with 4 naked setae and 4 large, spinulose spines; segment 5 with apical acrothek consisting of aesthetasc, naked seta and spinulose spine.

Antennary allobasis with abexopodal seta; exopod 3-segmented, armature formula [2-1-3]. Labrum with ornate frontal face. Mandibular endopod, maxillulary basis and maxillary endopod without sensory aesthetascs. Mandibular coxa robust, with blunt teeth on gnathobase; basis with 3 (possibly 4?) pinnate setae; endopod 1-segmented, with 3 lateral and 6 distal elements; exopod 1-segmented with 2 lateral and 3 apical elements. Maxillule with 3 setae on exopod; endopod larger than exopod. Maxillary syncoxa with 3 elements on middle endite. Maxilliped subchelate; syncoxa with 2 pinnate spines; basis with short pinnate seta on palmar margin; endopodal claw with 1 short accessory seta.

P1 exopod 3-segmented, exp-3 with 3 outer spines (distal outer spine longer than middle outer spine) and 1 bipinnate spine plus 1 plumose seta apically; endopod 2-segmented, longer than exopod with enp-1 shorter than enp-2. P2-P4 with squarish, heavily ornate intercoxal sclerites; rami 3-segmented; exp-1 with inner seta; enp-1 reduced in size (particularly in P3-P4). Armature formula of P1-P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.2.221
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

Female P5 with free exopod bearing 4 short pinnate spines and 1 long plumose seta; endopodal lobe large, with 5 short pinnate spines.

Female genital field with relatively small copulatory pore and genital slit covered by vestigial P6 bearing 1 plumose seta and 2 vestigial elements; seminal receptacles fused medially, multichambered.

Etymology. - The generic name is derived from the Greek *prion*, meaning saw, and refers to the distinct serrate hyaline frills on the thoracic somites. Gender: feminine.

Type and only species. - *Prionos ornata* gen. *et* sp. nov.

Prionos ornata gen. *et* sp. nov.

Type locality. - Merbok river estuary, opposite Bukit Kechik, Kedah, Malaysia (5°38' N, 100°24' E); on slightly decomposed leaves of *Rhizophora apiculata* lying on muddy mangrove forest floor between HWTN and HWST.

Material. - Holotype ♀ dissected on 10 slides; deposited in The Natural History Museum, London under no. 1996.128; coll. J.M. Gee, March 1995.

Description.

FEMALE

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami: 410 µm. Body dorsoventrally depressed with prosome distinctly wider than urosome (Fig. 1A-B). Cephalothorax large and wide; pleural area well developed; posterior margin with deeply serrate hyaline frill (Fig. 1C); posterolateral corners angular. P2- to P4-bearing somites with strongly developed pleurotergites covering bases of swimming legs in lateral aspect; with transverse row of denticuliform spinules. Hyaline frill of P2- and P3-bearing somites deeply serrate, of P4- and P5-bearing somites plain.

Genital double-somite wider than long; original segmentation marked by internal chitinous ribs dorsolaterally, laterally and ventrally and similarly arranged spinular rows dorsolaterally and ventrolaterally (Figs 2C-D; 5D); anterior half with paired rows of tiny spinules laterally (Fig. 5D); posterior margin with tiny spinules ventrally, coarse spinules laterally and spinular row dorsolaterally. Hyaline frill serrate dorsally and dentate ventrally. Genital apertures fused medially forming common transverse genital slit; closed off by paired operculae derived from vestigial P6, each bearing outer pinnate seta and 2 vestigial elements (Fig. 2D). Midventral copulatory pore located closely to genital slit; relatively small; leading via short copulatory duct to multi-chambered median seminal receptacle (with ventral unpaired chamber leading to dorsal paired reservoirs posteriorly; Fig. 2E); seminal receptacle largely located anterior to genital slit.

Postgenital somites (Fig. 2D) with small spinules midventrally and paired ventrolateral groups of coarse spinules around posterior margin; first postgenital somite also with dorsolateral spinules; hyaline frills serrate dorsally and dentate ventrally. Anal somite deeply cleft medially (Figs 2C-D); ventral hind margin with minute spinules; anal operculum absent but replaced by membranous, irregularly serrate pseudoperculum derived from dorsal posterior margin of penultimate somite (Fig. 2C).

Caudal ramus (Figs 2C-D; 5D) slightly divergent, short, wider than long; with ventrolateral extension bearing 2 tube pores and overlying base of seta IV; with 7 setae. Seta I minute; setae II, III and VI slender and bare; setae IV and V well developed, broken but presumably spinulose or pinnate in posterior two-thirds, not fused basally, with predesigned fracture planes; seta VI bare; seta VII tri-articulate at base, naked.

Rostrum (Figs 1A-B; 2A) large and elongate, about 1.7 times as long as basal width; defined at base, anteriorly directed; not hyaline but with membranous margins laterally; rounded anteriorly; with 1 pair of minute dorsal sensilla and 1 pair of large frontal ones; with 1 median and 2 anterolateral pores dorsally.

Antennule (Fig. 3A-D) short, indistinctly 5-segmented with segments 4 and 5 partly fused along anterior margin; segment 1 with 3 spinular rows; segment 3 with large aesthetasc (62.5 µm); segment 4 with 4 naked setae and 4 large, spinulose spines; segment 5 with apical acrothek consisting of slender aesthetasc (33 µm), naked seta and spinulose spine. Armature formula: 1-[1 pinnate], 2-[1 naked + 7 pinnate + 1 spinulose spine], 3-[6 naked + 6 pinnate + (1+ae)], 4-[4 naked + 4 spinulose spines], 5-[5 + acrothek].

Antenna (Fig. 4A). Coxa represented by small sclerite with 2 spinular rows. Basis and proximal endopod segment completely fused forming allobasis; abexopodal margin with 1 bipinnate seta. Exopod 3-segmented; exp-1 and -3 with spinular row; hyaline frill of exp-2 dentate; armature formula [2-1-3]; proximal seta of exp-1 diminutive. Endopod (Fig. 4B) with 2 spinular rows laterally; lateral armature consisting of minute seta, and 1 geniculate spine flanked by 2 pinnate spines equipped with lateral flagella; distal armature represented by 1 naked and 4 geniculate setae (largest spiniform, with large spinules proximal to geniculation, and fused basally to vestigial seta), and 1 pinnate spine.

Labrum (Fig. 6A) strongly developed; anterior face with median secretory pore and raised spinular rows as figured; with patch of fine spinules between bases of antennae; distal margin with overlapping rows of fine spinules.

Mandible (Fig. 5A-B). Coxal gnathobase robust with multicuspidate blunt teeth as figured and 1 swollen bipinnate seta at dorsal corner. Palp biramous, consisting of basis and 1-segmented rami. Basis with 2 spinular rows and 3 setae (proximal plumose, middle and distal bipinnate); additional weakly defined scar (arrowed in Fig. 5B) found

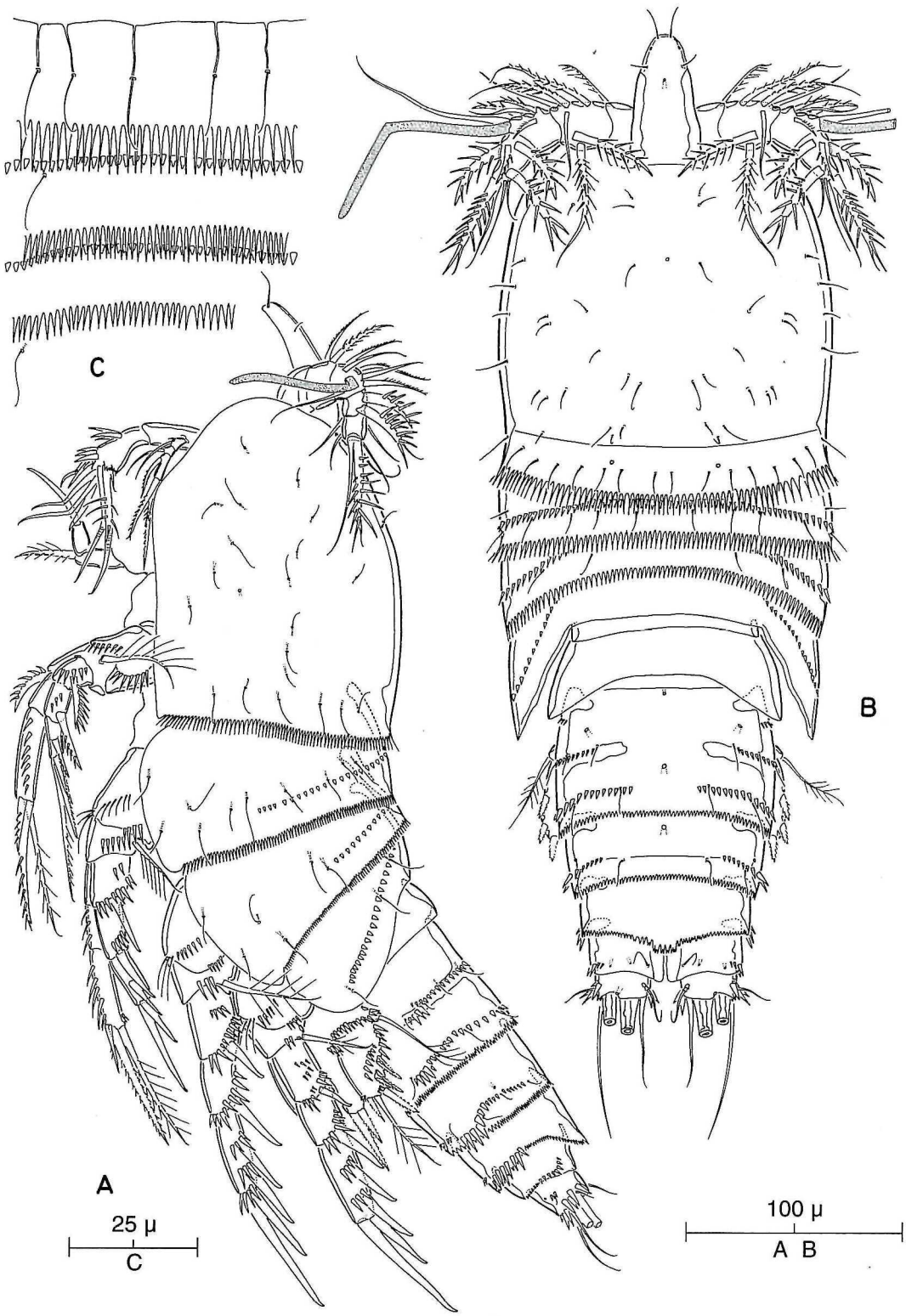

Figure 1. *Prionos ornata* gen. *et* sp. nov. (♀). A, habitus, lateral; B, same, dorsal; C, hyaline frills of cephalothorax and somites bearing P2-P3.

Figure 1. *Prionos ornata* gen. *et* sp. nov. (♀). A, habitus, vue latérale ; B, vue dorsale ; C, bords hyalins du céphalothorax et des somites portant P2-P3.

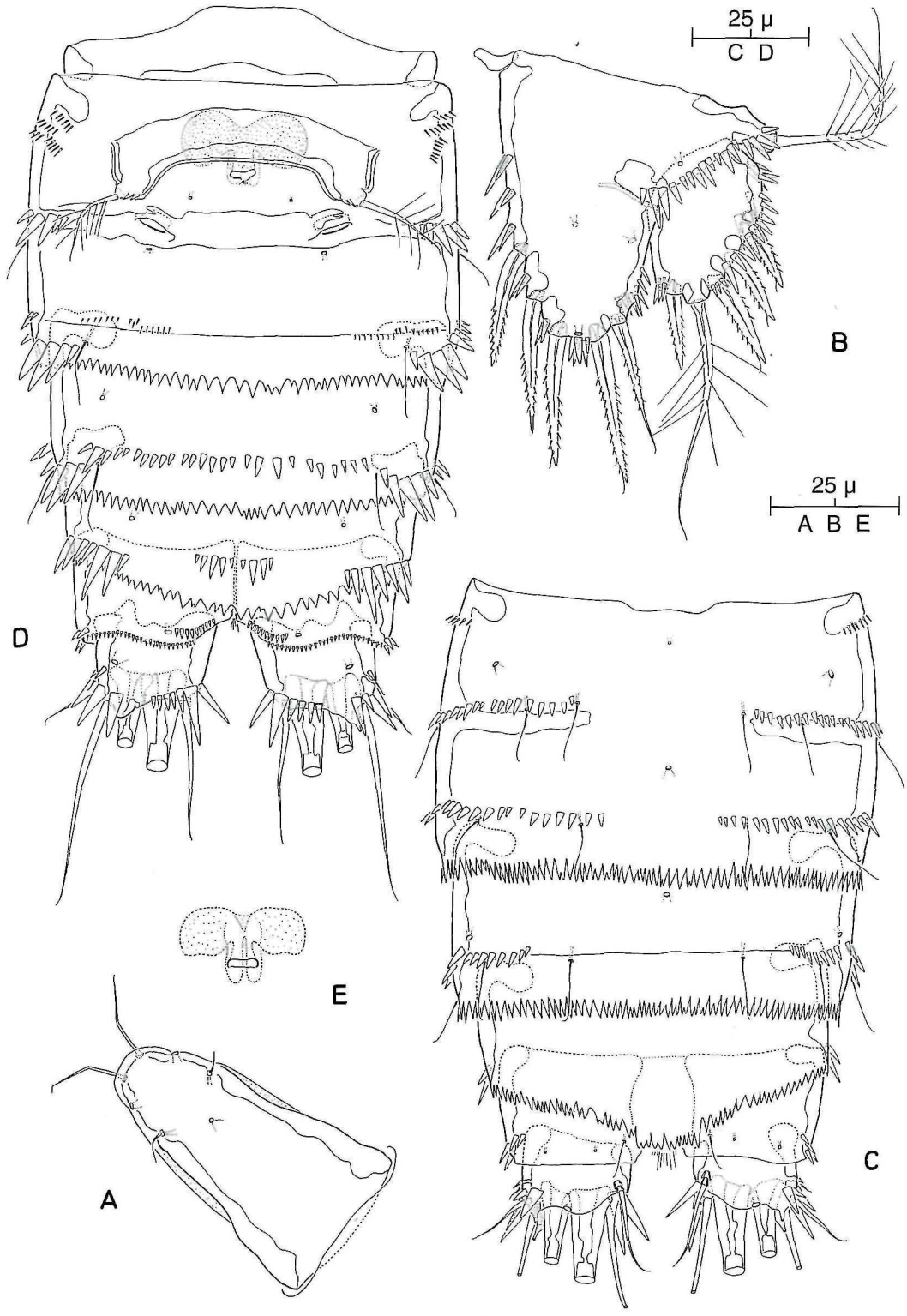

Figure 2. *Prionos ornata* (♀). A, rostrum; B, P5, anterior; C, urosome [excluding P5-bearing somite], dorsal; D, same, ventral; E, copulatory pore and seminal receptacles.

Figure 2. *Prionos ornata* (♀). A, rostre ; B, P5, vue antérieure ; C, urosome [sauf le somite portant P5], vue dorsale ; D, même région en vue ventrale ; E, orifice copulateur et réceptacles séminaux.

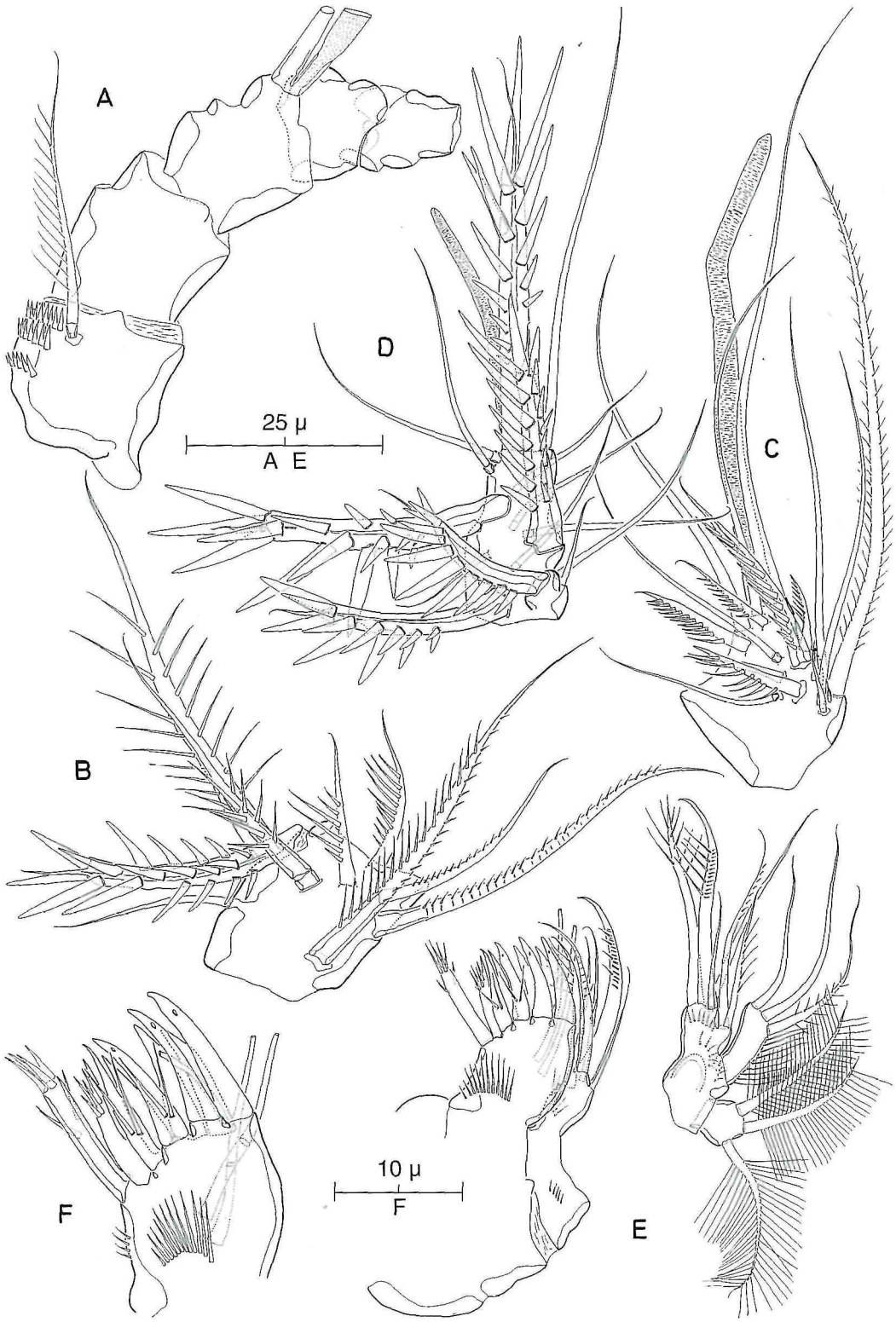

Figure 3. *Prionos ornata* (♀). A, antennule [armature of segments 2-5 omitted], ventral; B, antennulary segment 2, anterior; C, antennulary segment 3, anterior; D, antennulary segments 4 and 5, anterior; E, maxillule with disarticulated palp, posterior; F, maxillulary arthrite, posterior.

Figure 3. *Prionos ornata* (♀). A, antennule [armature des articles 2-5 omise], vue ventrale ; B, article antennulaire 2, vue antérieure ; C, article antennulaire 3, vue antérieure ; D, articles antennulaires 4-5, vue antérieure ; E, maxillule, avec palpe détaché, vue postérieure ; F, maxillule, arthrite, vue postérieure.

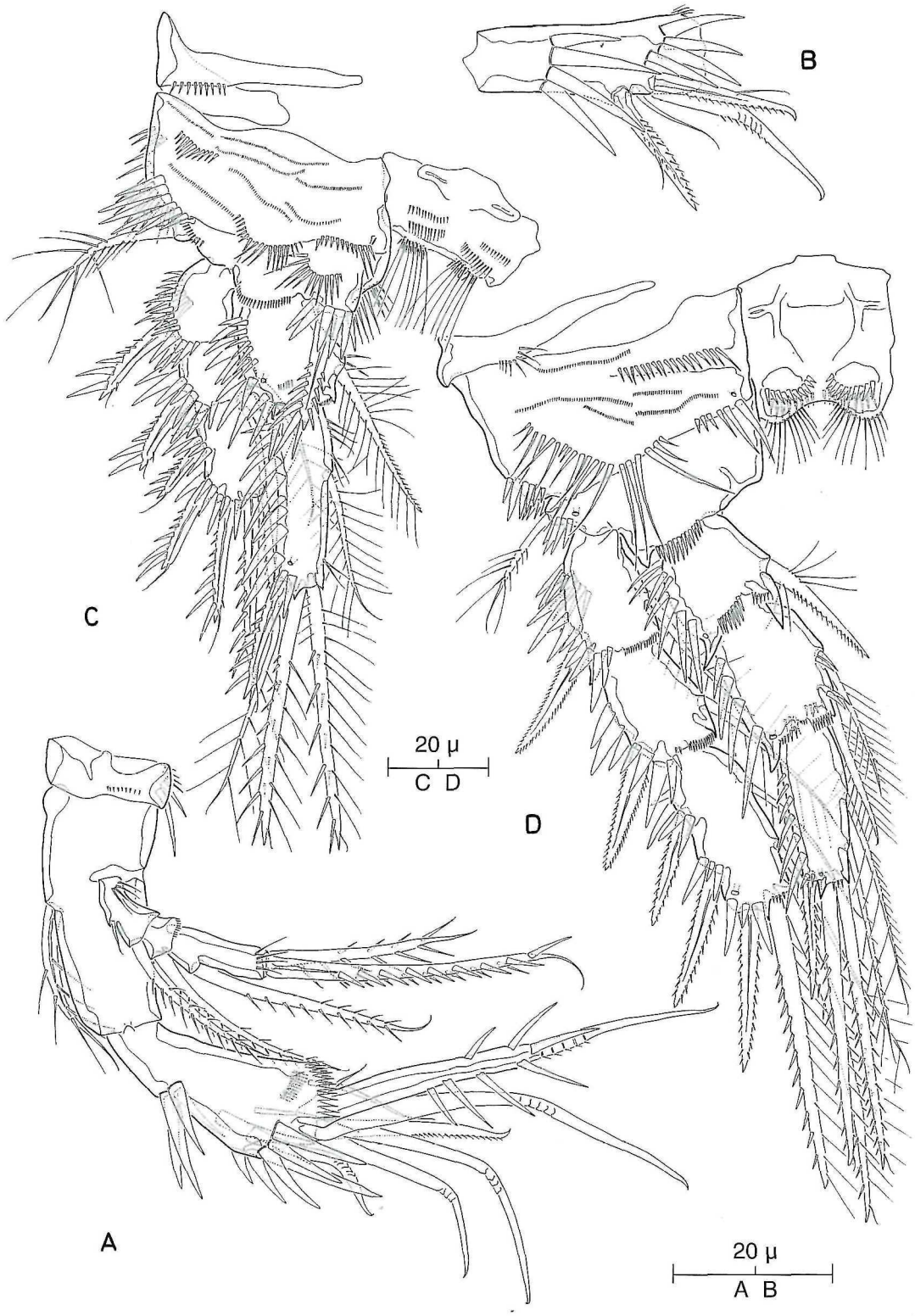

Figure 4. *Prionos ornata* (♀). A, antenna; B, antennary endopod [distal armature omitted]; C, P1, anterior; D, P2, anterior.

Figure 4. *Prionos ornata* (♀). A, antenne ; B, endopodite de l'antenne [armature distale omise] ; C, P1, vue antérieure ; D, P2, vue antérieure.

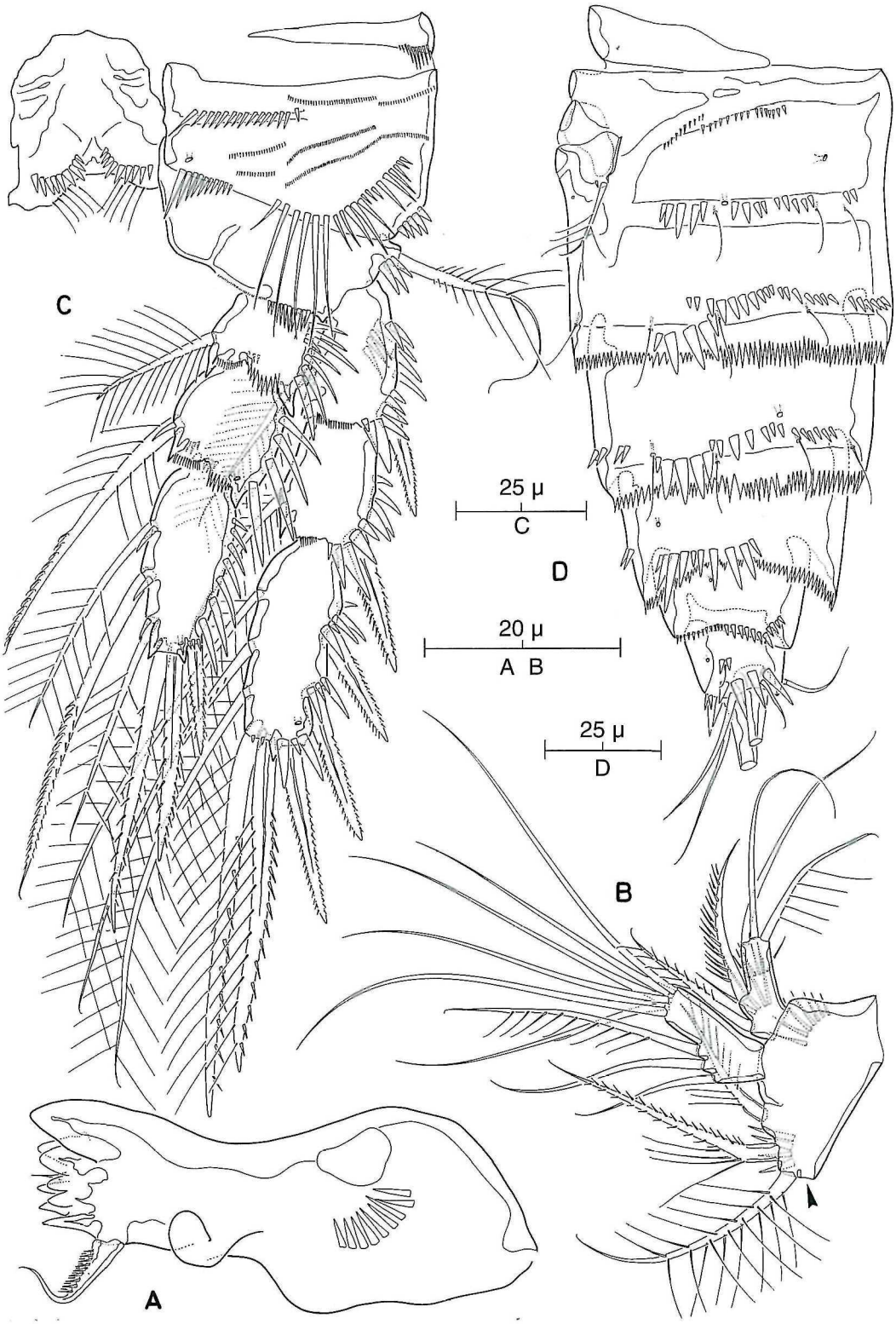

Figure 5. *Prionos ornata* (♀). A. mandibular gnathobase; B, mandibular palp [scar indicating possible fourth element on basis arrowed]; C, P3, anterior; D, urosome [excluding P5-bearing somite], lateral.

Figure 5. *Prionos ornata* (♀). A, gnathobase mandibulaire ; B, palpe mandibulaire [la flèche indique la soie manquante sur la base] ; C, P3, vue antérieure ; D, urosome [sauf le somite portant P5], vue latérale.

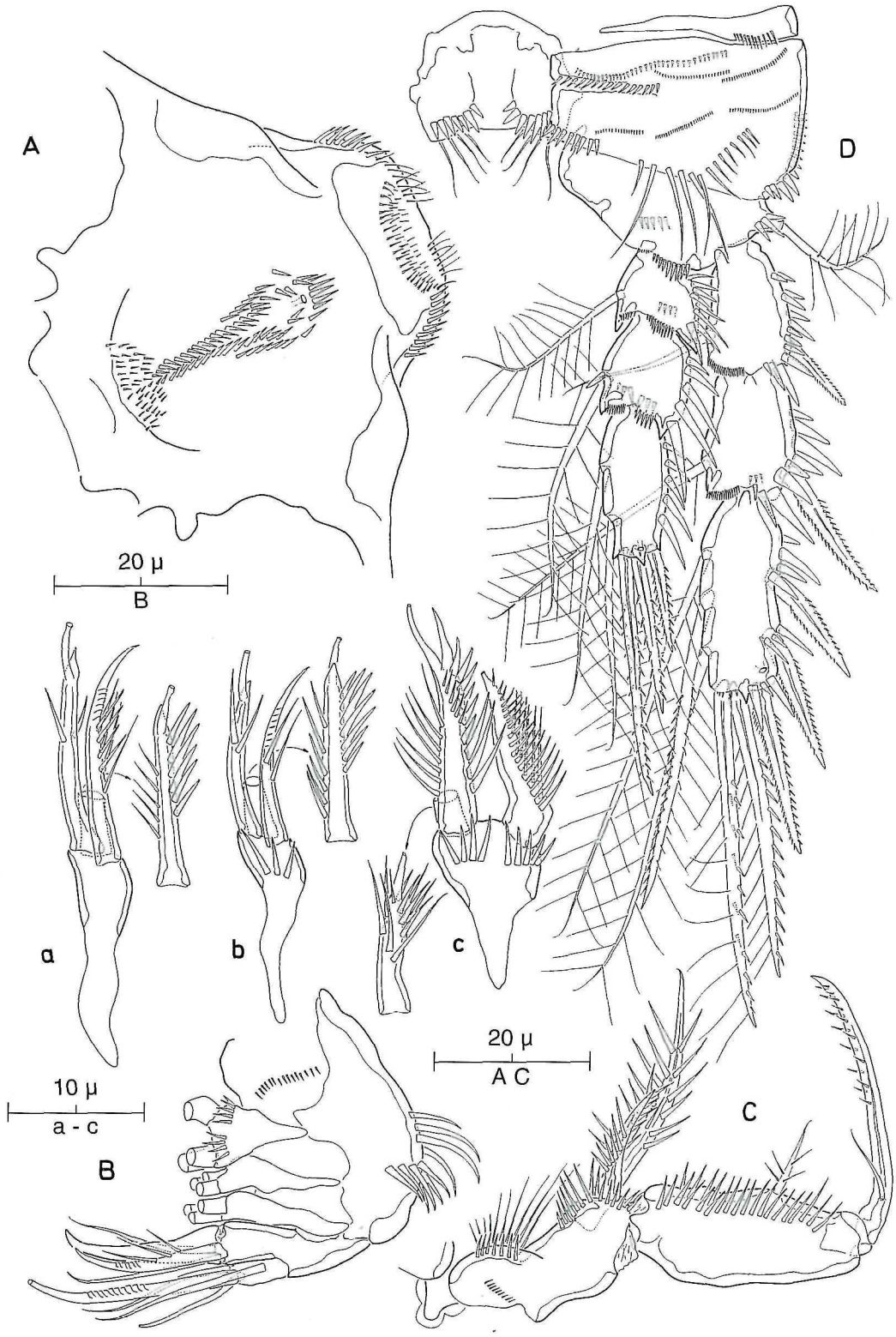

Figure 6. *Prionos ornata* (♀). A, labrum, anterior; B, maxilla [armature of syncoxal endites omitted], insets a-c showing distal, middle and proximal endites, respectively; C, maxilliped; D, P4, anterior.

Figure 6. *Prionos ornata* (♀). A, Labre, vue antérieure ; B, maxille [armature des endites syncoxaux omise], a-c : endite distal, médial et proximal ; C, maxillipède ; D, P4, vue antérieure.

proximal to plumose seta possibly indicating presence of fourth element. Exopod distinctly smaller than endopod; with 2 pinnate setae laterally, and 1 pinnate plus 2 naked setae apically; with 2 spinular rows on anterior surface. Endopod not elongate; lateral armature consisting of 1 pinnate and 2 naked setae; distal armature consisting of 6 naked setae.

Maxillule (Fig. 3E). Praecoxal arthrite represented by rectangular lobe with spinular comb on posterior and 2 geniculate tube setae on anterior surface (Fig. 3F); distal margin with 9 spines, dorsal ones with coarse spinules arranged around apex. Coxa with cylindrical endite bearing spinules along inner margin and 2 pinnate and 3 naked setae plus 1 pinnate claw distally. Basis with 2 closely set endites and 2 anterior spinular rows; proximal endite with 2 pinnate setae; distal endite with 1 geniculate, 1 pinnate and 2 naked setae. Exopod smaller than endopod; with 3 plumose setae. Endopod elongate; with 1 pinnate and 2 naked setae distally.

Maxilla (Fig. 6B, a-c). Syncoxa with 3 endites; proximal endite with 3 strongly pinnate spines (all elements defined at base and with tubular extension); middle and distal endites with 3 pinnate spines (2 with tubular extension); with spinular rows on proximal anterior surface, along outer margin and on proximal and middle endites. Allobasis drawn out into bare claw, largely defined at base; accessory armature consisting of 2 naked setae and 1 geniculate spine. Endopod 1-segmented, well defined at base; with 3 naked setae plus 1 swollen, pinnate tube seta.

Maxilliped (Fig. 6C) subchelate, inserted on small pedestal. Syncoxa with 4 spinular rows as figured, and 2 spinulose spines of unequal length. Basis with spinular row along palmar margin and short bipinnate seta. Endopod drawn out into strong, slightly curved bipinnate claw; accessory armature consisting of 1 short naked seta.

P1 (Fig. 4C). Intercoxal sclerite with long setules along distal margin, and spinules on both anterior and posterior surface. Praecoxa well developed, with spinular row. Coxa with complex pattern of spinules on anterior surface as indicated in Fig. 4C. Basis with pinnate outer seta and strong pinnate spines at inner distal corner. Exopod 3-segmented; outer spines with coarse spinules increasing in length towards apex and with subapical flagella; exp-3 with 4 unipinnate spines and 1 sparsely plumose seta. Endopod 2-segmented, distinctly longer than exopod; enp-1 wider and clearly shorter than enp-2, with spinulose distal and outer margins and with distally serrate, plumose seta along inner margin; enp-2 with inner plumose seta and distal armature consisting of plumose seta and 2 strong pinnate spines.

P2-P4 (Figs 4D; 5C; 6D) with squarish intercoxal sclerites ornamented with setules distally and coarse spinules anteriorly (in P2 also with spinules posteriorly). Praecoxae with anterior spinular row. Coxae with spinular pattern as figured. Basis with outer pinnate or plumose seta. Rami 3-segmented; outer margins of segments with coarse spinules. Endopods distinctly shorter than exopods in P3-P4. P2-P4 enp-1 reduced in size; inner margin with pinnate spine (P2), plumose spine (P3) or plumose seta (P4). Middle inner seta of P4 exp-3 spiniform and pinnate. Armature formula as for genus.

P5 (Fig. 2B) biramous, comprising oval exopod and large baseoendopod. Intercoxal sclerite minute. Exopod not extending beyond endopodal lobe; inner margin with short bipinnate spine; outer margin with 3 short bipinnate setae, equipped with subapical flagella and increasing in length distally; apex with long sparsely plumose seta. Baseoendopod with anterior secretory pores at distal margin and near articulation with exopod, with 2 posterior ones on endopodal lobe; outer basal seta slender and sparsely plumose, inserted on short setophore; endopodal lobe with slightly stepped inner margin bearing 3 short bipinnate spines, outer distal margin with 1 bipinnate seta and 1 bipinnate spine. Spinular ornamentation around insertion sites of spines, along inner margin of endopodal lobe, around articulation of exopod.

MALE. Unknown.

Etymology. - The specific name refers to the elaborate ornamentation of the body and swimming legs.

Discussion

Prionos is one of the few parannanopid genera that has retained the most primitive armature on the swimming legs. The ancestral formula combining the presence of three inner setae on P3-P4 exp-3 and P3 enp-3, and two inner setae on P2 enp-2 has thus far been found only in representatives of the genus *Jonesiella* Brady and in the problematic species *Psammis borealis* which is to be referred to a new genus *Anapophysia* (see below). The presence of two inner setae on the middle endopod segment of P2 is also found in *Psammis* and *Bathypsammis* Huys & Gee, however these two genera exhibit significant reductions on other swimming leg segments.

One of the main characteristics separating *P. ornata* from other paranannopids is the presence of typically incised hyaline frills on the cephalothorax and free body somites. Distinctive somatic frills have only been reported for a few genera such as *Danielssenia* where the P5-bearing somite displays a deeply serrate frill (Huys & Gee, 1993; Gee & Huys, 1994) and in the advanced genera *Micropsammis*, *Telopsammis* and *Leptotachidia* where it forms distinct lappets on the urosomites (Gee & Huys, 1991). The condition in *Prionos* resembles that of *Afrosenia spinipes* (Wells, 1967) where all body somites are bordered with an incised hyaline frill (Huys & Gee, 1996), however in the latter the frills form large lappets which differ in form and shape between the prosome and urosome.

Identification of the sistergroup of *Prionos* is severely hampered by the lack of information on the male. Knowledge on the structure and homology of sexual dimorphism has proven pivotal in reconstructing the evolutionary history of the Paranannopidae (Huys & Gee, in prep.) and taxa that are known from one sex only are therefore difficult to position on the phylogenetic tree. Such taxa, whose relationships have to be regarded as tentative, include the genera *Bathypsammis* and *Mucrosenia* which are known from females only and *Danielssenia spitsbergensis* Gee & Huys, 1994 for which only the male has been recorded (Huys & Gee, 1993; Gee & Huys, 1994).

Within the Paranannopidae a well defined genus group can be recognized which is characterized by the presence of sensory aesthetascs on the mouthparts (Huys & Gee, 1996). This lineage includes *Jonesiella*, *Paradanielssenia* Soyer, *Leptotachidia* Becker, *Micropsammis* Mielke, *Telopsammis* Gee & Huys, *Peltisenia* Huys & Gee and *Sentiropsis* Huys & Gee. The absence of such oral aesthetascs precludes *Prionos* from being accommodated in this complex, consequently narrowing down the discussion on relationships to the other genera contained in the danielsseniid lineage: *Danielssenia* Boeck, *Psammis*, *Archisenia* Huys & Gee, *Mucrosenia* Gee & Huys and *Afrosenia* Huys & Gee. The deepwater genera *Fladenia* Gee & Huys and *Bathypsammis* are not considered here for reasons explained below (see discussion of *Anapophysia*).

An appendage of central importance in determining the possible affiliations of *Prionos* is the female antennule. Within the danielsseniid lineage the 5-segmented condition of this appendage is found only in *Prionos*, *Afrosenia* and *Leptotachidia*, however, only in the former this condition has arisen through fusion of segments 2 and 3 of the ancestral 6-segmented condition (as found in e.g. *Archisenia*). Using the position of the large aesthetasc as a reference point in *Afrosenia* and *Leptotachidia* shows the distal segment to be a compound one resulting from fusion (or failure to separate) of ancestral segments 5 and 6. In *P. ornata* the antennule can be regarded as indistinctly 5-segmented due to the incomplete suture between the apical segments and is therefore a transitionary stage leading to the 4-segmented condition found in *Psammis*, *Danielssenia* and *Mucrosenia*. The fusion of ancestral segments 2 and 3 is regarded here as a synapomorphy linking *Prionos* to these genera. Within this group there is little doubt that *Mucrosenia* and *Danielssenia* are most closely related. This sistergroup relationship is supported by the shared lack of the inner seta on P2-P4 exp-1, the presence of only 3 setae on the mandibular basis, the loss of an inner seta on P2 enp-2 and by a [1-1-2] armature formula on the antennary exopod (Gee & Huys, 1994). *Psammis* can be related to this clade on the basis of the following synapomorphies: (a) 4-segmented ♀ antennule, (b) P3 exp-3 with maximum of 2 inner setae. The primitive setation pattern of the swimming legs in conjunction with the 5-segmented antennule, the [2-1-3] antennary exopod formula and the probable presence of 4 setae on the mandibular basis indicate that *Prionos* occupies a basal position in the *Psammis-Danielssenia-Mucrosenia* clade. The characteristic shape of the rostrum, the somatic frills on the cephalothorax and free body somites (except P5-bearing somite) and the stubby facies of the setation elements on the female P5 serve as autapomorphies to define the new genus.

Anapophysia gen. nov.

Diagnosis. - Paranannopidae. Body very large, not dorsoventrally depressed; with prosome not distinctly wider than urosome. Rostrum large, rectangular, slightly longer than wide, defined at base; rounded anteriorly, not hyaline; with 1 pair of long frontal and 1 pair of minute dorsal sensilla. Pleural area of cephalothorax and pleurotergites of thoracic somites bearing P2-P4 hyaline. Somatic hyaline frills plain on cephalothorax and somites bearing P2-P4, minutely dentate on P5-bearing somite, genital double-somite and remaining urosomites. Female genital and first abdominal somites completely fused forming genital double-somite; original segmentation marked by lateral and laterodorsal sub-cuticular transverse ridges. Pseudoperculum moderately developed with minutely dentate margin. Caudal rami wider than long; with 7 setae: seta I vestigial, setae II and VI naked, setae IV-V well developed and multipinnate (seta IV swollen at base); seta VII triarticulate at base. Sexual dimorphism in antennule, P2 endopod (inner distal seta of enp-3 modified), P3 endopod (enp-3 with long spinous apophysis), P5, P6 and in genital segmentation.

Antennule ♀ short, 4-segmented; with large aesthetasc on segment 3; segment 4 with apical acrothek consisting of aesthetasc, naked seta and spinulose spine; all segments with pinnate setae and/or spines. Antennule ♂ 7-segmented and subchirocer; geniculation between segments 5 and 6; with aesthetasc on segment 3 and as part of apical acrothek on segment 7.

Antennary allobasis with abexopodal seta; exopod 3-segmented, armature formula [2-1-3]. Labrum with ornate frontal face. Mandibular endopod, maxillulary basis and maxillary endopod without sensory aesthetascs. Mandibular coxa robust, with sharp and multicuspidate blunt teeth on gnathobase; basis with 4 pinnate setae; endopod 1-segmented, with 3 lateral and 6 distal elements; exopod 1-segmented with 2 lateral and 3 apical elements. Maxillule with 3 setae on exopod. Maxillary syncoxa with 3 elements on middle endite. Maxilliped subchelate; syncoxa with 2 pinnate spines; basis with short pinnate seta on palmar margin; endopodal claw with 1 short accessory seta.

P1 exopod 3-segmented, exp-3 with 3 outer spines (distal outer spine as long as middle outer spine) and 1 bipinnate spine plus 1 plumose seta apically; endopod 2-segmented, shorter than exopod with enp-1 and enp-2 equally long. P2-P4 with rectangular intercoxal sclerites; rami 3-segmented; exp-1 with inner seta. Armature formula of P1-P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.2.221
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

P5 with exopod and baseoendopod fused forming slightly bilobed plate in both sexes; exopodal lobe with 1 small and 3 large setae/spines; endopodal lobe with 2 pinnate spines and accessory spinous process in ♀, with 2 pinnate spines in ♂. Fifth pair of legs medially fused in ♂.

Female genital field with relatively small copulatory pore and genital slit covered by vestigial P6 bearing 1 plumose seta and 2 short naked setae; seminal receptacles fused medially, multichambered. Male P6 slightly asymmetrical, with 3 setae.

Etymology. - The generic name is derived from the Greek *an*, not, *apo*, away, and *phyein*, to grow, and refers to the absence of a spinous apophysis on P2 enp-2. Gender: feminine.

Type species. - *Psammis borealis* Klie, 1939 = *Anapophysia borealis* (Klie, 1939) comb. nov.

Other species. - *A. segonzaci* sp. nov.

Anapophysia borealis (Klie, 1939) comb. nov.

Type locality. - North Atlantic; off Iceland.

Material. - Syntypes deposited in the Zoologisches Museum der Universität Kiel: (a) Stn 126, 67°19 N, 15°52' W; depth 527 m; 30 July 1896: 1 ♀ dissected on 2 slides (Cop. 214-215) and 1 ♀ dissected on 1 slide (Cop. 212); (b) Stn 128; 66°50' N, 20°02' W; depth 349 m; 02 August 1896: 1 ♂ (Cop. 211) and 1 ♀ (Cop. 213) dissected on 1 slide each; collected during Danish Ingolf Expedition.

Redescription

The following redescription is intended to supplement Klie's (1939, 1941) original descriptions which are detailed and accurate in most aspects but present illustrations only of the mandible, maxilliped, ♀ genital field, ♂ P2 and P5 of both sexes.

FEMALE

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami 1.8 mm according to Klie (1939, 1941).

Genital double-somite wider than long (but slightly squashed in Fig. 7D); original segmentation marked by internal chitinous ribs laterodorsally and laterally, and by transverse spinular rows dorsally and ventrolaterally (Fig. 7D); anterior half with paired rows of tiny spinules dorsolaterally. Hyaline frill minutely dentate. Genital apertures fused medially forming common transverse genital slit; closed off by paired operculae derived from vestigial P6, each bearing outer sparsely plumose seta and 2 short naked setae (Fig. 9D). Midventral copulatory pore located halfway the genital double-somite; relatively small; leading via short copulatory duct to multi-chambered median seminal receptacle (with ventral unpaired chamber leading to dorsal paired reservoirs posteriorly); seminal receptacle largely located anterior to genital slit.

Postgenital somites (Fig. 7D) with minutely dentate hyaline frill and with dorsal spinule row around posterior margin. Anal somite deeply cleft medially (Fig. 7D), outer distal corners with spinular rows; anal operculum absent but replaced by membranous, minutely dentate pseudoperculum derived from dorsal posterior margin of penultimate somite.

Caudal ramus (Fig. 7D) slightly divergent, short, wider than long; with 7 setae. Seta I minute; setae II and VI short and bare; seta III unipinnate; setae IV and V well developed and multipinnate, base of seta IV distinctly swollen (Fig. 7D).

Rostrum (Fig. 9A) large, rectangular, about 1.2 times as long as basal width; defined at base, anteriorly directed; not hyaline; rounded anteriorly; with 1 pair of minute dorsal sensilla at about halfway the rostrum length and 1 pair of large frontal ones; with 1 middorsal and 2 anteroventral pores.

Antennule short, 4-segmented; segment 3 with large aesthetasc; segment 4 (Fig. 7A) with apical acrothek consisting of slender aesthetasc (50 µm), naked seta and spinulose spine. Armature formula: 1-[1 pinnate], 2-[1 naked + 7 pinnate + 1 plumose], 3-[7 naked + 8 pinnate + (1+ae)], 4-[2 naked + 5 plumose + 6 spinulose + acrothek].

Antenna (Fig. 8A). Coxa represented by sclerite with spinular row. Basis and proximal endopod segment completely fused forming allobasis; abexopodal margin with 1 bipinnate seta; outer surface with row of long spinules. Exopod 3-segmented; armature formula [2-1-3]. Endopod with 2 spinular rows laterally; lateral armature consisting of sparsely plumose seta, and 1 geniculate spine flanked by 2 spines (1 bipinnate, 1 smooth) equipped with lateral flagella; distal armature represented by 1 naked and 4 geniculate spines (longest with large spinules proximal to geniculation, and fused basally to unipinnate seta), and 1 bipinnate spine (indicated by filled circle in Fig. 8A).

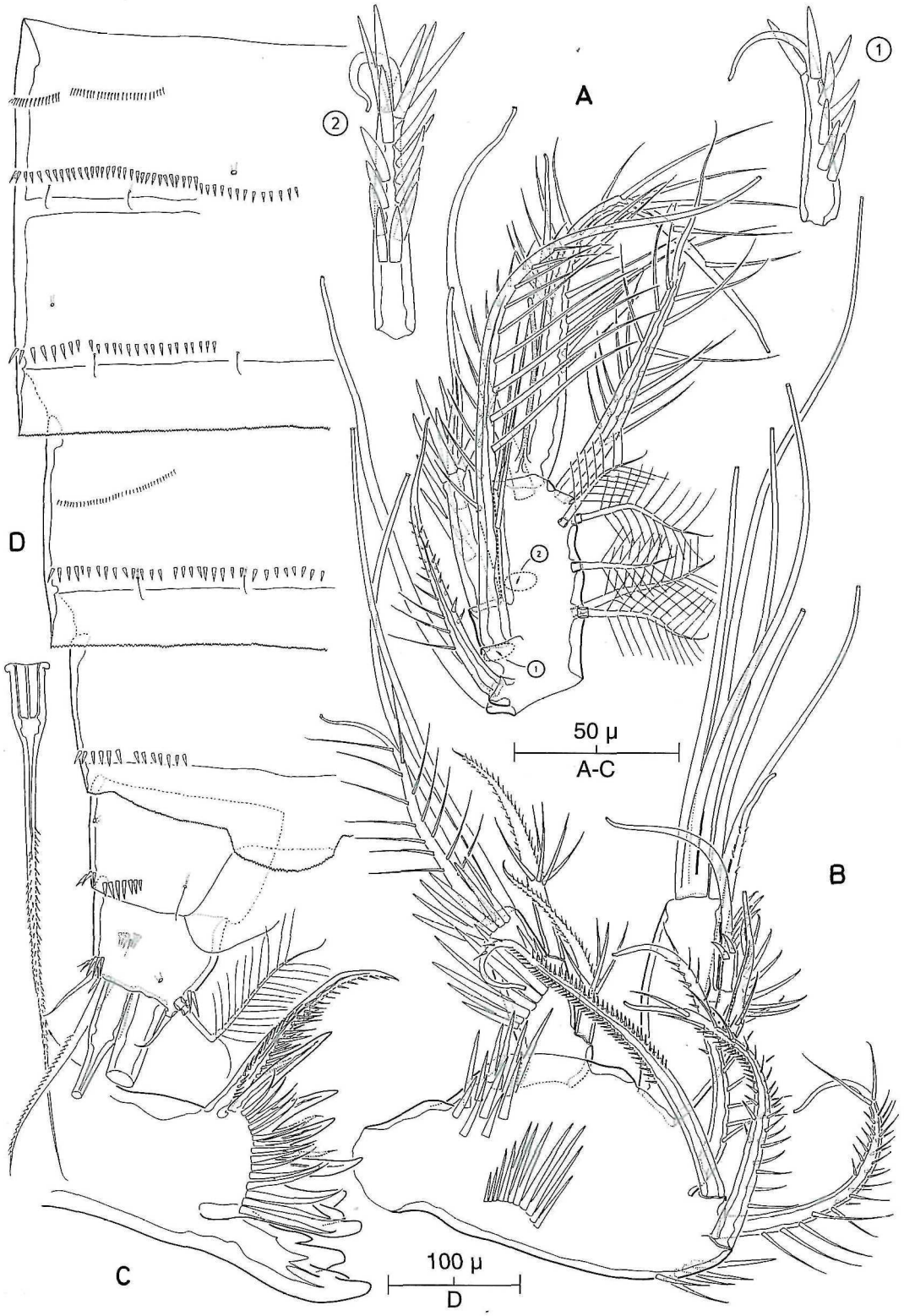

Figure 7. *Anapophysia borealis* (Klie, 1939) comb. nov. (♀). A, antennulary segment 4 [insets 1-2 showing spinulose spines]; B, mandibular palp; C, mandibular gnathobase; D, urosome [excluding P5-bearing somite], dorsal [inset showing seta IV].

Figure 7. *Anapophysia borealis* (Klie, 1939) comb. nov. (♀). A, article antennulaire 4 [encarts 1-2 : épines barbelées] ; B, palpe mandibulaire ; C, gnathobase mandibulaire ; D, urosome [sauf le somite portant P5], vue dorsale [encart : soie IV].

Mandible (Figs 7B-C). Coxal gnathobase robust with multicuspidate blunt teeth ventrally and sharper teeth plus 1 bipinnate seta dorsally. Palp biramous, consisting of basis and 1-segmented rami. Basis with 3 spinular rows and 4 large pinnate setae. Exopod slightly smaller than endopod; with 2 pinnate spines (with radiating spinules) laterally, and 1 pinnate plus 2 naked setae apically; with 2 spinular rows on anterior surface. Endopod not elongate; lateral armature consisting of 1 minutely pinnate and 2 spinulose setae; distal armature consisting of 6 naked setae fused basally in two clusters (4+2).

Paragnaths (Fig. 8B) strongly developed; with elaborate ornamentation as figured.

Maxillule (Fig. 9B). Praecoxal arthrite represented by rectangular lobe with proximal spinular row on posterior and 2 geniculate tube setae on anterior surface; distal margin with 9 spines and 1 tube seta. Coxa with cylindrical endite bearing spinules along inner margin and 3 pinnate and 2 naked setae plus 1 pinnate claw distally. Basis with endites completely amalgamated, bearing total 4 pinnate and 2 naked setae. Exopod oval-shaped, larger than endopod; with 3 plumose setae. Endopod elongate; with 1 naked and 2 pinnate setae distally.

Maxilla (Fig. 8C). Syncoxa with 3 endites; proximal endite with 3 strongly pinnate spines (2 defined at base, 1 fused to endite; proximal spine enlarged with medially directed spinules); middle and distal endites with 3 pinnate spines (2 with tubular extension; anterior one partly fused to endite). Allobasis drawn out into minutely pinnate claw; accessory armature consisting of 1 naked and 1 pinnate seta. Endopod 1-segmented, well defined at base; with 1 pinnate plus 3 naked setae.

Maxilliped (Fig. 8D) subchelate. Syncoxa with 4 spinular rows as figured, and 2 spinulose spines of unequal length. Basis with spinular row along palmar margin and 2 shorter spinule rows near or around outer margin; with short pinnate seta. Endopod drawn out into strong, slightly curved pinnate claw; accessory armature consisting of 1 long (basally fused) and 1 short naked seta.

P1 (Fig. 9C). Intercoxal sclerite bare. Praecoxa well developed, with spinular row. Coxa with complex pattern of spinules on anterior surface as indicated in Fig. 9C. Basis with pinnate spine at both outer and inner distal corner. Exopod 3-segmented; exp-3 with 4 unipinnate spines and 1 plumose seta. Endopod 2-segmented, slightly shorter than exopod; enp-1 wider than and about as long as enp-2, with spinulose distal and outer margins and with distally serrate, plumose seta along inner margin; enp-2 with inner plumose seta and distal armature consisting of plumose seta and 2 pinnate spines.

P2-P4 with rectangular intercoxal sclerites ornamented with paired spinule rows anteriorly. Basis with outer pinnate spine (P2) or plumose seta (P3-P4). Rami 3-segmented; outer margins of segments with coarse spinules; endopods about as long as exopods. P2 endopod (Fig. 10A) with 2 inner setae on enp-2; apical armature of enp-3 consisting of outer pinnate spine, outer distal pinnate spine and inner distal plumose seta. P3 endopod as for male (Fig. 10E). Armature formula as for genus.

P5 (Fig. 10F) with exopod and baseoendopod fused forming slightly bilobate plate; outer basal seta plumose, arising from short pedestal; exopodal lobe with pinnate seta flanked by 2 strong, minutely pinnate spines, and short inner seta; endopodal lobe with incomplete suture on posterior surface; armature consisting of short spinous process (representing vestigial element) flanked by 2 strong, minutely pinnate spines. Secretory pores distributed as in Fig. 10F. Intercoxal sclerite absent.

MALE

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami 1.6 mm according to Klie (1939, 1941).

Antennule 7-segmented and subchirocer; geniculation between segments 5 and 6; with aesthetasc on segment 3 and as part of apical acrothek on segment 7.

P2 endopod (Fig. 10B) slightly modified. Enp-1 and -2 as in ♀; no apophysis present. Enp-3 with inner distal plumose seta of ♀ being replaced by short spinous element (Fig. 10C); this element was slightly longer and unipinnate on the left endopod (Fig. 10D); spinules around bases of inner setae shorter than in ♀.

P3 endopod (Fig. 10E) not modified. The absence of the recurved process on the distal outer corner of enp-2 might well be an aberration (see *A. segonzaci* below).

P5 (Fig. 10G) with exopod and baseoendopod fused forming slightly bilobate plate; outer basal seta plumose, arising from short pedestal; exopodal lobe with similar armature as in ♀; endopodal lobe with 1 short naked spine and 1 long, minutely bipinnate spine. Inner margin of endopodal lobe with 2 coarse spinules. Secretory pores distributed as in Fig. 10G. Fifth pair of legs fused medially.

Sixth pair of legs slightly asymmetrical, represented by hyaline flaps fused to supporting somite; armature consisting of 3 setae.

Anapophysia segonzaci sp. nov.

Type locality. - Indian Ocean, off La Réunion; stn DS 151; 20°51'0 S, 56°03'3 E; depth 3300 m.

Material. - Holotype ♀ (dissected on 6 slides) and paratypes (1 ♂ dissected on 6 slides; 1 ♀ and 1 cop V♀ in alcohol); deposited in the Muséum National d'Histoire Naturelle, Paris under nos MNHN-Cp 1121-1123; collected at type locality during Cruise MD32, R/V *Marion-Dufresne* (Chief scientist: Dr Alain Guille); 05 September 1982.

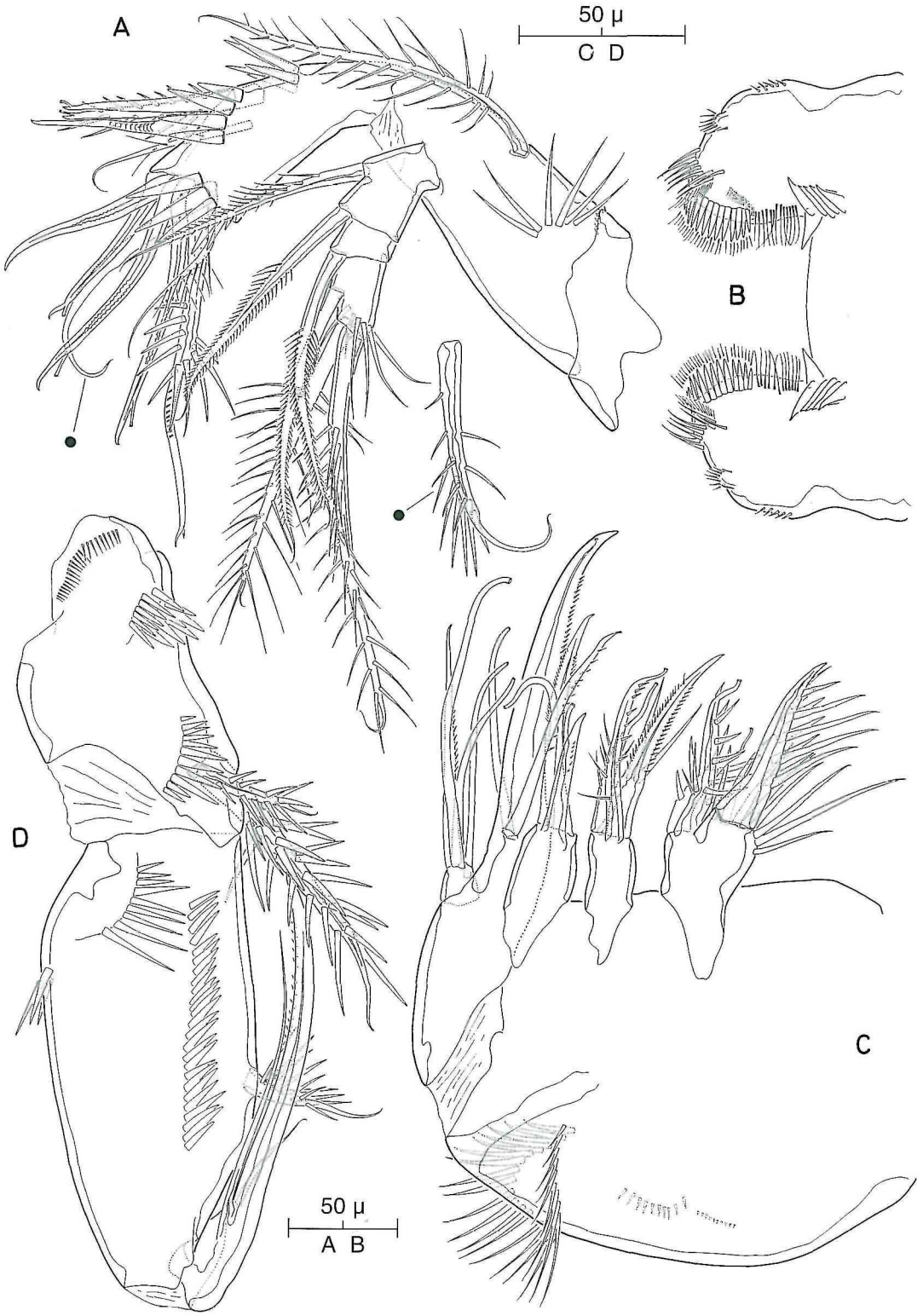

Figure 8. *Anapophysia borealis* (♀). A, antenna [filled circle symbol indicating subapical spine]; B, paragnaths, anterior; C, maxilla; D, maxilliped.

Figure 8. *Anapophysia borealis* (♀). A, antenne [le symbole circulaire noir indique l'épine subapicale] ; B, paragnathes, vue antérieure ; C, maxille ; D, maxillipède.

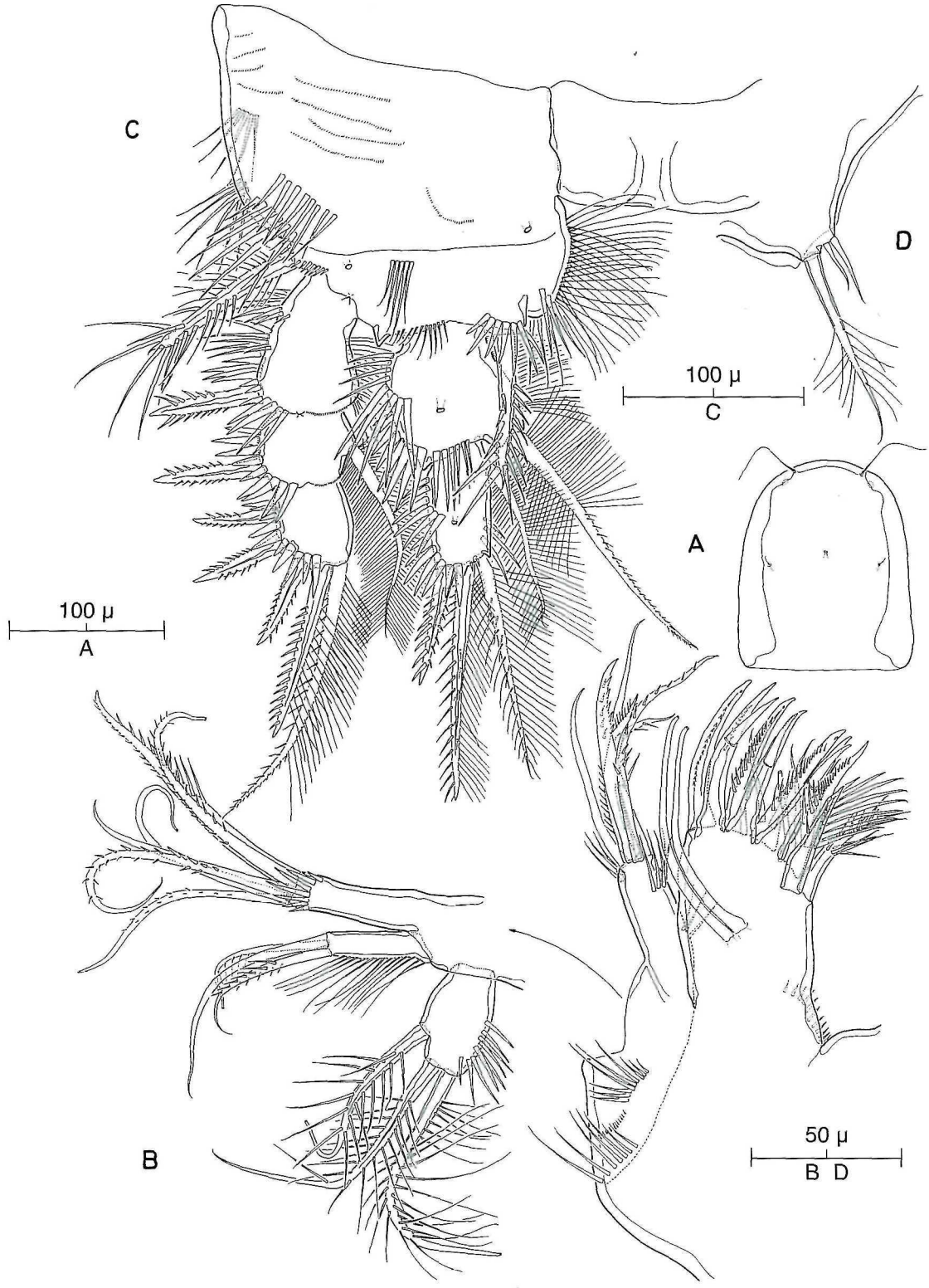

Figure 9. *Anapophysia borealis* (♀). A, rostrum, dorsal; B, maxillule with palp disarticulated, anterior; C, P1, anterior [praecoxa not figured]; D, armature of P6.

Figure 9. *Anapophysia borealis* (♀). A, rostre, vue dorsale ; B, maxillule, avec palpe détaché, vue antérieure ; C, P1, vue antérieure [praecoxa omise] ; D, armature de P6.

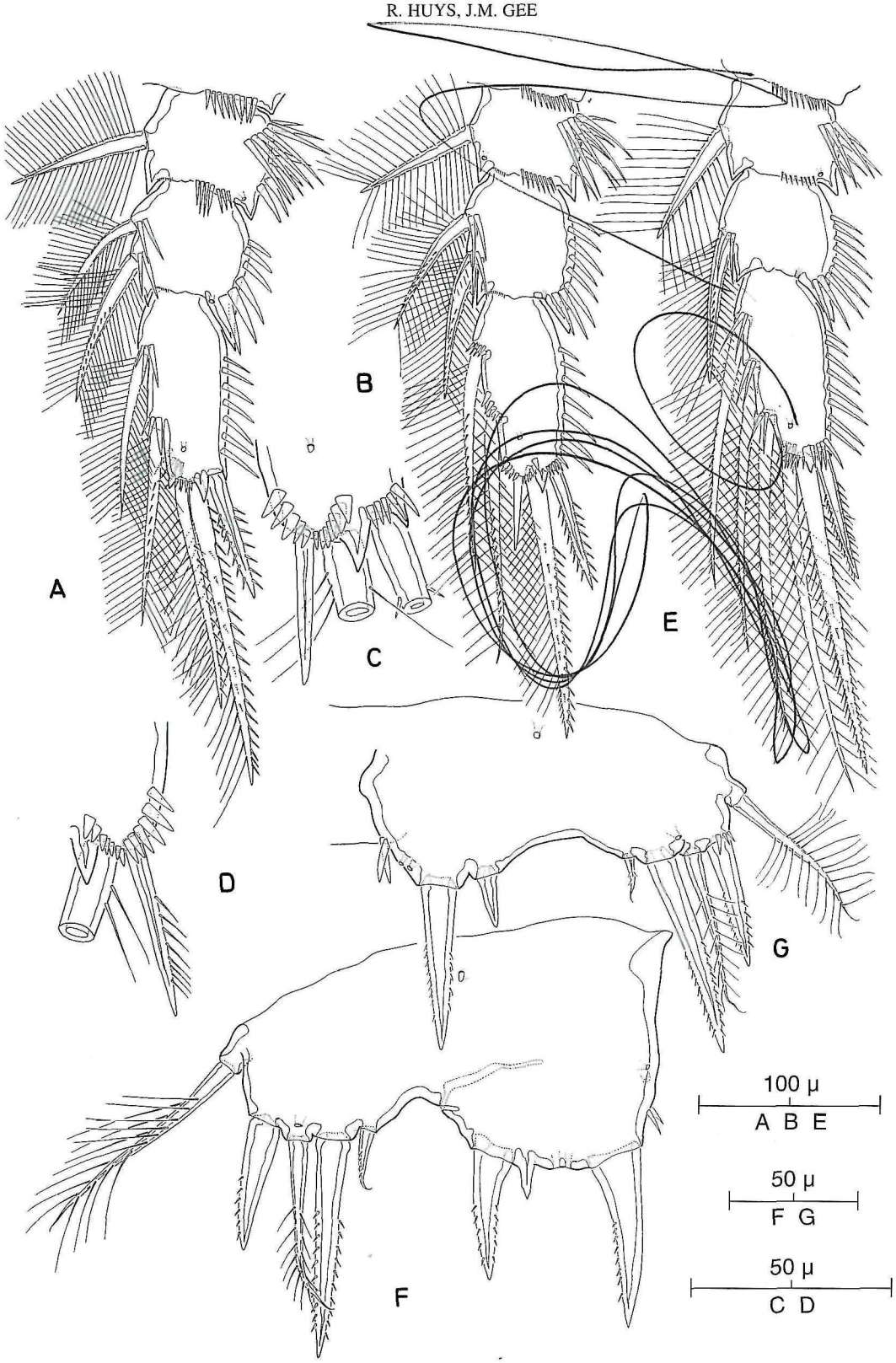

Figure 10. *Anapophysia borealis*. A, P2 endopod (♀), anterior; B, P2 endopod (♂), anterior; C, P2 endopod (♂), detail of distal margin of enp-3; D, same, other side; E, P3 endopod (♂), anterior; F, P5 (♀), anterior; G, P5 (♂), anterior.

Figure 10. *Anapophysia borealis*. A, P2, endopodite (♀), vue antérieure ; B, P2, endopodite (♂), vue antérieure ; C, P2, endopodite (♂), détail du bord distal d'enp-3 ; D, même région sur l'autre P2 ; E, P3, endopodite (♂), vue antérieure ; F, P5 (♀), vue antérieure ; G, P5 (♂), vue antérieure.

Etymology. - The species is dedicated to Dr Michel Segonzac (CENTOB, Brest) who placed the material at our disposal.

Description

A. segonzaci sp. nov. is closely related to the type species and consequently only the major differences are described here.

FEMALE

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami: 2.61 mm (Fig. 11A). Genital double-somite about as wide as long; original segmentation marked by internal chitinous ribs dorsally and laterally and similarly arranged spinular rows dorsolaterally. Urosomal spinule rows as illustrated in Fig. 11A.

Caudal ramus as in *A. borealis* except that the base of seta IV is less swollen.

Rostrum (Fig. 12A) slightly shorter than in type species but sensillar pattern and pore arrangement identical.

Antennule, mandible and maxillule as in type species.

Antenna (Fig. 12B-D) differing in following aspects: (a) proximal spinule row on allobasis consisting of finer and shorter spinules (Fig. 12B); (b) relative size of exopod larger (Fig. 12B); (c) distal spines of exp-3 longer in relation to total exopod length (Fig. 12C); (d) subapical spine (see inset Fig. 12D) longer.

Maxillary allobasis with additional element (arrowed in Fig. 11B).

Maxilliped (Fig. 12E) similar to type species but endopodal claw shorter.

P1 (Fig. 12F) and P2-P4 as in type species.

P5 (Fig. 11E) with exopod and baseoendopod fused forming slightly bilobate plate; outer basal seta plumose; exopodal lobe with 3 strong, minutely pinnate spines (middle one longest), and very short spine at inner corner; endopodal lobe with incomplete suture on posterior surface; armature consisting of diminutive spur (representing vestigial element) flanked by 2 strong, minutely pinnate spines. Secretory pores distributed as in Fig. 11E. Intercoxal sclerite absent.

MALE

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami 2.11 mm. Antennule and P6 as in *A. borealis*.

P2 endopod (Fig. 11C) slightly modified. Enp-1 and -2 as in ♀; no apophysis present. Enp-3 with inner distal plumose seta of ♀ being replaced by short spinous element.

P3 endopod (Fig. 11D) with outer distal corner of enp-2 extremely attenuated forming very long (compared to other genera), bifid apophysis surrounded by membranous area at base modified and bearing inner pore in proximal quarter.

P5 (Fig. 11F) with exopod and baseoendopod fused forming slightly bilobate plate; outer basal seta plumose; exopodal lobe with similar armature as in ♀ except that inner apical spine is longest and inner vestigial element is bare; endopodal lobe with 1 short outer spine and 1 long inner spine. Inner margin of endopodal lobe with 2 spinules. Secretory pores distributed as in Fig. 11F. Fifth pair of legs fused medially.

Discussion

Huys & Gee (1993) redefined the taxonomic concept of the genus *Psammis* and excluded *P. borealis* by ranking it *species incertae sedis* in the Paranannopidae. Their failure to place this species more confidently was largely caused by the confusion that existed over the identity of the type material. Klie (1939, 1941) had reported 11 ♀♀ and 1 ♂ from two localities, yet the male syntype slide contained three mounted antennules and only part of one seemed to display male characteristics. Moreover, both P2 and P3 did not exhibit clear sexual dimorphism on the endopodal segments, rising the suspicion that the male syntype is either a preadult or an aberrant adult. Scrutinous re-examination of the types of *P. borealis* and comparison with the newly described material of the closely related *A. segonzaci* provides support in favour of the latter possibility. The recurved process on the male P3 enp-2 is a diagnostic character for the Paranannopidae. It can vary considerably in size, ranging from the minute process in e.g. *Paradanielssenia* and *Afrosenia* to the extremely long apophysis in *A. segonzaci*. We regard it extremely unlikely that the complete absence of this apophysis in the morphologically very similar *P. borealis* is genuine and consider this an aberration. The differences found between the left and right sides of the P2 enp-3 (compare Fig. 10C and D) also testify to the aberrant nature of the male syntype.

The absence of a spinous apophysis on the male P2 endopod in both species of *Anapophysia* is remarkable. This structure attains its maximum development in *Danielssenia* and *Archisenia* but can be very small in genera that possess sensory aesthetascs on the mouthparts such as *Sentiropsis* and *Paradanielssenia*. Only in *Telopsammis secunda* and *Leptotachidia ibericus* the sexually dimorphic apophysis is completely lost. The male apophysis usually bears an apical pore (see e.g. Huys & Gee (1992), Fig. 6B) which represents the homologue of the pore found on the anterior surface of the middle endopod segment in the female. In *Telopsammis* and *Leptotachidia* the secretory (?) pore is lost in the female and this absence might well be related to the secondary loss of the spinous apophysis in the males of these genera. A similar explanation would not apply to *Anapophysia* since the surface pore is clearly

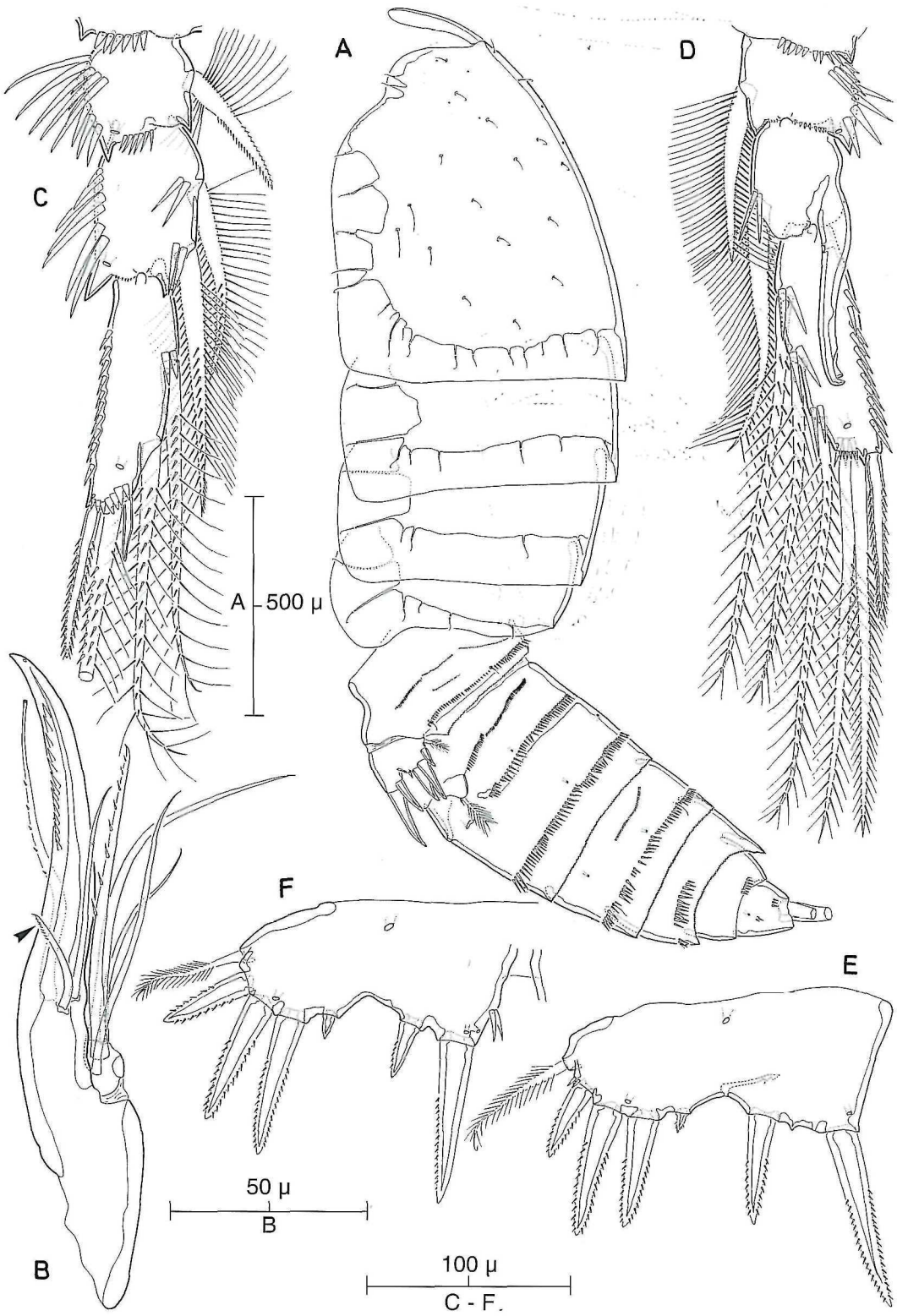

Figure 11. *Anapophysia segonzaci* sp. nov. A, habitus (♀), lateral; B, maxillary allobasis [small seta arrowed]; C, P2 endopod (♂), anterior; D, P3 endopod (♂), anterior; E, P5 (♀), anterior; F, P5 (♂), anterior.

Figure 11. *Anapophysia segonzaci* sp. nov. A, habitus (♀), vue latérale ; B, allobase maxillaire [la flèche indique la soie rudimentaire] ; C, P2, endopodite (♂), vue antérieure ; D, P3, endopodite (♂), vue antérieure ; E, P5 (♀), vue antérieure ; F, P5 (♂), vue antérieure.

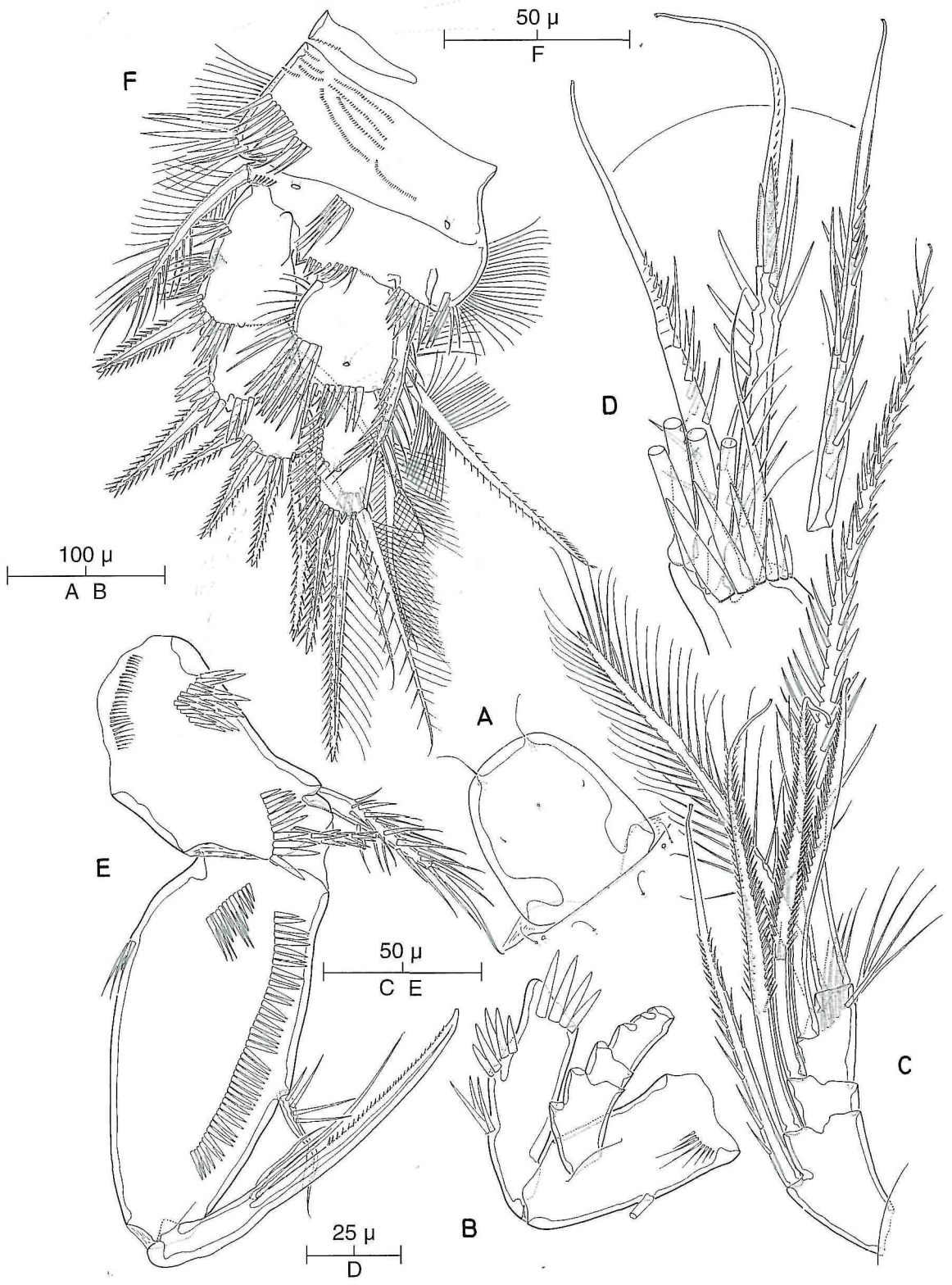

Figure 12. *Anapophysia segonzaci* (♀). A, rostrum, dorsal; B, antennary contours showing relative size of exopod; C, antennary exopod; D, antennary endopod, distal part; E, maxilliped; F, P1, anterior.

Figure 12. *Anapophysia segonzaci* (♀). A, rostre, vue dorsale ; B, contours de l'antenne montrant la taille relative de l'exopodite ; C, exopodite antennaire ; D, endopodite antennaire, région distale ; E, maxillipède ; F, P1, vue antérieure.

present in the female (Fig. 10A) and hence the underlying developmental process for the absence of sexual dimorphism could be different.

Two major lineages can be recognized within the Paranannopidae: the paranannopid branch grouping *Parannanopus* Lang and *Cylindronannopus* Coull, and the danielsseniid branch grouping all other genera. Gee & Huys (1990) considered *Fladenia* as a missing link between these two lineages and used primarily swimming leg sexual dimorphism to reinforce this position. Despite their usefulness, sexually dimorphic patterns in the paranannopid lineage are difficult to interpret and the situation is exacerbated by the fact that the majority of its constituent taxa are known from one sex only. However, careful comparison of the armature on the antenna has revealed an additional character that serves to reinforce the distinctiveness of the two lineages currently recognized in the Paranannopidae. The setation on the antennary endopod is highly conservative in the family. The lateral armature consists of a geniculate spine flanked by two pinnate spines and accompanied by a naked seta. The distal armature invariably consists of four geniculate setae (the largest of which is fused basally to a seta of variable size), a (pinnate) spine at the inner distal corner, and a subapical element. The ornamentation of the latter is of central importance and shows a clearcut difference between both lineages. In the danielsseniid branch it is represented by a setiform element which is naked in the majority of the genera. In species of *Paranannopus* and *Cylindronannopus* the element is typically enlarged and modified into a bipinnate or multipinnate spine. This state is regarded here as the apomorphic condition, and the polarity of this character was determined by outgroup comparison with the Pseudotachidiinae and Donsiellinae (currently subfamilies in the Thalestridae which will be upgraded to family level in a forthcoming paper). The subapical element in *Anapophysia* clearly resembles the *Paranannopus* condition and is indicated in Figs 8A and 12D. In the original description of *Fladenia intermedia* (Wells, 1965) (= *F. robusta* (Sars, 1921)) Gee & Huys (1990) illustrated this element as a sparsely plumose seta (cf. their Fig. 4A). However, re-examination has revealed that this element is exactly as in *Anapophysia* and therefore would link *Fladenia* with the paranannopid branch rather than with the danielsseniid grouping. Since this feature is not sexually dimorphic it can be applied to place certain genera that are known from females only such as *Bathypsammis*. Huys & Gee (1993) did not illustrate the antennary endopod of *B. longifurca* (Bodin, 1968), however Bodin's (1968) original description clearly shows that this element is multipinnate and spiniform and this has subsequently been confirmed by re-examination of the holotype. On the basis of antennary armature the following genera can thus be assigned to the paranannopid branch: *Paranannopus*, *Cylindronannopus*, *Fladenia*, *Bathypsammis* and *Anapophysia*. This relationship is reinforced by other characters such as the size of the distal outer spine of P1 exp-3. In the former genera this spine is at most as long as (but usually distinctly shorter than) the middle outer spine. In the danielsseniid genera the outer exopodal spines gradually increase in size with the distal one being the longest. Another character shared by these five genera is the fused P5 although this character has evolved convergently in a number of other genera such as *Psammis*, *Micropsammis*, *Leptotachidia* and *Telopsammis*.

Within the paranannopid branch there is a clear trend towards reduction in the number of endopodal segments in the swimming legs. *Fladenia*, *Bathypsammis* and *Anapophysia* show the ancestral 3-segmented condition which is also retained in all genera of the danielsseniid lineage. On the basis of the setation of P2-P4 exopods it would appear that *Bathypsammis* and *Anapophysia* are the most primitive genera in the paranannopid branch, and moreover, certain details in the structure of the mouthparts indicate that they might well be sistertaxa. Evidence for such a relationship is found in for example the presence of an additional surface spinule row on the maxillipedal basis near the coxa-basis joint (compare Huys & Gee's (1993) Fig. 18D with Figs 8D, 12E), and in the reduction (or complete loss in *A. borealis*) of one of the setae on the maxillary allobasis (compare Huys & Gee's (1993) Fig. 18B with Figs 8C, 11B). The intermediate position of *Fladenia* between these two genera and *Paranannopus-Cylindronannopus* will require reconsideration upon the discovery of the male of *B. longifurca*, yet it seems to be supported at present by swimming leg setation and sexual dimorphism and a number of other characters outlined by Gee & Huys (1990).

Both species of *Anapophysia* are known from their respective type localities only. The two female specimens provisionally identified as *P. borealis* by Prof. B.C. Coull and deposited in the Smithsonian Institution (reg. no. 00231018) do not belong to *Anapophysia* but show close similarities with certain species of *Pseudotachidius* T. Scott (Huys & Gee, 1993).

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