

# Systematics and phylogeny of *Zausodes* C.B. Wilson, 1932 (Copepoda, Harpacticoida, Harpacticidae), including three new species from the northern Gulf of Mexico

LORI BOUCK

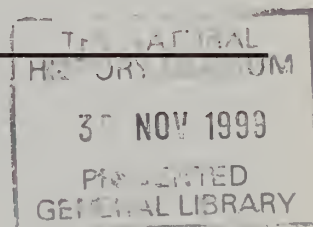
Department of Oceanography, Florida State University, Tallahassee, FL 32306–4320, USA

DAVID THISTLE\*

Department of Oceanography, Florida State University, Tallahassee, FL 32306–4320, USA

RONY HUYS

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD



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**SYNOPSIS.** Re-examination of copepod material, collected from the northern Gulf of Mexico and previously identified as *Zausodes arenicolus* C.B. Wilson, 1932 (Harpacticoida, Harpacticidae), resulted in the discovery of three new species of the *Zausodes* complex. Phylogenetic analysis identified four distinct lineages within this complex which are attributed generic status. *Zausodes* C.B. Wilson, 1932 is redefined to include only *Z. septimus* Lang and the type species *Z. arenicolus* which is completely redescribed. A new genus *Mucropedia* is proposed to accommodate two new species from the Gulf of Mexico, *M. kirstenae* and *M. cookorum*. *Z. biarticulatus* Itô, 1979 from the Japanese Bonin Islands is transferred to *Archizausodes* gen. nov. and regarded as the most primitive member of the *Zausodes* complex. All other species are grouped in *Neozausodes* gen. nov., including *N. shulenbergeri* sp. nov. from the Gulf of Mexico and *N. areolatus* (Geddes, 1968a) comb. nov. which is completely redescribed on the basis of type material. *Z. cinctus* Krishnaswamy, 1954 is ranked *species incertae sedis* in the family Harpacticidae. The sister group relationship between *Perissocope* Brady, 1910 and the *Zausodes* complex is discussed. Lang's (1944, 1948) subfamilial division of the Harpacticidae is abandoned.

\*Author for correspondence

## INTRODUCTION

Species of *Zausodes* C.B. Wilson are typical inhabitants of sandy substrata in shallow subtidal localities, however, some records indicate that their horizontal zonation extends into the infralittoral of sandy beaches (Wilson, 1932; Mielke, 1990, 1997). Although the genus was originally proposed for the type species *Z. arenicolus* from the Woods Hole area (Wilson, 1932), most species that have been added since are subtropical in distribution. The genus currently comprises nine species but only two of them, *Z. arenicolus* and *Z. septimus* Lang, 1965, have been recorded again since their original description (Bell & Woodin, 1984; Coull, 1971a–b; Foy & Thistle, 1991; Mielke, 1990, 1997). The taxonomy and phylogenetic position of the genus within the family Harpacticidae are not well understood for a variety of reasons. First, species of *Zausodes* are amongst the smallest Harpacticidae and males often do not exceed 0.4 mm in size. Second, Wilson's (1932) generic diagnosis contains a number of significant inconsistencies which originate from his imperfect description of *Z. arenicolus*. Lang (1965) clarified some of the erroneous statements but did not present a complete redescription. Third, several subsequent descriptions are grossly inadequate and severely hamper both species identification and phylogenetic reconstruction of relationships. This is particularly the case for the species described by Jakobi (1954) and Krishnaswamy (1954). Finally, the current subfamilial classification of the Harpacticidae introduced by Lang (1948) is inadequate. The genus *Zausodes* was placed in the Zausodiinae together with *Zaus* Goodsir and *Zausopsis* Lang, however recent discoveries of new taxa (Itô, 1979; Watkins, 1987) have provided strong indications for a close relationship between *Zausodes* and *Perissocope* Brady, a genus currently assigned to the Harpacticinae.

While examining a collection of harpacticoids from the northern Gulf of Mexico, previously identified by D. Thistle and co-workers as *Z. arenicolus* (Foy & Thistle, 1991; Ravenel & Thistle, 1981; Thistle, 1980; Thistle *et al.*, 1995), we found several other species of *Zausodes* which could not be assigned to the type species. Although *Z. arenicolus* was present among the specimens, as confirmed by comparison with Wilson's type material, three species new to science were found. Since one of these was very similar to *Z. areolatus* Geddes, the type locality of which is in the relatively nearby Caribbean (Geddes, 1968a), the type material of the latter was obtained for comparison.

This paper describes the three new species from the Gulf of Mexico, provides complete redescriptions for both *Z. arenicolus* and *Z. areolatus* and analyses the phylogenetic relationships between the species. The genus *Zausodes* is redefined in the light of these findings.

## MATERIALS AND METHODS

Samples were taken by SCUBA divers with a 15.5 cm<sup>2</sup> corer. The top 3 cm of each core were preserved in sodium-borate-buffered formalin. In the laboratory, harpacticoids were concentrated from each sample with a modified Barnett (1968) extraction technique combined with a 0.062-mm mesh sieve. After rose bengal staining, harpacticoids were sorted under a dissecting microscope and mounted in glycerol on slides.

Specimens were dissected in lactic acid, and the dissected parts were placed in Hoyer's mounting medium (Pfannkuche & Thiel, 1988) on H-S mounts (Shirayama *et al.*, 1993) or Cobb slide frames

(Westheide & Purschke, 1988). Drawings were prepared with a camera lucida on a Zeiss Standard 16 compound microscope equipped with differential interference contrast. Habitus views were drawn at 800 $\times$ ; other illustrations were drawn at 2000 $\times$ . Body size was measured along a line halfway between the dorsal and ventral margins in lateral view at 256 $\times$  with the aid of a camera lucida. Terminology follows Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae = aesthetasc; P1–P6 = first to sixth thoracopods; exp(enp)–1(2,3) to denote the proximal (middle, distal) segment of a ramus.

Phylogenetic relationships between taxa were analyzed using the phylogenetic computer package PAUP 3.1 prepared by David L. Swofford of the Laboratory of Molecular Systematics, Smithsonian Institution (Swofford, 1993; Swofford & Begle, 1993). Since evolution within the Copepoda is assumed to proceed typically by oligomerization (Huys & Boxshall, 1991), all characters were set irreversible using the CAMIN–SOKAL option. This option suppresses character reversals at the expense of introducing extra convergences and thereby increasing the tree-length. The options employed in the analysis were BRANCH AND BOUND, which guaranteed to find all most parsimonious trees, and the MINF optimization, which assigns character states so that the f-value is minimized.

## SYSTEMATICS

For practical reasons the systematics section of this paper is arranged according to the conclusions arrived at in the phylogeny section below. Species are allocated to genera following the topology of the most parsimonious cladogram obtained by the phylogenetic analysis (Fig. 33A).

### Family Harpacticidae Dana, 1846

#### Genus *Zausodes* C.B. Wilson, 1932

In its revised concept (see below) the genus is restricted here to the type species and *Z. septimus*. Lang (1965) had already recognized the close relationship between these species, pointing out their similarity in the ♀ P5. *Z. arenicolus* displays two characters which are not found in any of the species of the former *Zausodes* complex: (1) the 3-segmented P4 endopod, and (2) the presence of a mucroniform process on enp-2 of the male P2. The former is an evolutionary labile character, frequently showing intermediate states in other species (Lang, 1965), whilst the latter is regarded here as a plesiomorphy retained within the former *Zausodes* complex only in *Z. arenicolus*, but being present in many other harpacticid genera such as *Perissocope*, *Harpacticus* Milne-Edwards and *Tigriopus* Norman (Huys *et al.*, 1996). It is assumed that in all other species of the former *Zausodes* complex this process was secondarily lost.

**DIAGNOSIS.** Harpacticidae. Antennule ♀ 8-segmented, with pinnate or plumose setae on segments 1–6; without strong, modified spines on segments 3–5 or enlarged pectinate or pinnate spines on segment 6. Antennule ♂ without modified spines on segment 3. Antennary exopod 1-segmented, with 2 apical setae. Maxilla with 4 spines/etae on praecoxal endite. P2–P3 endopods 3-segmented, P4 endopod 2- or 3-segmented. P2 ♀ enp-3 with 2 inner setae. P3 ♀ enp-2 without inner seta. P4 exp-3 with 3 outer spines in both sexes. P4 enp-3 (or enp-2 when 2-segmented) with 1 inner seta in both sexes.

P2♂enp-2 with or without apophysis, inner seta not modified; enp-3 with 1 apical seta (inner one lost), outer spine not fused to segment. P3♂enp-2 outer distal corner not attenuated.

Swimming leg setal formula:

	exopod	endopod
P2	0.1.223	0.1.221 [♀] 0.1.211 [♂]
P3	0.1.323	1.0.221
P4	0.1.323	1.0.121 or 1.121

P5 exopod elongate-oval in both sexes. P5 endopodal lobe ♀ expressed; 3rd and 4th inner setae much shorter than others (or 1 seta lost in *Z. septimus*).

Sexual dimorphism in rostrum, antennule, P2 endopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Zausodes arenicolus* C.B. Wilson, 1932 (by monotypy).

OTHER SPECIES. *Z. septimus* Lang, 1965.

### *Zausodes arenicolus* C.B. Wilson, 1932

TYPE LOCALITY. Katama Bay, Martha's Vineyard, Woods Hole (Massachusetts); beach sand washings.

#### MATERIAL EXAMINED.

National Museum of Natural History (Smithsonian Institution), Washington, D.C.: Woods Hole region; type series consisting of one vial containing >50 specimens (USNM 63877); 1 ♀ and 1 ♂ dissected for examination. According to the USNM catalogue files the holotype ♂ has gone missing since at least 1983 when the harpacticoid collections were inventoried. It is assumed that in reality the holotype was never segregated by C.B. Wilson although the empty vial, which supposedly contained the specimen, received a separate registration number (no. 63423).

The Natural History Museum, London: syntypes (4 ♀ ♀, 4 ♂ ♂) in alcohol; from type locality; coll. C.B. Wilson, 15 August 1927; BMNH 1948.9.10.37.

Gulf of Mexico: 29°51'N, 84°31'W (about 50 m north of day mark #2), St. George Sound, Florida, 5 m depth, unvegetated medium sand (median grain size = 0.254 mm); a seagrass meadow occurs about 150 m to the north; see Foy & Thistle (1991) for additional description. Deposited at the Natural History Museum, London are 9 ♀ ♀ and 3 ♂ ♂ in ethanol (BMNH 1999.176–187) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.188–191). Deposited at the Smithsonian, Washington, D.C. are 9 ♀ ♀ and 2 ♂ ♂ in ethanol (USNM 288445–446) and 1 ♀ and 2 ♂ ♂ dissected on slides (USNM 288444).

REDESCRIPTION. All illustrations and text are based on specimens from the Gulf of Mexico. Illustrations were compared to type material obtained from the Smithsonian in order to verify the species identification.

FEMALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 433 µm ( $\bar{x}$  = 0.499, n = 4); without rostrum and caudal rami: 394 µm ( $\bar{x}$  = 0.456, n = 4). Body (Figs 1A–B, 2C–D) dorsoventrally flattened. Greatest width 200 µm ( $\bar{x}$  = 0.202, n = 4), measured near posterior margin of cephalothorax. Nauplius eye distinct; reddish brown in fresh, unstained specimens; invisible in cleared specimens. Integument with surface ornamentation/sculpturing consisting of irregular pattern of fine striations (not illustrated). Sensillae present dorsally and dorsolaterally on cephalothorax and body somites except penultimate one (not all

shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of thoracic somites thickly chitinized laterally. All somites but anal with fine spinular rows dorsally and dorsolaterally; penultimate somite with ventral spinular row; anal somite with spinular rows dorsally, ventrally, and laterally on the posterior margin. Lateral margins of free thoracic somites with 3 sensillae. Ventral posterolateral corners of urosomites 3–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is partially exposed in dorsal aspect; with two ventral pores near posterior margin; anal operculum rounded, smooth; pseudoperculum present, weakly developed. Caudal rami (Figs 1A–B, 2C–D) approximately as long as wide, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string (Figs 1A–B) extending posteriorly from each caudal ramus present in some specimens.

Rostrum (Fig. 1C) prominent, bell-shaped in dorsal view, with membranous fringe, defined at base; with two short sensillae anteriorly and one sensilla on each mediolateral margin; with mid-dorsal pore.

Antennule (Fig. 2B) 8-segmented; segments 2 and 3 longest; first segment widest with several spinular rows; fourth segment with an aesthetasc (50 µm long); eighth segment with acrothek consisting of 3 elements (probably 2 setae and 1 aesthetasc, however, we were unable to distinguish which elements were setae and which was an aesthetasc); with armature formula 1–[1], 2–[9 + 1 pinnate], 3–[7 + 2 pinnate], 4–[3 + 1 pinnate + (1 + ae)], 5–[1 + 1 pinnate], 6–[2 + 2 pinnate], 7–[4], 8–[4 + acrothek].

Antenna (Fig. 2A). Coxa short and unornamented; allobasis with several spinular rows, abexopodal spinulose seta, and membranous insert marking original segment boundary between basis and first endopodal segment; free endopod 1-segmented; lateral armature consisting of a spine, 1 short seta and 1 long seta; distal armature comprising 1 seta, 1 pinnate, curved spine, and 4 geniculate spines, longest one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinular rows and hyaline surface frill as indicated in Fig. 2A; exopod 1-segmented with 2 distal, unequal setae.

Labrum well developed, medially incised.

Mandible (Fig. 3A). Gnathobase with seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod longer than exopod, with 1 bare and 1 pinnate lateral seta and 6 apical setae; exopod with 1 pinnate and 2 bare lateral setae, 3 distal setae, and spinules subdistally and along outer margin.

Maxillule (Fig. 3C). Prae-coxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 4 setae and a spinular row; basal endite with 6 setae; endopod with 1 bare and 2 pinnate setae distally; exopod with 1 bare inner seta, 1 pinnate outer seta, 2 distal setae, and a spinular row.

Maxilla (Fig. 3B). Syn-coxa with spinular row along outer margin and 3 endites; praecoaxal endite with 2 bare and 2 bipinnate setae; coxal endites each with 2 bare setae and 1 pinnate spine; allobasis with claw and 3 bare setae; endopod 1-segmented with 4 bare setae.

Maxilliped (Fig. 3D). Syn-coxa with a bipinnate seta and numerous spinular rows as indicated; basis with a spinular row and seta along palmar margin, with spinules along outer distal margin and on anterior face; endopod represented by acutely recurved claw with spinules along inner margin and proximal accessory seta.

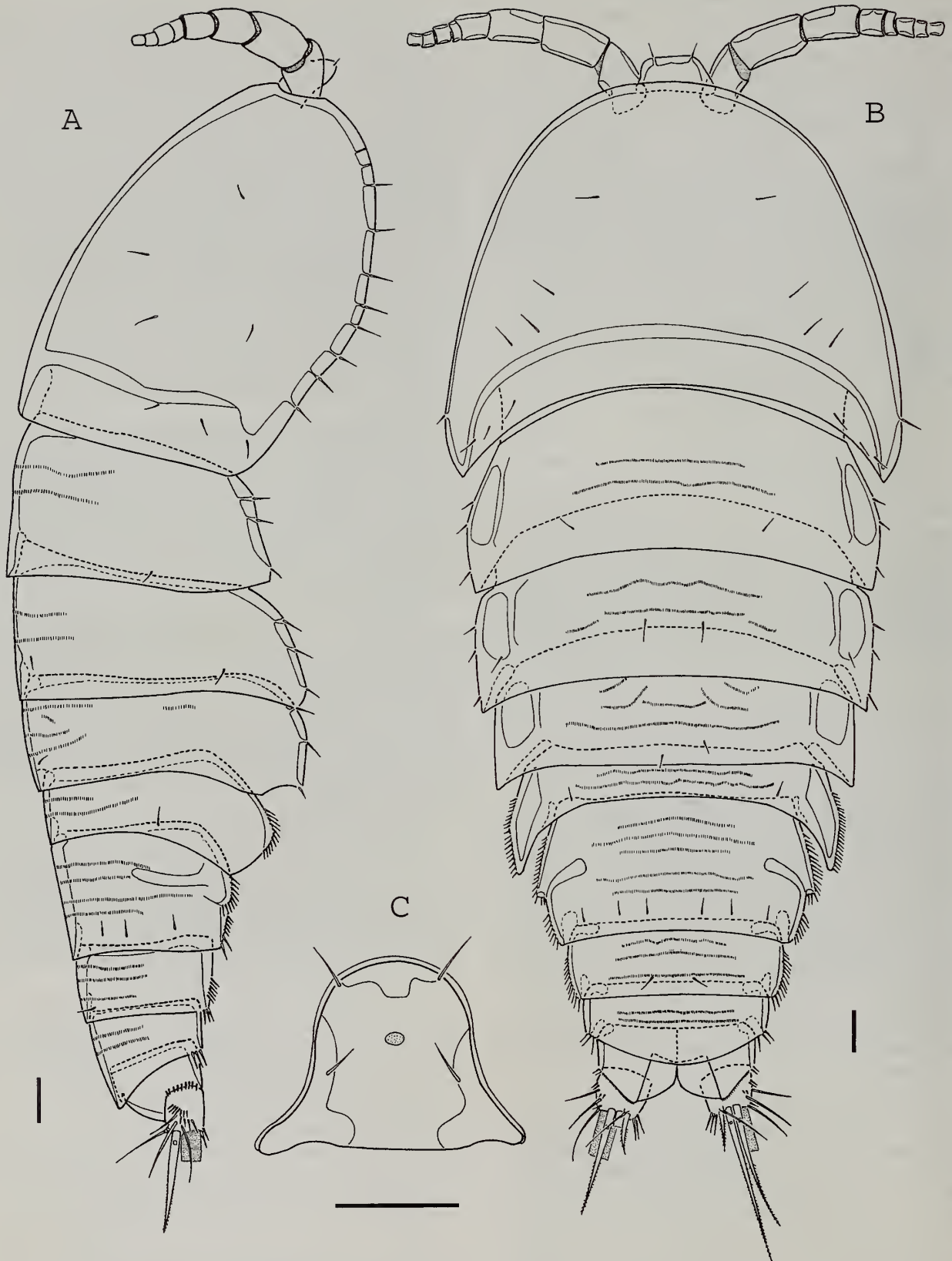
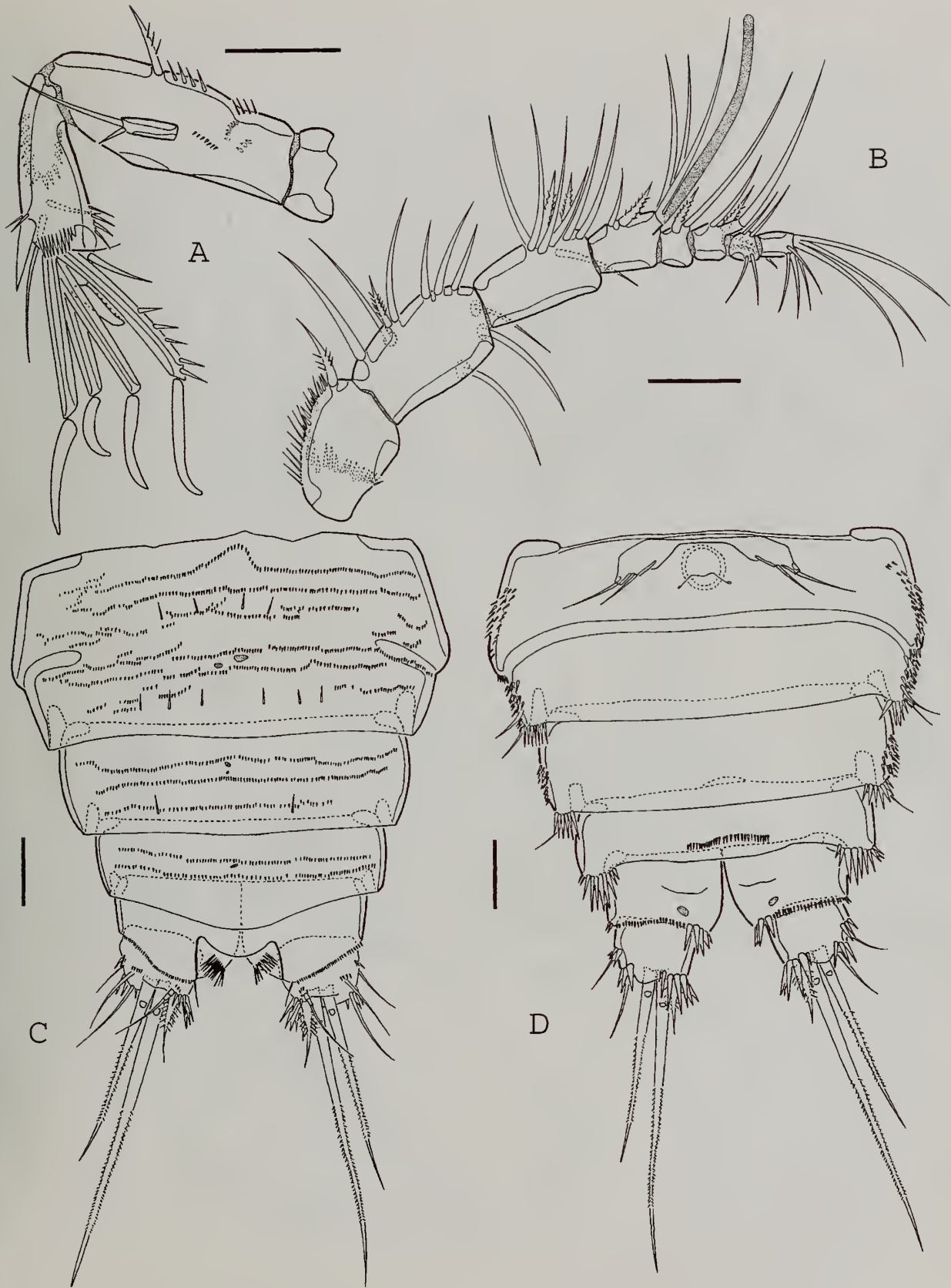


Fig. 1 *Zausodes arenicolus* C.B. Wilson, 1932 (♀). A, Habitus, lateral view; B, habitus, dorsal view; C, rostrum. Scale bars = 20  $\mu$ m.



**Fig. 2** *Zausodes arenicolus* C.B. Wilson, 1932 (♀). A, Antenna; B, antennule; C, urosome (excluding P5-bearing somite), dorsal view; D, urosome (excluding P5-bearing somite), ventral view; Scale bars = 20  $\mu\text{m}$ .

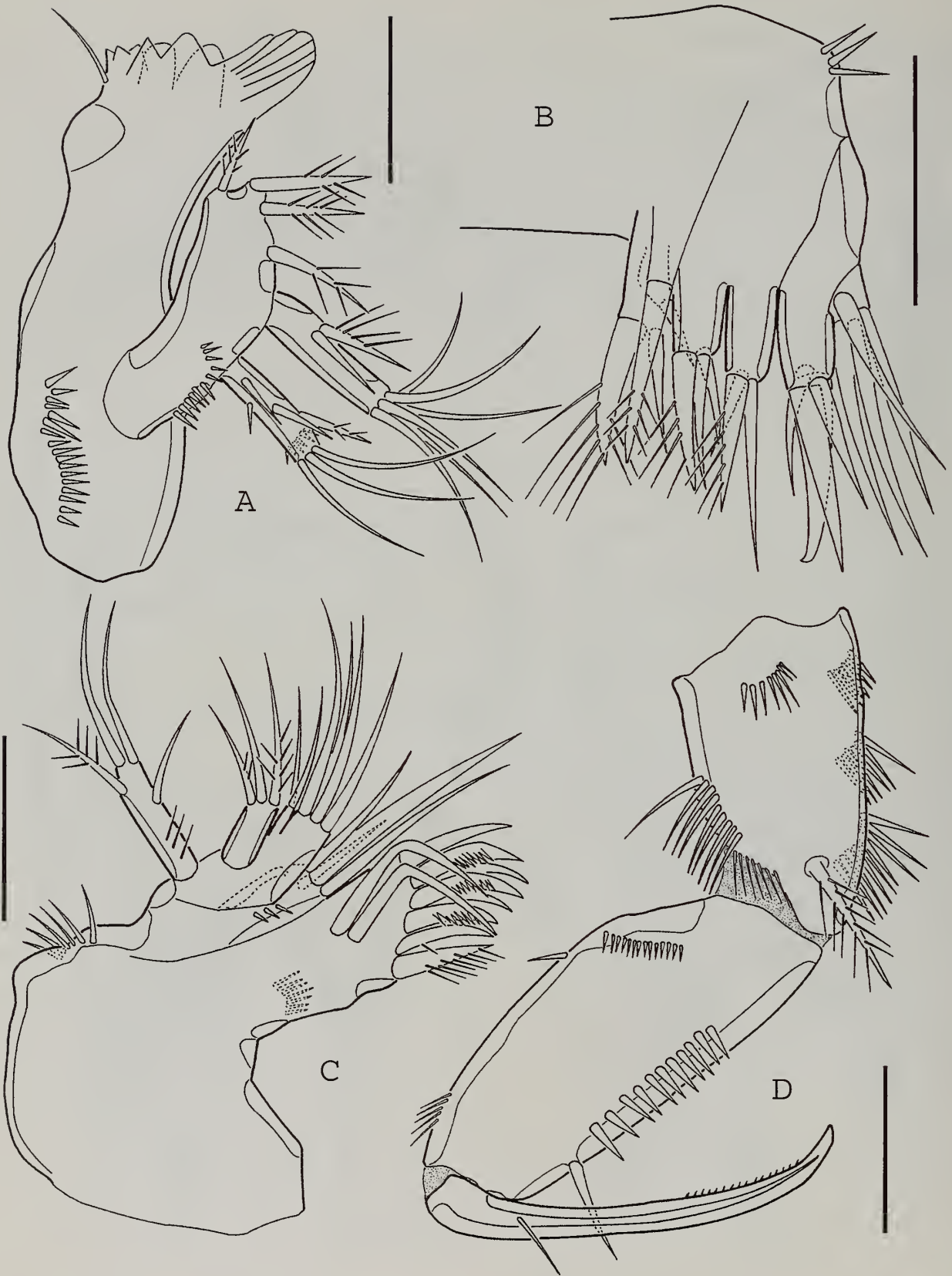


Fig. 3 *Zausodes arenicolus* C.B. Wilson, 1932 (♀). A, Mandible; B, maxilla; C, maxillule; D, maxilliped. Scale bars = 20 µm.

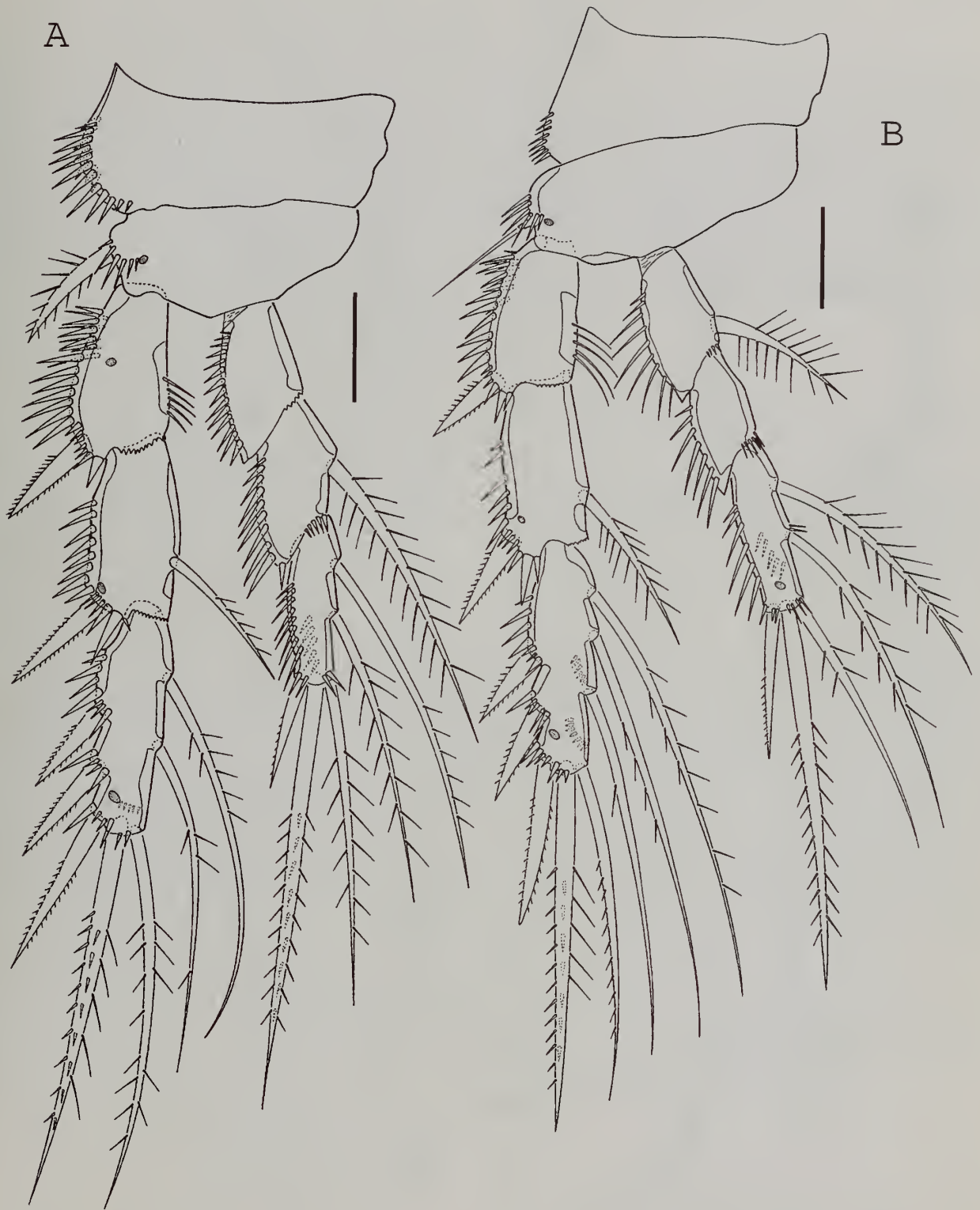


Fig. 4 *Zausodes arenicolus* C.B. Wilson, 1932 (♀). A, P2; B, P3. Scale bars = 20 μm.



Fig. 5 *Zausodes arenicolus* C.B. Wilson, 1932 (♀). A, P5 exopod, posterior view; B, P4; C, P1 (arrow indicating rudimentary seta); D, P5, anterior view. Scale bars = 20  $\mu$ m.



P1 (Fig. 5C). Rami prehensile; coxa with spinular rows along inner, outer, and distal margins and on anterior face, with pore at inner distal corner; basis with bipinnate seta near mid-point of outer margin and bipinnate spine at inner distal corner; spinular rows present along inner and outer margins and around articulation with endopod; with pore near outer proximal corner. Exopod 3-segmented, 1.5 times as long as endopod (excluding apical elements); exp-1 with distal pinnate seta and spinular rows along outer margin; exp-2 elongate, 2.6 times as long as exp-1, with short, slender inner seta distally (arrowed) and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate, with outer spinular row; enp-2 0.2 times as long as enp-1, with outer spinular row and bearing geniculate spine, claw, and short, slender inner seta distally.

P2–P4 (Figs 4A–B, 5B) with 3-segmented rami. Coxae with spinular rows at outer distal corner of P2–P3 and posteriorly near outer edge of P4. Bases with outer bipinnate spine (P2) or naked seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P2–P4 exp-3, P4 exp-1 and -2, P2–P4 enp-3. Outer distal spine of P2–P4 exp-3 and P2 enp-3 tripinnate. Pores present as illustrated (Figs 4A–B, 5B). Seta and spine formula of P2–P4 as in Table 1.

P5 (Figs 5A, D) biramous, not fused medially. Baseoendopod with numerous anterior surface and marginal spinular rows; endopodal lobe triangular, with 2 sparsely plumose and 2 short bare setae along inner margin and 1 distally pinnate seta apically; outer basal seta slender and arising from cylindrical process. Exopod 1.9 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer bipinnate spines, apical one with flagellate tip; posterior surface with proximal pore near outer margin.

Genital double somite (Figs 2C–D) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 2 naked setae.

**MALE.** Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 366  $\mu\text{m}$  ( $\bar{x}$  = 0.379  $\mu\text{m}$ ,  $n$  = 4); without rostrum and caudal rami: 294  $\mu\text{m}$  ( $\bar{x}$  = 338  $\mu\text{m}$ ,  $n$  = 4). Body width 147  $\mu\text{m}$  ( $\bar{x}$  = 149  $\mu\text{m}$ ,  $n$  = 4). Not all sensillae shown in habitus views (Figs 6A–B). Sexual dimorphism in body size, rostrum, antennule, P2 endopod, P5, P6, and urosome segmentation (Figs 7A–B).

Rostrum (Fig. 6A) trapezoid, defined at base.

Antennule (Figs 6C–D) 6-segmented, chirocer; segment 5 bearing aesthetasc, not conspicuously swollen; segments 3 and 5 longest; with geniculation between segments 5 and 6; first segment with several spinular rows along anterior margin; with armature formula 1–[1], 2–[1], 3–[9], 4–[10], 5–[6 + (1 + ae)], 6–[6 + acrothek].

P2 (Fig. 7E) as in ♀ except for endopod. Enp-1 with outer row of spinules. Enp-2 with outer distal corner produced into spinous apophysis, extending to distal margin of enp-3; outer margin spinulose; inner margin with subdistal bipinnate seta. Enp-3 with spinulose outer margin, short outer pinnate spine, long bipinnate spine distally and 2 pinnate inner setae; with spinules on posterior face and at bases of distal inner and apical elements.

P5 (Figs 7C–D) biramous. Baseoendopods fused medially forming transversely elongate plate; endopodal lobe slightly developed, with 1 outer, distally pinnate seta and 1 inner, bipinnate seta; outer basal seta slender and arising from cylindrical process; with spinules

around articulation with exopods. Exopod as in ♀ except for an additional small, bipinnate seta along the outer margin, and fewer spinular rows.

P6 (Fig. 7B) symmetrical; with distal seta and spinules along outer margin; located more laterally than in ♀.

#### NOTES.

Wilson (1932) noted sexual dimorphism in the first pair of swimming legs and the exopods of P3–P4 and further claimed that none of the other rami was genuinely modified in the male. Lang (1965) re-examined type specimens of *Z. arenicolus* and concluded that neither P1 nor P3–P4 displayed sexual dimorphism and that Wilson had overlooked the modification of the male P2 endopod.

Coull's (1971b) numerous records from the North Carolina shelf, Bell & Woodin's (1984) record from Virginia, Bell's records from Tampa Bay (e.g. Bell *et al.*, 1989), and this paper suggest that *Z. arenicolus* assumes a continuous distribution along the American east coast from Massachusetts, around the Florida peninsula, and into the northern Gulf of Mexico.

#### *Zausodes septimus* Lang, 1965

**TYPE LOCALITY.** California, Monterey Bay, off Hopkins Marine Station, about 7 m depth.

#### NOTES.

The few disjunct records of this species suggest a wide distribution both in the Caribbean and along the Pacific seaboard of the U.S. and Latin America. Mielke (1990) found *Z. septimus* along both Pacific and Caribbean coasts of Panamá and subsequently recorded the species also from Punta Morales in Costa Rica (Mielke, 1997). Coull (1971a) identified *Z. septimus* from sediment samples taken on St. Thomas (U.S. Virgin Islands).

Mielke's (1990) specimens from Panamá (particularly from the Caribbean side; Isla Nalunega) are remarkably smaller than those from the type locality in California but otherwise agree in most aspects with Lang's (1965) description. Significant discrepancies are found in (1) the shape of the rostrum which is squarish and truncate in the Californian material but elongate bell-shaped and pointed in Mielke's material, (2) the proportional lengths of the antennular segments in the ♀ (particularly segments 3–4 are distinctly shorter in the Panamá females), (3) the length of P1 endopod which is markedly shorter in Lang's specimens, and (4) the shape and length of outer and apical spines of P2–P4 exp-3 which are stouter and shorter in the Panamá population. A further study based on material from a wider range of localities is required to confirm whether these differences originate from intraspecific variability as Mielke (1990, 1997) advocates, or reflect the existence of two closely related species.

*Z. septimus* can be differentiated from *Z. arenicolus* by the segmentation of the P4 endopod and by the shape of the P5 baseoendopod and the relative position of its setae. Males of both species can be distinguished by their P2 endopod (i.e. enp-2 with mucroniform process in *Z. arenicolus*).

#### Genus *Neozausodes* gen. nov.

Lang (1965) remarked on the close similarity between *Z. sextus* and the three Brazilian species *Z. limigenus*, *Z. stammeri* and *Z. paranaguaensis*. Geddes (1968a) regarded *Z. areolatus* as morphologically closest to *Z. sextus*. As a result of the phylogenetic analysis these 5 species together with *N. shulenbergeri* sp. nov. are grouped here in a new genus.

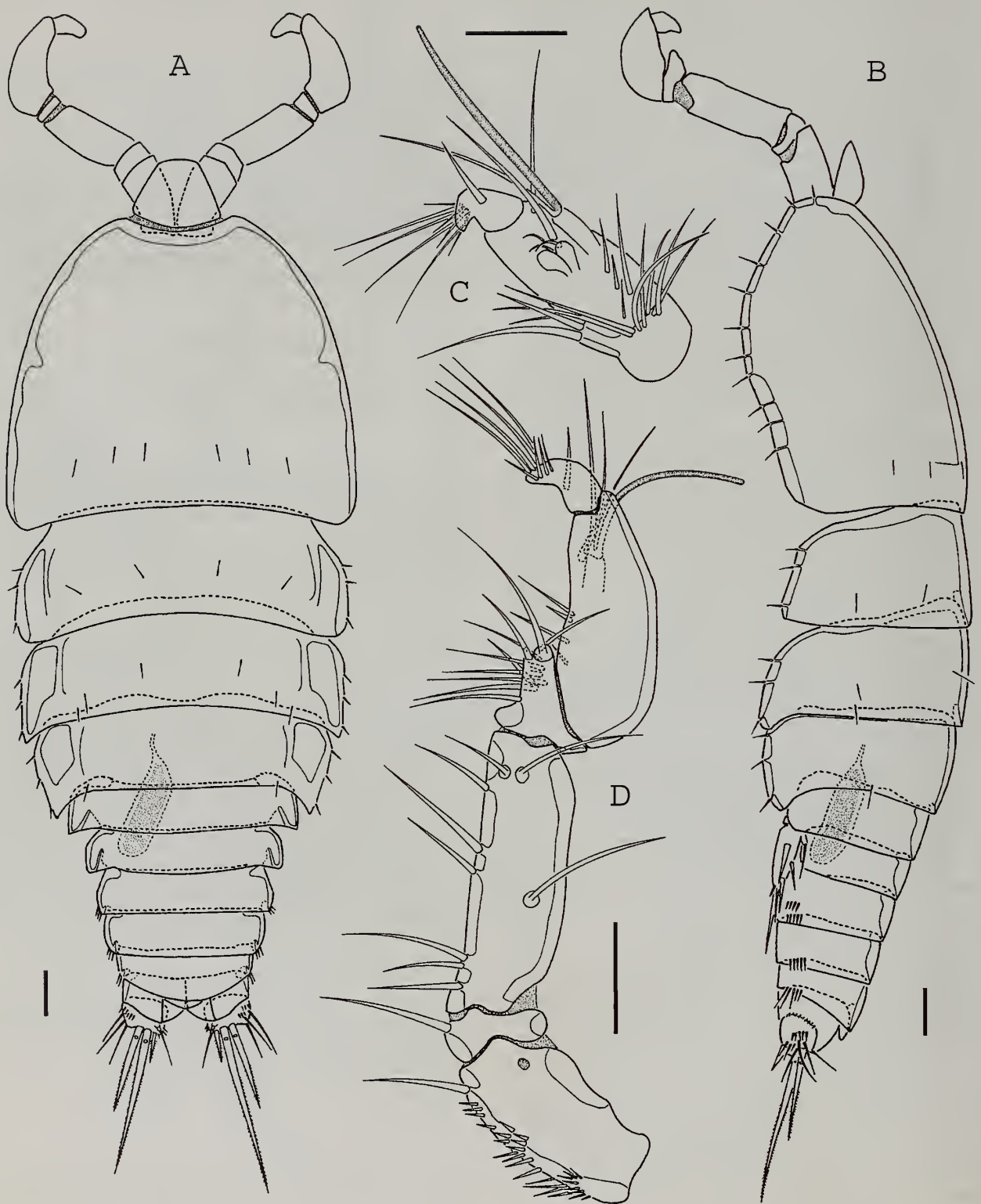


Fig. 6 *Zausodes arenicolus* C.B. Wilson, 1932 (♂). A, Habitus, dorsal view; B, habitus, lateral view; C, antennule, fifth and sixth segments, anterior view; D, antennule, dorsal view. Scale bars = 20  $\mu$ m.

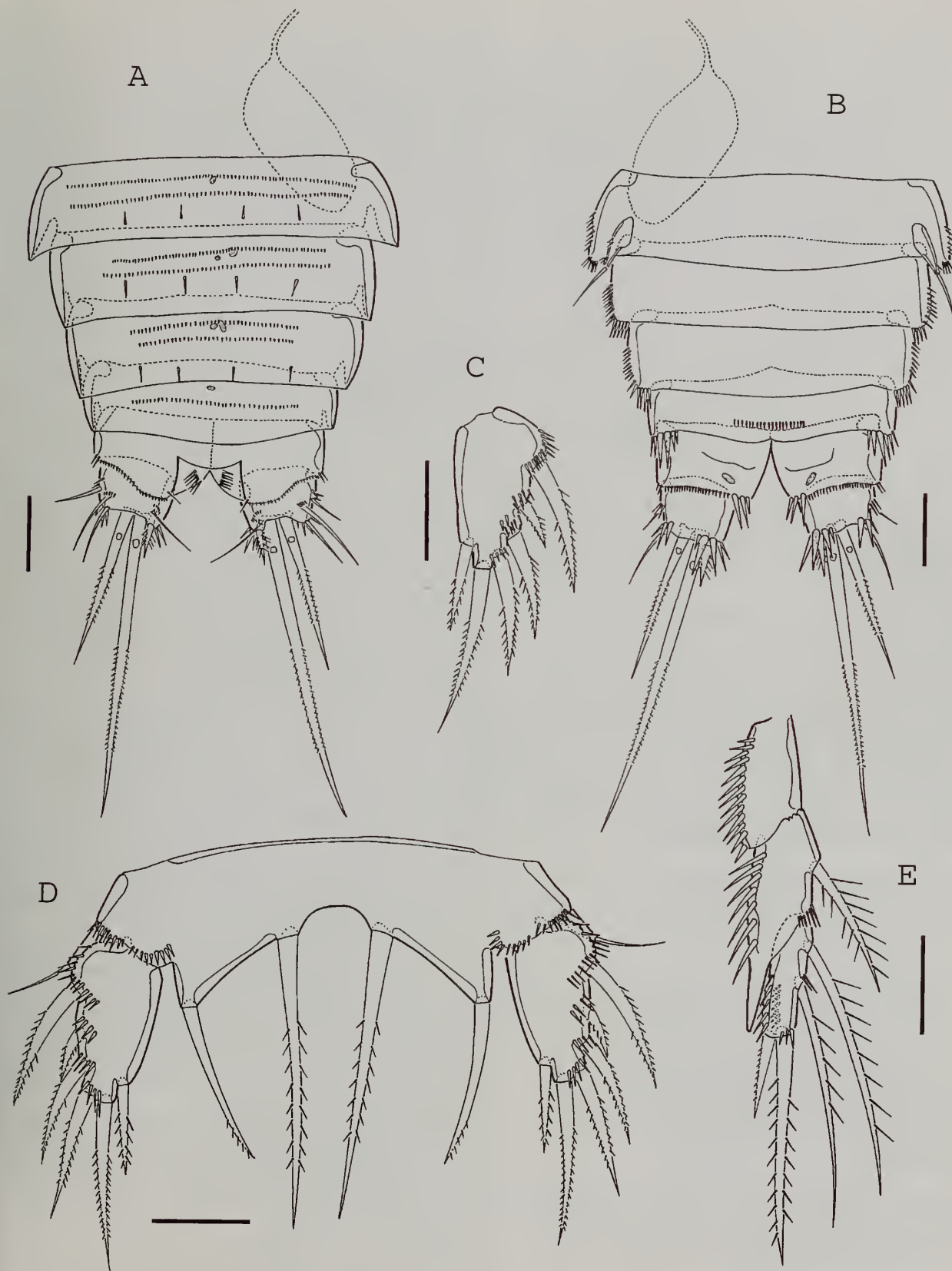


Fig. 7 *Zausodes arenicolus* C.B. Wilson, 1932 (♂). A, Urosome, dorsal view; B, urosome, ventral view; C, P5 exopod, posterior view; D, P5, anterior view; E, P2 endopod. Scale bars = 20  $\mu$ m.

DIAGNOSIS. Harpacticidae. Antennule ♀ 6- or 7-segmented, without pinnate or plumose setae on segments 1–6; with strong, modified spines on segments 3–5 and enlarged pectinate or pinnate spines on segment 6. Antennule ♂ with modified spine on segment 3. Antennary exopod 1-segmented, with 2 apical setae. Maxilla with 3 spines/ setae on praecoxal endite. P2 endopod 3-segmented (2- in ♂ of *N. areolatus*), P3 endopod 2- or 3-segmented, P4 endopod 2-segmented. P2 ♀ enp-3 with 1–2 inner setae. P3 ♀ enp-2 without inner seta. P4 exp-3 with 3 outer spines in both sexes. P4 enp-2 with 1 inner seta in both sexes. P2 ♂ enp-2 without apophysis, inner seta (proximal one in 2-segmented endopod of *N. areolatus*) not modified; enp-3 (-2 in *N. areolatus*) with 1 apical seta (inner one lost), outer spine not fused to segment. P3 ♂ enp-2 outer distal corner not attenuated.

Swimming leg setal formula:

	exopod	endopod	
P2	0.1.223	0.1.221 or 0.1.121	[♀]
		0.1.211	[♂ <i>sextus</i> ]
		0.311	[♂ <i>areolatus</i> ]
		0.1.111	[♂ ♂ other species]
P3	0.1.323	1.0.221 or 1.221	
P4	0.1.323	1.121	

P5 exopod round in both sexes. P5 endopodal lobe ♀ expressed; all setae well developed.

Sexual dimorphism in rostrum, antennule, P2 endopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Zausodes areolatus* Geddes, 1968a = *Neozausodes areolatus* (Geddes, 1968a) comb. nov.

OTHER SPECIES. *Z. limigenus* Jakobi, 1954 = *N. limigenus* (Jakobi, 1954) comb. nov.; *Z. paranaguaensis* Jakobi, 1954 = *N. paranaguaensis* (Jakobi, 1954) comb. nov.; *Z. stammeri* Jakobi, 1954 = *N. stammeri* (Jakobi, 1954); *Z. sextus* Lang, 1965 = *N. sextus* (Lang, 1965) comb. nov.; *N. shulenbergi* sp. nov.

ETYMOLOGY. The generic name is derived from the Greek prefix *neos*, meaning new, and alludes to the advanced position of this genus within the *Zausodes*-group. Gender: masculine.

*Neozausodes areolatus* (Geddes, 1968a) comb. nov.

TYPE LOCALITY. Bahamas, Eleuthera, SW of Glass Window; 25°26'03"N, 76°36'10"W; 5 m depth, sand bottom.

MATERIAL EXAMINED.

American Museum of Natural History: holotype ♀ dissected and mounted on 3 slides (AMNH 12944); paratypes are 1 ♀ and 1 ♂ dissected on 3 slides each, and 8 ♀ ♀ in alcohol, collected from type locality (AMNH 12945). Note that the holotype registration number was inadvertently misprinted in Geddes (1968a) as 12949.

Zoological Museum of the University of Bergen: paratypes (2 ♂ ♂, 3 ♀ ♀) from Exuma Cays, Great Guana Cay, between White Point and Black Point, 24°04'25"N, 76°23'45"W; 3–4 m depth, sand bottom (ZMUB 49315).

REDESCRIPTION. All female illustrations are from the holotype except Figs 8B–C, which are from paratypes. Male habitus and P5 illustrations are from a Bergen Museum paratype; other male illustrations are from an AMNH paratype.

FEMALE. Body length measurements from AMNH paratypes: measured from anterior margin of rostrum to posterior margin of caudal rami:  $\bar{x}$  = 606  $\mu$ m (n = 3); without rostrum and caudal rami:

$\bar{x}$  = 561  $\mu$ m (n = 3). Body (Figs 8B–C, 9B–C) dorsoventrally flattened. Body width:  $\bar{x}$  = 314  $\mu$ m (n = 3). Integumental surface (e.g. A1, rostrum, urosome) with areolated ornamentation/sculpturing (not illustrated). Sensillae present dorsally and dorsolaterally on urosomites 2–4 and anal somite. Urosomites 2–5 with fine denticle rows dorsally and dorsolaterally; antepenultimate and penultimate somites with ventral spinular rows; anal somite with spinular rows dorsally, ventrally, and laterally on the posterior margin. Ventral posterolateral corners of urosomites 4–5 and lateral margins of urosomites 2–4 with spinules. Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is partially exposed in dorsal and ventral aspects; with two ventral pores near posterior margin; anal operculum and reduced pseudoperculum present. Caudal rami (Figs 8B–C, 9B–C) wider than long, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. No gelatinous string was present.

Rostrum (Fig. 9A) prominent, lateral margins roughly parallel, defined at base; with two short sensillae anteriorly and two sensillae subdistally; with middorsal pore.

Antennule (Fig. 8A) 6-segmented; segments 1 and 2 longest; first segment widest with spinules; fourth segment with an aesthetasc (50  $\mu$ m long), a surface indentation running from the anterior margin towards, but not reaching, the posterior margin, and an uninterrupted cuticle extending the length of the posterior margin; with setal formula 1–[1], 2–[10], 3–[8 + 2 unipinnate], 4–[4 + 2 unipinnate + (1 + ae)], 5–[6 + 2 pinnate], 6–[5 + acrothek]. The setal formula was based on the holotype, but setae missing in the holotype specimen that were found in the paratypic slides were added to the formula. Added setae include 1 seta from segment 2, 1 unipinnate seta from segment 3, and 1 seta from segment 5. The setation in the illustration is a composite, showing all setae.

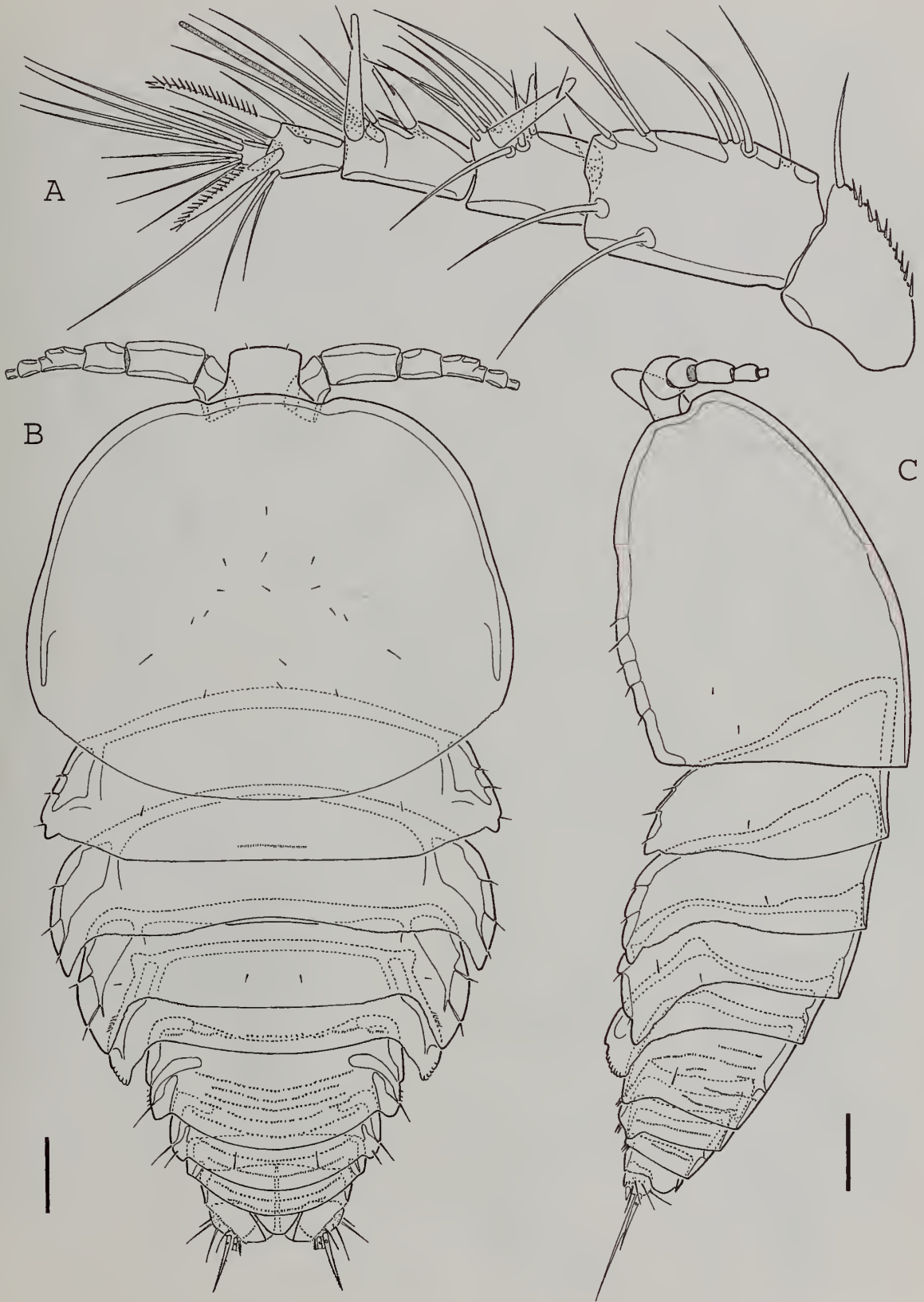
Antenna (Fig. 9D). Coxa short and unornamented; allobasis with spinular row, abexopodal seta, and membranous insert marking original segment boundary between basis and first endopod segment; free endopod 1-segmented; lateral armature consisting of a pinnate spine and 1 pinnate, 1 short bare, and 1 long bare seta; distal armature comprising 1 seta, 1 unipinnate, curved spine, and 4 geniculate spines, longest one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinular rows and hyaline surface frill as indicated in Fig. 9D; exopod 1-segmented with 2 distal, unequal setae and a spinular row. The short, bare, lateral seta of the endopod was found on the paratype but could not be discerned on the holotype.

Mandible (Fig. 10A). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 3 bipinnate setae (one of which broken off in the holotype but observed in the paratype); endopod longer than exopod, with 1 bare and 1 pinnate lateral seta and 6 apical setae; exopod with 3 lateral and 4 distal setae and subdistal spinules.

Maxillule (Fig. 10C). Praecoxa with spinular row along outer edge and with arthritis bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 5 setae; basal endite with 6 setae; endopod with 3 pinnate setae distally and a lateral spinular row; exopod with 1 pinnate inner seta, 1 bare and 2 pinnate distal setae.

Maxilla (Figs 10E–F). Syncoxa with 3 endites; praecoxal endite with 3 bipinnate setae; coxal endites each with 1 bare seta and 2 pinnate setae; allobasis with claw and 3 bare setae; endopod 1-segmented with 1 distally pinnate and 3 bare setae.

Maxilliped (Fig. 10D). Syncoxa with a pinnate seta and numerous



**Fig. 8** *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, Antennule; B, habitus, dorsal view (somewhat distorted); C, habitus, lateral view. Scale bars = 50 µm.

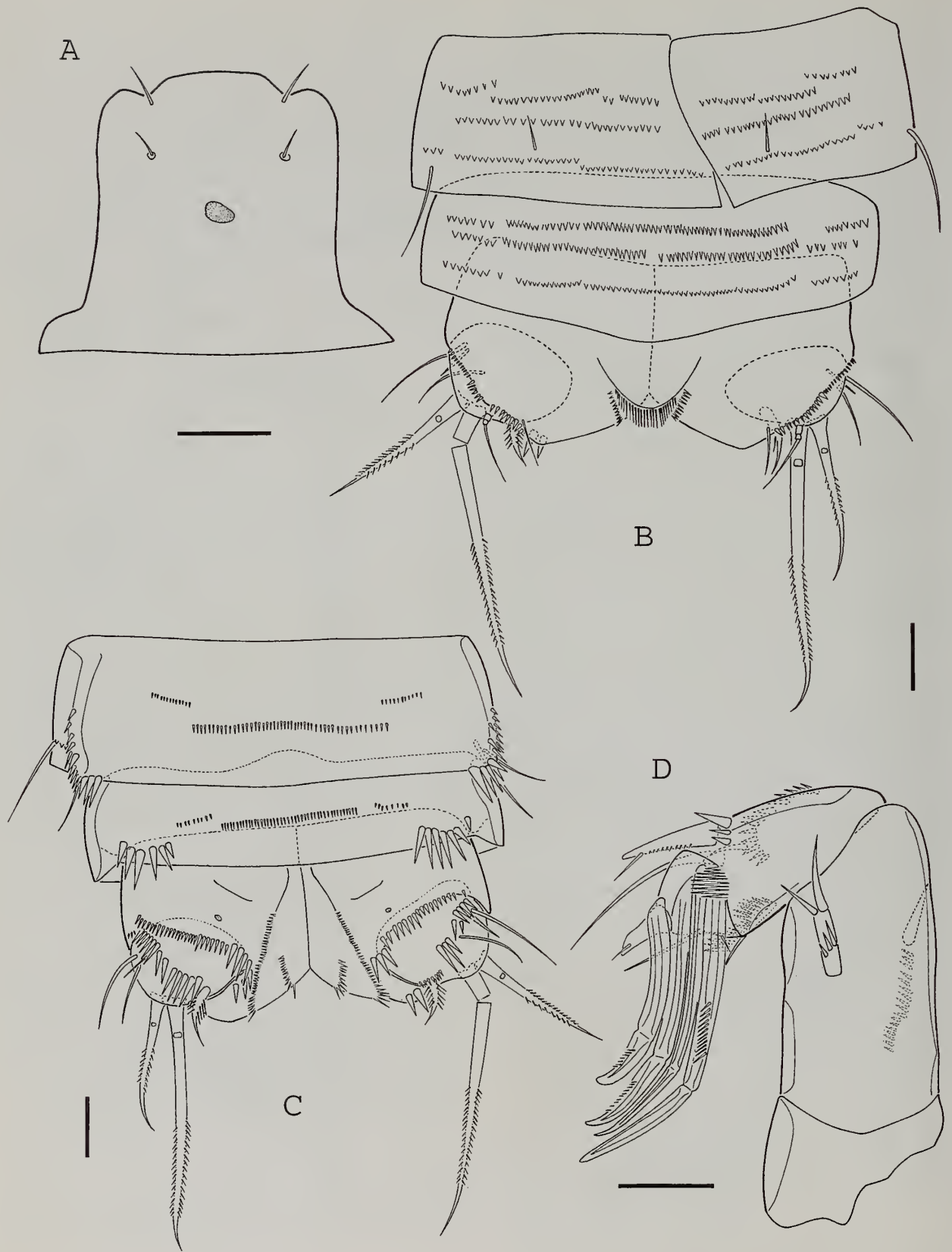


Fig. 9 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, Rostrum; B, last 3 urosomites and caudal rami, dorsal view; C, same, ventral view; D, antenna. Scale bars = 20  $\mu$ m.

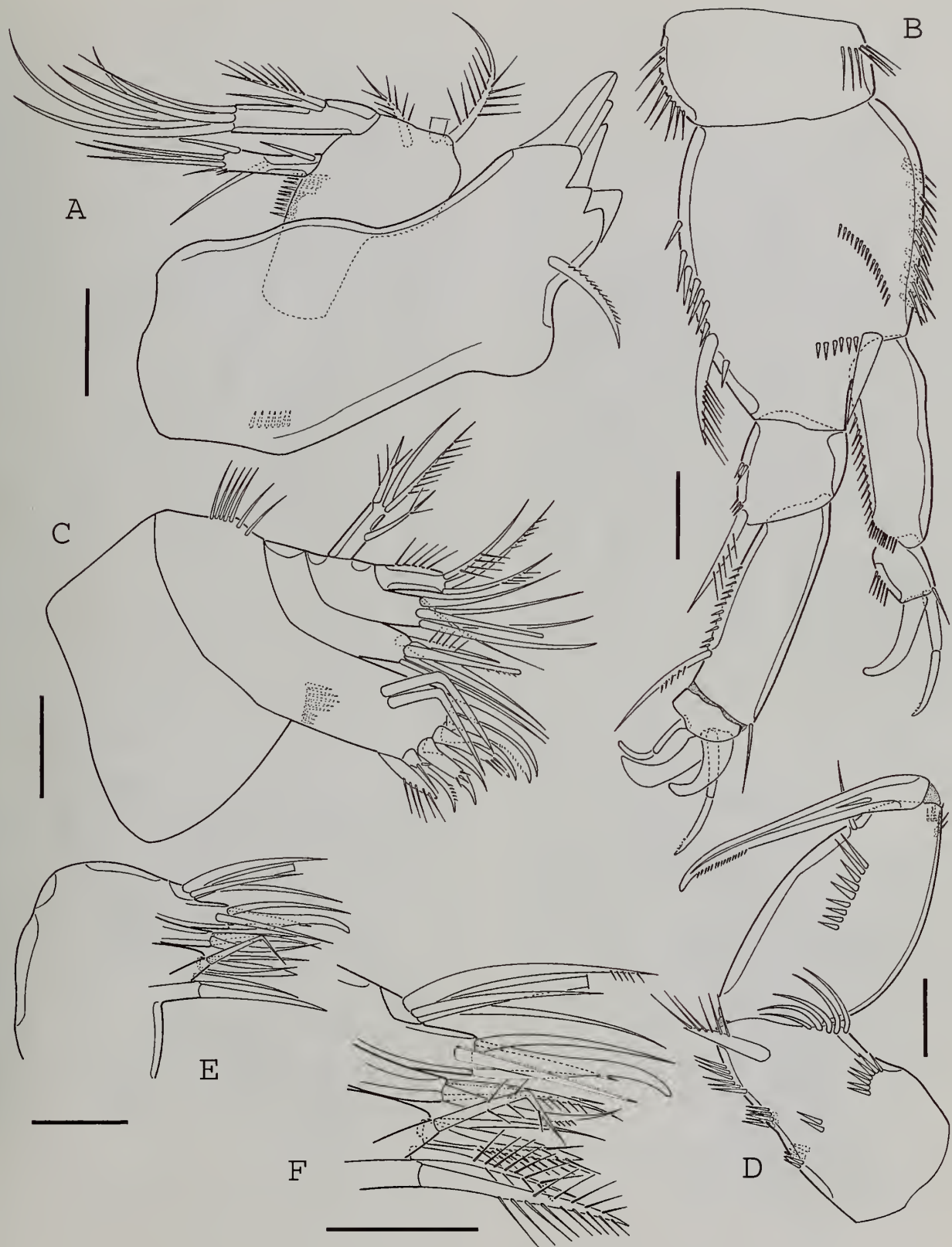


Fig. 10 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, Mandible; B, P1; C, maxillule; D, maxilliped; E, maxilla; F, maxillary endites. Scale bars = 20 μm.

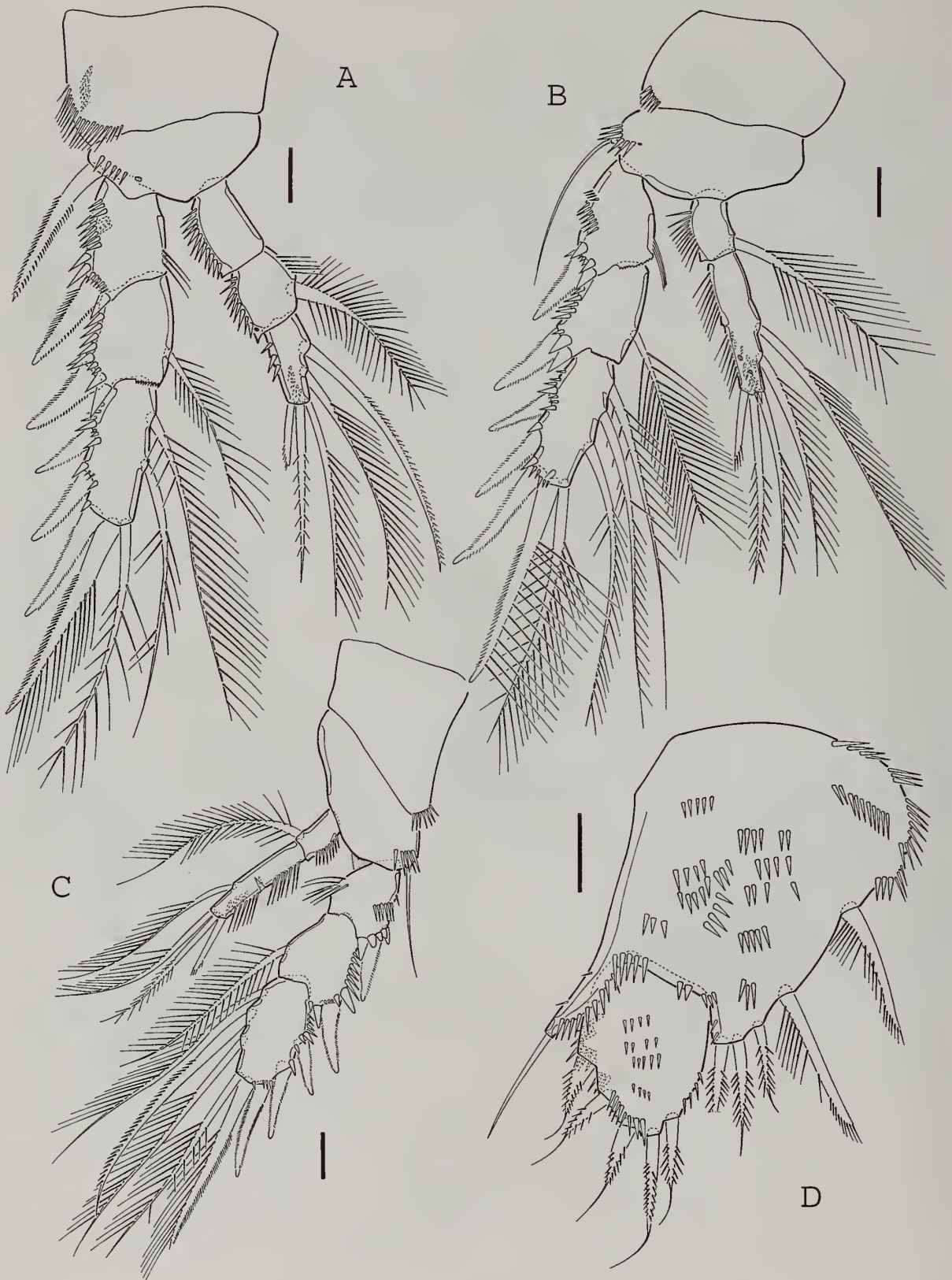


Fig. 11 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♀). A, P2; B, P3; C, P4; D, P5. Scale bars = 20 µm.



spinular rows as indicated in Fig. 10D; basis with a spinular row and seta along palmar margin, with spinules along outer distal margin; endopod represented by acutely recurved claw, spinulose along the distal inner margin, with proximal accessory seta.

P1 (Fig. 10B) Rami prehensile; coxa with spinular rows along inner and outer margins; basis with pinnate seta subdistally at outer margin and spine near articulation with endopod; spinular rows present along inner and outer margins and on anterior face. Exopod 3-segmented, 1.3 times as long as endopod (excluding apical elements); exp-1 with distal pinnate seta and spinular rows along outer margin; exp-2 elongate, 2.1 times as long as exp-1, with short, slender inner seta distally and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate, with outer spinular row; enp-2 0.3 times as long as enp-1, with outer spinular row and bearing geniculate spine, claw, and short, slender inner seta distally.

P2–P4 (Figs 11A–C) with 3-segmented exopods; endopod 3-segmented in P2 and 2-segmented in P3–P4 with the distal segment comprised of two fused segments; indentations mark the plane of fusion. Coxae with spinular rows at outer distal corner and posteriorly near outer margin of P2. Bases with outer bipinnate spine (P2) or naked seta (P3–P4), spinules, and a pore (P2–P3) near outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P2–P4 terminal endopodal segments. Spinular rows present on posterior surfaces of P4 exp-1, -2, and -3 in the paratype. Pores present as illustrated (Figs 11A–C). Seta and spine formula of P2–P4 as in Table 1.

P5 (Fig. 11D) biramous, not fused medially. Baseoendopod with numerous anterior surface and marginal spinular rows; endopodal lobe triangular, with 3 bipinnate and 2 pinnate setae; outer basal seta slender and arising from cylindrical process. Exopod 1.2 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer bipinnate spines with flagellate tips. A posterior margin row of spinules on the baseoendopod was left out of the illustration to increase clarity.

**MALE.** Body length (from Bergen museum paratypes) measured from anterior margin of rostrum to posterior margin of caudal rami:  $\bar{x}$  = 506  $\mu$ m ( $n$  = 2); without rostrum and caudal rami:  $\bar{x}$  = 454  $\mu$ m ( $n$  = 2). Body width:  $\bar{x}$  = 264  $\mu$ m ( $n$  = 2). Not all sensillae shown in habitus views (Figs 12A–B). Sexual dimorphism in body size, rostrum, antennule, P2 endopod, P5, and urosome segmentation (Figs 12A–B). The P6 could not be observed.

Rostrum (Fig. 12B) oval, twice as wide as long; with two sensillae anteriorly and one sensilla on each mediolateral margin; with mid-dorsal pore.

Antennule (Figs 12E–F) 6-segmented, chirocer; segment 5 not conspicuously swollen; segments 3 and 5 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; segment 5 with aesthetasc (55  $\mu$ m long) and anterior distal corner produced into blunt apophysis; with setal formula 1–[1], 2–[1], 3–[9], 4–[9], 5–[8 + (1 + ae) + 4 modified], 6–[6 + acrothek].

P2 (Fig. 12D) as in ♀ except for endopod. Endopod 2-segmented with the distal segment derived by fusion of two segments. Enp-1 with outer row of spinules. Enp-2 with pronounced indentations marking the plane of fusion and continuous cuticle between fused segments; with spinulose outer margin; inner margin with 3 pinnate setae; distal margin with short distally pinnate spine and long bipinnate spine; posterior face with spinules. Pore present as illustrated (Fig. 12D).

P5 (Fig. 12C) baseoendopods fused medially forming transversely elongate plate (one half of plate illustrated); each side with 2 setae, slender outer basal seta arising from cylindrical process, and spinules around articulation with exopod. Exopod as in ♀ except for an additional small, bipinnate seta along the outer margin, and fewer spinular rows.

#### NOTES.

The holotype urosome is damaged showing a break between urosomites 3 and 4. The distal portion of the urosome is reillustrated here to provide additional information for the anal somite and caudal rami.

Inspection of the holotype and paratypes revealed that what Geddes (1968a) illustrated as discrete segments 4 and 5 of the female antennule is in reality a single segment. This segment has a surface suture, which Geddes illustrated as a functional articulation between two segments, running subdistally from the anterior towards the posterior margin. However, the surface suture is incomplete and does not reach the posterior margin. Also, the continuity of the cuticle along the posterior margin further supports the interpretation of a single compound segment rather than two distinct segments.

The male P2 endopod also has a fusion not described by Geddes (1968a). The two distal segments are fused into a single segment indicated by a continuous cuticle running through the plane of fusion. The membranous insert indicating the line of fusion (Fig. 12D) and the outer corner projection on what Geddes illustrated as the second segment may have been the source of his misinterpretation of the endopod segmentation.

This redescription has revealed additional setae, not found in Geddes' description, on the following appendages in the female: antennule (segments 2–6), antenna (allobasis and endopod), mandible (exopod and endopod), maxillule (coxal and basal endites), maxilla (syncoxal endites and endopod), maxilliped (endopodal claw), P1 and P4 (basis), and caudal rami. Additional setae were also found on the male antennule (segments 2–6).

#### *Neozausodes limigenus* (Jakobi, 1954) comb. nov.

**TYPE LOCALITY.** Brazil, Paraná State; Baía de Paranaguá, Ilha do Mel, Mar de Dentro.

#### NOTES.

Jakobi's (1954) deficient description is very brief and contains several internal inconsistencies (Lang, 1965). According to the author the male is unknown but in the description of *Z. paranaguaensis* he states that there is no sexual dimorphism in the swimming legs. He further claims that the armature formula of P2–P4 is identical in *Z. limigenus* and *Z. stammeri*, however, according to his table on p. 223 the outer spine of P4 enp-2 is missing in the former. This character, which was not figured by Jakobi, is unique within the former *Zausodes* complex and requires confirmation. The species is placed in *Neozausodes* on account of the 7-segmented ♀ antennule, the presence of large uniserrate spines on the penultimate segment of this appendage, and the round P5 exopod.

#### *Neozausodes paranaguaensis* (Jakobi, 1954) comb. nov.

**TYPE LOCALITY.** Brazil, Paraná State; Baía de Paranaguá, Ilha do Mel, Mar de Dentro.

#### NOTE.

According to Jakobi (1954) males of this species possess a small inner seta on P3–P4 exp-1. Since the author did not illustrate but only tabulated this character, and none of the other species of the

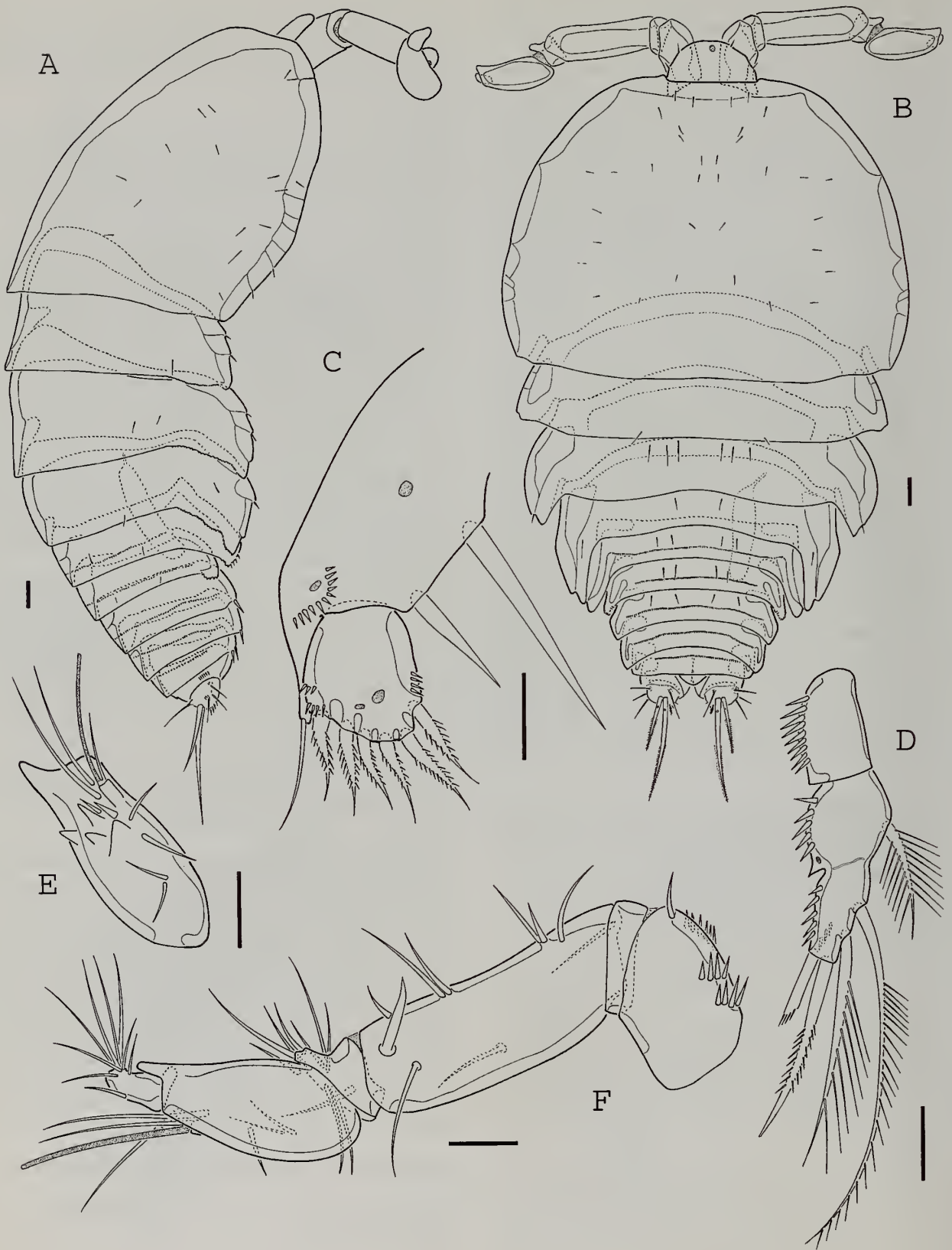


Fig. 12 *Neozausodes areolatus* (Geddes, 1968a) comb. nov. (♂). A, Habitus, lateral view; B, habitus, dorsal view; C, P5; D, P2 endopod; E, antennule, segment 5, anterior view; F, antennule, dorsal view. Scale bars = 20  $\mu$ m.

former *Zausodes* complex displays such kind of sexual dimorphism, we regard this observation as extremely doubtful. The first exopod segment of legs 2–4 often has an inner tuft or row of long setules which can easily be misinterpreted as a small seta. The species is placed in *Neozausodes* on the same grounds as for the previous one.

*Neozausodes stammeri* (Jakobi, 1954) comb. nov.

TYPE LOCALITY. Brazil, Paraná State; Baía de Paranaguá, Ilha do Mel, Mar de Dentro.

NOTE.

This is the most completely described of Jakobi's (1954) species. There is, however, no doubt that this species requires redescription before it can be unambiguously identified. Given the limited detail in the illustrations, the differences between *N. limigenus* and *N. stammeri* are not impressive, raising the suspicion that both are conspecific.

*Neozausodes sextus* (Lang, 1965) comb. nov.

TYPE LOCALITY. California, Monterey Bay, off Hopkins Marine Station; sand at about 7 m depth.

*Neozausodes shulenbergeri* sp. nov.

SYNONYMY. *Zausodes* cf. *arenicolus sensu* Ravenel & Thistle (1981) [ecology]. *Zausodes arenicolus sensu* Varon & Thistle (1988) [ecology].

TYPE LOCALITY. Gulf of Mexico: 29°51'N, 84°31'W (about 50 m north of day mark #2), St. George Sound, Florida, 5 m depth, unvegetated medium sand (median grain size = 0.254 mm); a seagrass meadow occurs about 150 m to the north; see Foy & Thistle (1991) for additional description.

MATERIAL EXAMINED.

The Natural History Museum: holotype ♀ in alcohol (BMNH 1999.192); allotypic paratype ♂ in alcohol (BMNH 1999.193); other paratypes are 1 ♀ in ethanol (BMNH 1999.194) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.195–198).

National Museum of Natural History (Smithsonian Institution, Washington, D.C.): additional paratypes represented by 2 ♀ ♀ and 1 ♂ in alcohol (USNM 288448–449) and 2 ♀ ♀ and 2 ♂ ♂ on slides (USNM 288447).

DESCRIPTION. All illustrations are from paratypes except Figs 13C–D which are from the holotype.

FEMALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 443 µm ( $\bar{x}$  = 451 µm,  $n$  = 4); without rostrum and caudal rami: 411 µm ( $\bar{x}$  = 419 µm,  $n$  = 4). Body (Figs 13C–D, 16A,C) dorsoventrally flattened. Greatest width: 193 µm ( $\bar{x}$  = 196 µm,  $n$  = 4) near posterior margin of cephalosome. Naupliar eye distinct; reddish brown in fresh, unstained specimens; invisible in cleared specimens. Integument with surface ornamentation/sculpturing consisting of irregular pattern of fine striations and cephalothorax pitted (not illustrated). Sensillae present dorsally and dorsolaterally on cephalothorax and body somites except penultimate one (not all shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of thoracic somites thickly chitinized laterally. Third thoracic somite and urosomites 1–5 with fine spinular rows dorsally and dorsolaterally; penultimate and antepenultimate somites with ventral spinular row (Fig. 16C); anal somite with spinular rows dorsally, ventrally, and laterally on the posterior margin (Fig. 16A,C). Lateral margins of free thoracic somites with

2 sensillae. Ventral posterolateral corners of urosomites 2–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is partially exposed in dorsal aspect; with ventral pore near posterior margin; anal operculum and pseudoperculum present. Caudal rami (Figs 13C–D, 16A,C) approximately as long as wide, with 7 setae; setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string (Figs 16A,C) extending posteriorly from each caudal ramus present in some specimens.

Rostrum (Fig. 13A) prominent, bell-shaped, defined at base; with two short sensillae anteriorly and one sensilla on each mediolateral margin; with middorsal pore.

Antennule (Figs 14A–B) 7-segmented; segments 1 and 2 longest; first segment widest with several spinular rows; segment 4 with aesthetasc (35 µm long); segment 7 with acrothek consisting of 3 elements (probably 2 setae and 1 aesthetasc, however, we were unable to distinguish which elements were setae and which was an aesthetasc); with setal formula 1–[1], 2–[10], 3–[7 + 2 unipinnate], 4–[3 + 1 unipinnate + (1 + ae)], 5–[1 + 1 unipinnate], 6–[6 + 2 pinnate], 7–[5 + acrothek].

Antenna (Fig. 13B). Coxa short and unornamented; allobasis with spinular row, abexopodal spinulose seta, and cuticular thinning marking original segmentation of basis and first endopodal segment; free endopod 1-segmented; lateral armature consisting of a pinnate spine, 1 long and 1 short seta; distal armature comprising 1 seta, 1 pinnate curved spine, and 4 geniculate spines, longest one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinular rows and hyaline surface frill as indicated in Fig. 13B; exopod 1-segmented with 1 lateral short seta and 1 distal bipinnate seta.

Labrum well developed, not medially incised.

Mandible (Fig. 14E). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod longer than exopod, with 1 bare and 1 pinnate lateral setae and 6 apical setae; exopod with 1 pinnate and 2 bare lateral setae, 1 pinnate and 2 bare distal setae, and subdistal spinular row.

Maxillule (Fig. 14D). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 4 setae and a spinular row; basal endite with 6 setae; endopod with 1 bare and 2 pinnate setae distally; exopod with 1 pinnate inner seta, 2 pinnate and 1 bare distal setae.

Maxilla (Fig. 14C). Syncoxa with spinular row along outer margin and 3 endites; praecoxal endite with 3 pinnate setae; coxal endites each with 2 bare setae and 1 pinnate seta; allobasis with claw and 3 bare setae; endopod 1-segmented with 4 bare setae.

Maxilliped (Fig. 14F). Syncoxa with a bipinnate seta and numerous spinular rows as indicated in Fig. 14F; basis with a spinular row and seta along palmar margin, with spinules along outer distal margin and on anterior face; endopod represented by acutely recurved claw with spinules along inner margin and proximal accessory seta.

P1 (Fig. 15C). Rami prehensile; coxa with spinular rows along outer margin and anterior face, with pore near inner distal corner; basis with bipinnate seta subdistally at outer margin and bipinnate spine at inner distal corner; spinular rows present along inner and outer margins, anterior face, and around articulation with endopod; with pore near outer seta. Exopod 3-segmented, 1.2 times as long as endopod (excluding apical elements); exp-1 with subdistal pinnate seta and spinular rows along outer margin; exp-2 elongate, 2.1 times

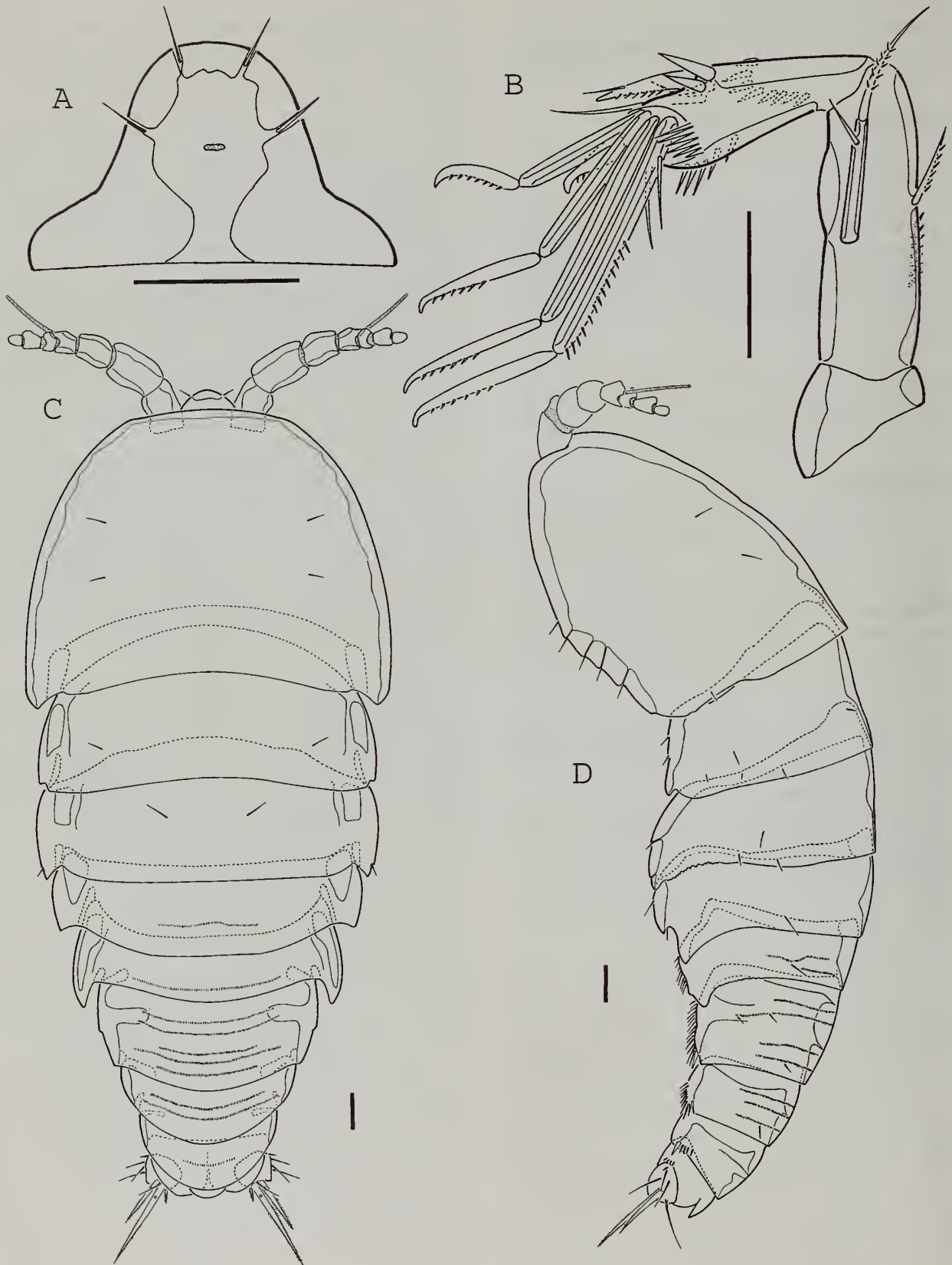


Fig. 13 *Neozausodes shulenbergeri* sp. nov. (♀). A, Rostrum; B, antenna; C, habitus, dorsal view; D, habitus, lateral view. Scale bars = 20  $\mu$ m.

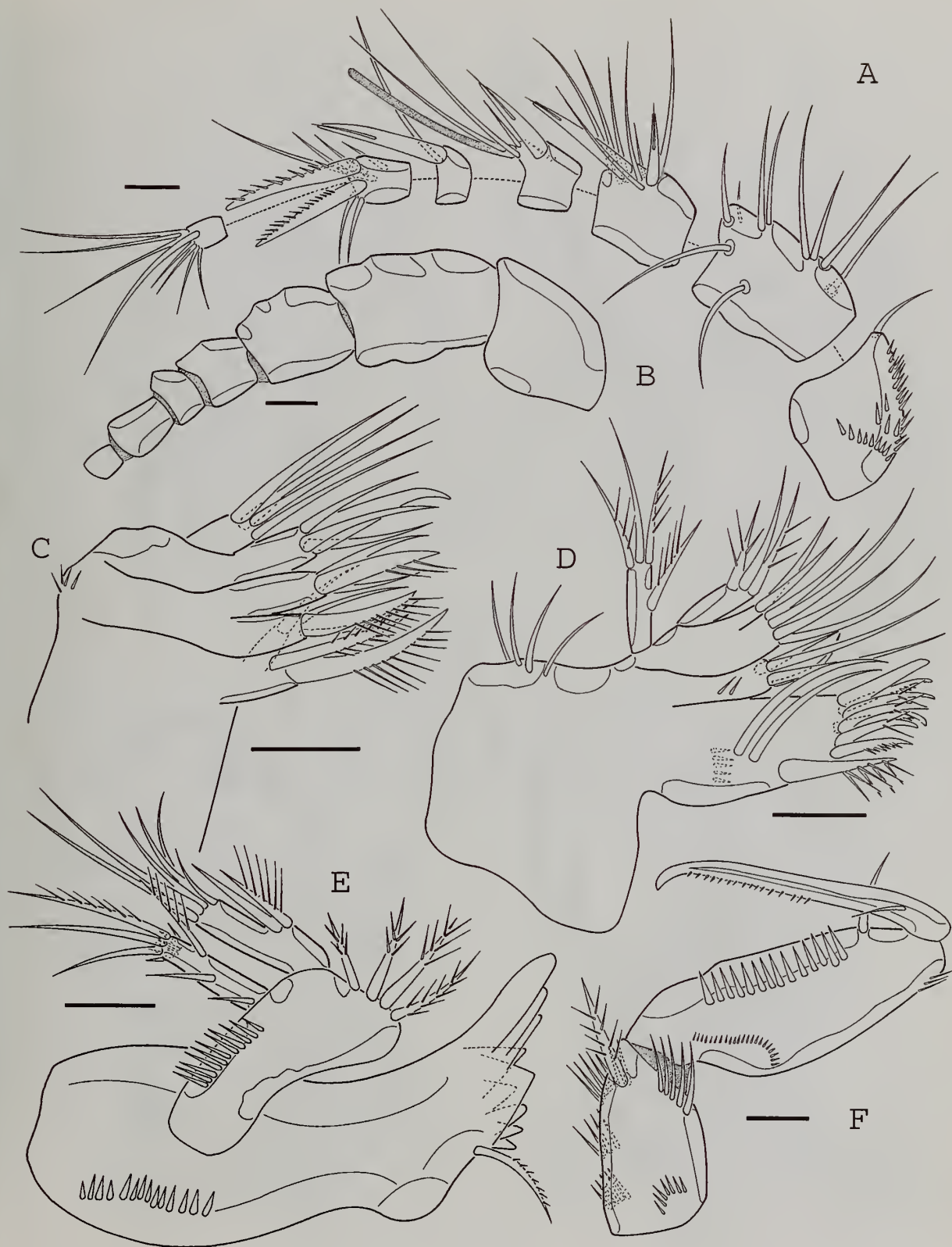


Fig. 14 *Neozausodes shulenbergeri* sp. nov. (♀). A, Antennule (disarticulated); B, antennule (armature omitted); C, maxilla; D, maxillule; E, mandible; F, maxilliped. Scale bars = 10  $\mu$ m.

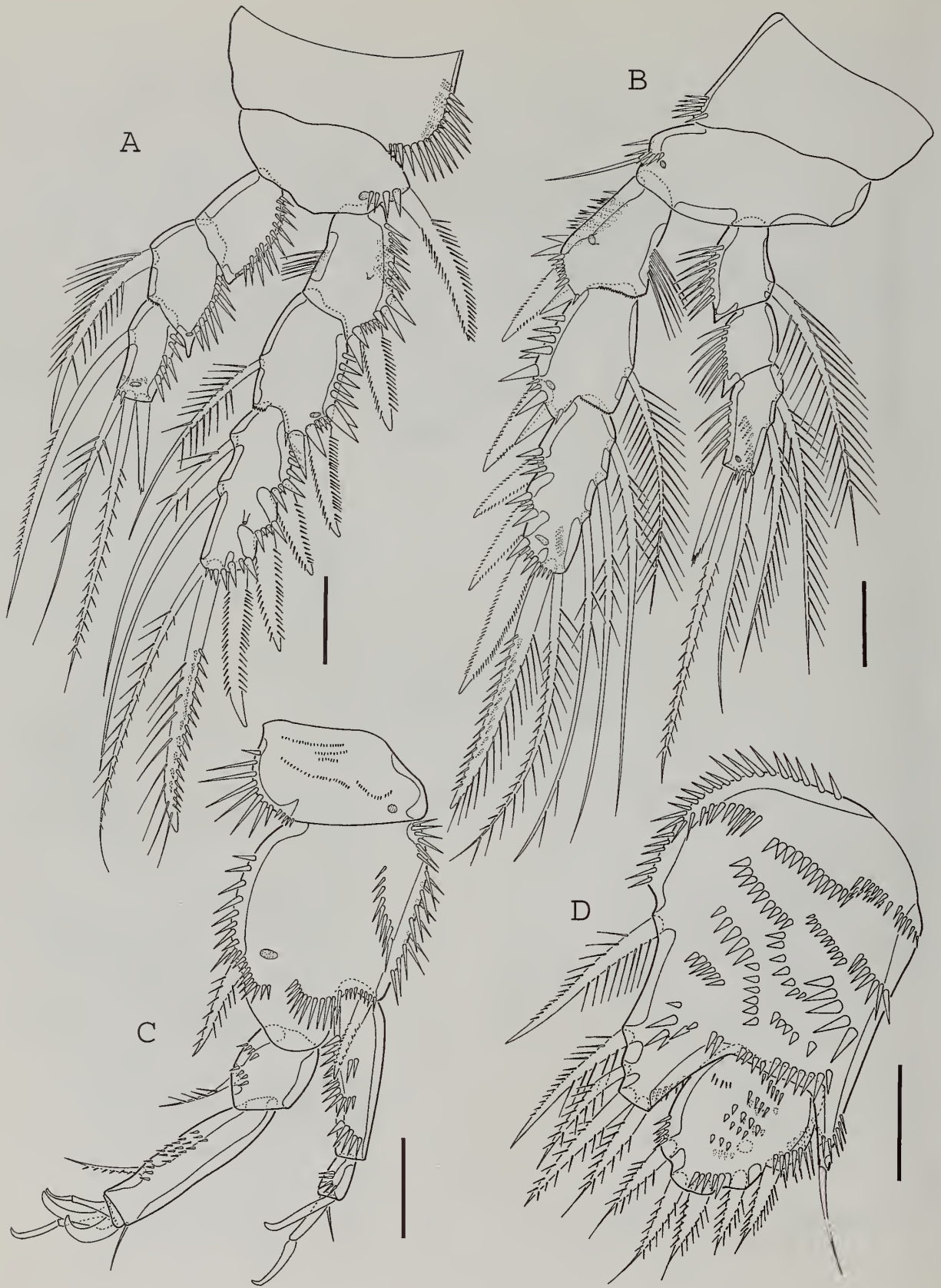


Fig. 15 *Neozausodes shulenbergeri* sp. nov. (♀). A, P2; B, P3; C, P1; D, P5. Scale bars = 20  $\mu$ m.

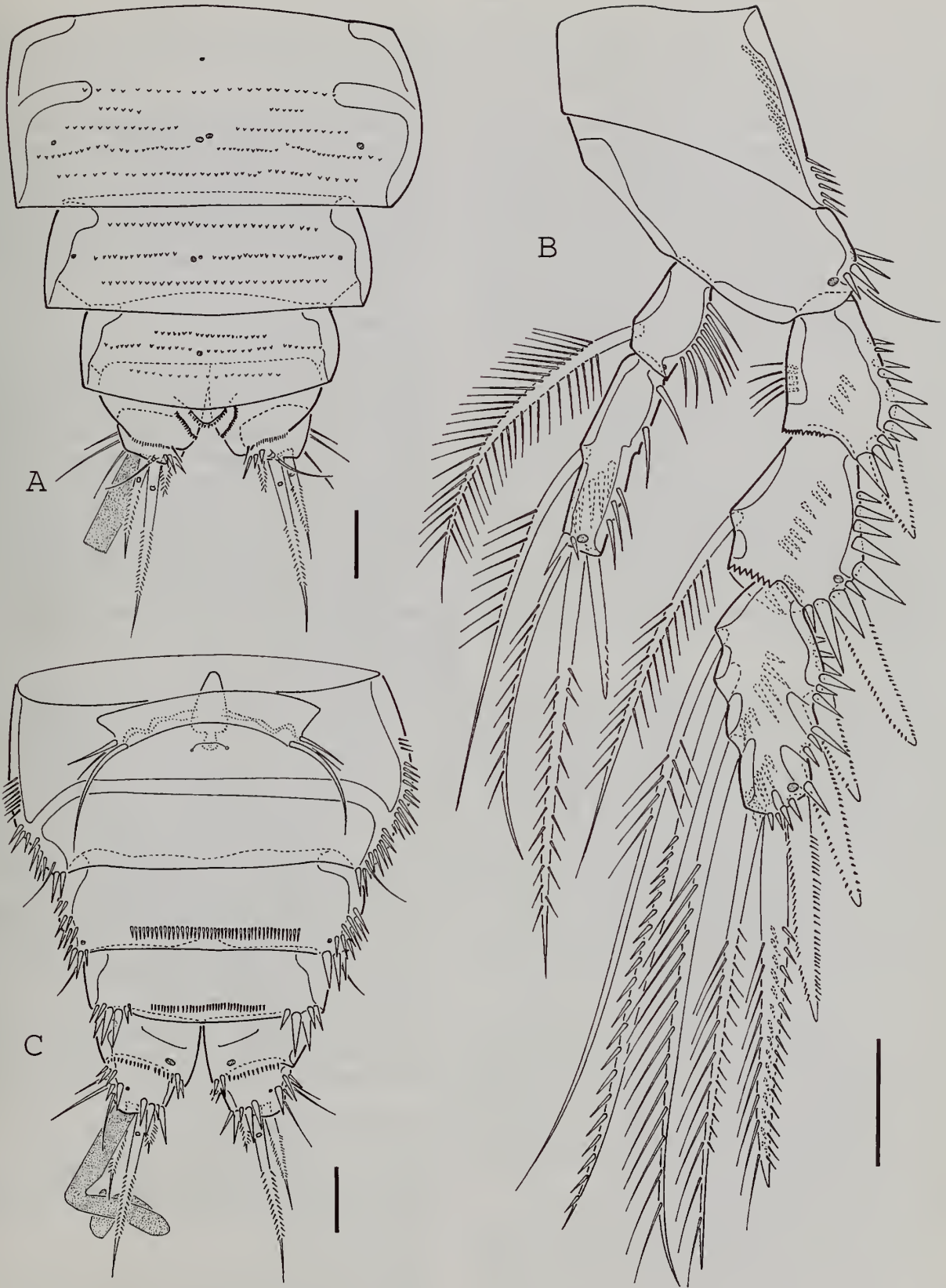


Fig. 16 *Neozausodes shulenbergeri* sp. nov. (♀). A, Urosome (excluding P5-bearing somite), dorsal view; B, P4; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20  $\mu$ m.

as long as exp-1, with short, slender inner seta distally and outer margin spinular rows extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate, with outer spinular rows extending to anterior face; enp-2 0.3 times as long as enp-1, with spinular row and bearing geniculate spine, claw, and short, slender inner seta distally.

P2–P4 (Figs 15A–B, 16B) with 3-segmented exopods and endopods 3-segmented in P2 and P3 and 2-segmented in P4 with the distal segment comprised of two fused segments; indentation at outer lateral margin marks the plane of fusion. Coxae with spinular rows at outer distal corner (P2–P4) and posteriorly near outer edge of P2 and P4. Bases with outer bipinnate spine (P2) or naked seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P3–P4 exp-3, P4 exp-1 and -2, P2–P4 terminal endopodal segments. Outer distal spine of P2–P4 exp-3 tripinnate. Pores present as illustrated (Figs 15A–B, 16B). Seta and spine formula of P2–P4 as in Table 1.

P5 (Fig. 15D) biramous, not fused medially. Baseopod with numerous anterior surface and marginal spinular rows; endopodal lobe triangular, with 5 bipinnate setae, outermost seta with flagellate tip; outer basal seta slender and arising from cylindrical process. Exopod 1.1 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer bipinnate spines, apical, inner, and distal outer ones with flagellate tips; posterior surface with pore.

Genital double somite (Figs 16A,C) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 3 naked setae.

**MALE.** Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 411  $\mu\text{m}$  ( $\bar{x}$  = 398  $\mu\text{m}$ ,  $n$  = 4); without rostrum and caudal rami: 367  $\mu\text{m}$  ( $\bar{x}$  = 362  $\mu\text{m}$ ,  $n$  = 4). Body width: 189  $\mu\text{m}$  ( $\bar{x}$  = 187  $\mu\text{m}$ ,  $n$  = 4). Not all sensillae shown in habitus views (Figs 17A–B). Sexual dimorphism in body size, rostrum (Fig. 17D), antennule, P2 endopod and exp-3, P3 enp-3 and exp-3, P5, P6, and urosome segmentation (Figs 18B–C).

Antennule (Fig. 18A) 6-segmented, chirocer ae-bearing segment not conspicuously swollen; segments 3 and 5 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; fifth segment with an aesthetasc (40  $\mu\text{m}$  long), 3 modified elements, and anterior distal corner produced into blunt apophysis; with armature formula 1–[1], 2–[1], 3–[8 + 1 unipinnate], 4–[9], 5–[9 + (1 + ae) + 3 modified], 6–[5 + acrothek].

P2 (Fig. 17C) as in  $\text{♀}$  except for endopod and exp-3. Enp-1 with 2 outer rows of spinules. Enp-2 with outer distal corner produced into apophysis, extending one half the length of enp-3; outer margin spinulose; inner margin with subdistal bipinnate seta. Enp-3 with spinulose outer margin, short distally pinnate outer spine, long bipinnate spine distally, and 1 bipinnate inner seta; with spinules at base of distal bipinnate spine. Exp-3 without posterior spinules found in  $\text{♀}$ . Pores present as illustrated (Fig. 17C).

P3 enp-3 and exp-3 without posterior spinules found in  $\text{♀}$ .

P5 (Fig. 18D) biramous. Baseopods fused medially forming transversely elongate plate; endopodal lobe slightly developed, with 1 outer, pinnate seta and 1 inner, bipinnate seta; outer basal seta slender, arising from cylindrical process; with spinules around articulation with exopods. Exopod as in  $\text{♀}$  except for an additional bipinnate seta along the outer margin, fewer spinular rows, and more pores.

P6 (Fig. 18C) symmetrical; with distal seta; located more laterally than in the  $\text{♀}$ .

**ETYMOLOGY.** Named for Dr. Eric Shulenberg, an administrator of scientific research who believed in the importance of taxonomy enough to fund some.

**NOTES.**

*N. shulenbergi* sp. nov. and the three Brazilian species (Jakobi, 1954) share the presence of only 1 inner seta on P2 enp-3. Species within this group are closely related and identification is best achieved by paying particular attention to the P1 endopod and the P5 in both sexes. The sexually dimorphic spinule rows on the posterior face of P2 exp-3 and P3 exp-3 and enp-3 are unique for this species but might well have been overlooked in some other congeners.

**Genus *Mucropedia* gen. nov.**

**DIAGNOSIS.** Harpacticidae. Antennule  $\text{♀}$  8-segmented, without pinnate or plumose setae on segments 1–6; without strong, modified spines on segments 3–5 or enlarged pectinate or pinnate spines on segment 6. Antennule  $\text{♂}$  without modified spines on segment 3. Antennary exopod 2-segmented, with armature formula [2, 2]. Maxilla with 4 spines/setae on praecoxal endite. P2–P3 endopods 3-segmented, P4 endopod 2- or 3-segmented. P2  $\text{♀}$  enp-3 with 2 inner setae. P3  $\text{♀}$  enp-2 without inner seta. P4 exp-3 with 2 outer spines in  $\text{♀}$  and 3 outer spines in  $\text{♂}$ . P4 enp-3 (or enp-2 when 2-segmented) with 2 inner setae in both sexes. P2  $\text{♂}$  enp-2 without distinct apophysis, inner seta modified into stout spine; enp-3 with 1 apical seta (inner one lost), outer spine fused to segment. P3  $\text{♂}$  enp-2 outer distal corner attenuated.

Swimming leg setal formula:

	exopod	endopod
P2	0.1.223	0.1.221 [ $\text{♀}$ ] 0.1.211 [ $\text{♂}$ ]
P3	0.1.323	1.0.221
P4	0.1.322 [ $\text{♀}$ ] 0.1.323 [ $\text{♂}$ ]	1.0.221 or 1.221

P5 exopod elongate-oval in both sexes. P5 endopodal lobe  $\text{♀}$  not developed; distalmost inner seta rudimentary.

Sexual dimorphism in rostrum, antennule, P2 endopod, P3 endopod, P4 exopod, P5, P6, genital segmentation and size.

**TYPE SPECIES.** *Mucropedia cookorum* gen. et sp. nov.

**OTHER SPECIES.** *M. kirstenae* sp. nov.

**ETYMOLOGY.** The generic name is derived from the Latin *mucro*, meaning sharp point, and *pes*, meaning foot, and refers to the apophysis present on P3 enp-2 in the male. Gender: feminine.

***Mucropedia cookorum* sp. nov.**

**TYPE LOCALITY.** Gulf of Mexico: 29°40.63'N, 84°22.80'W, northern Gulf of Mexico, 18 m depth, unvegetated medium sand; see Thistle *et al.* (1995) for additional description.

**MATERIAL EXAMINED.**

The Natural History Museum: holotype  $\text{♀}$  in alcohol (BMNH 1999.199); allotypic paratype  $\text{♂}$  in alcohol (BMNH 1999.200); other paratypes are 2  $\text{♀}$  and 1  $\text{♂}$  in ethanol (BMNH 1999.201–203) and 2  $\text{♀}$  and 2  $\text{♂}$  on slides (BMNH 1999.204–207).



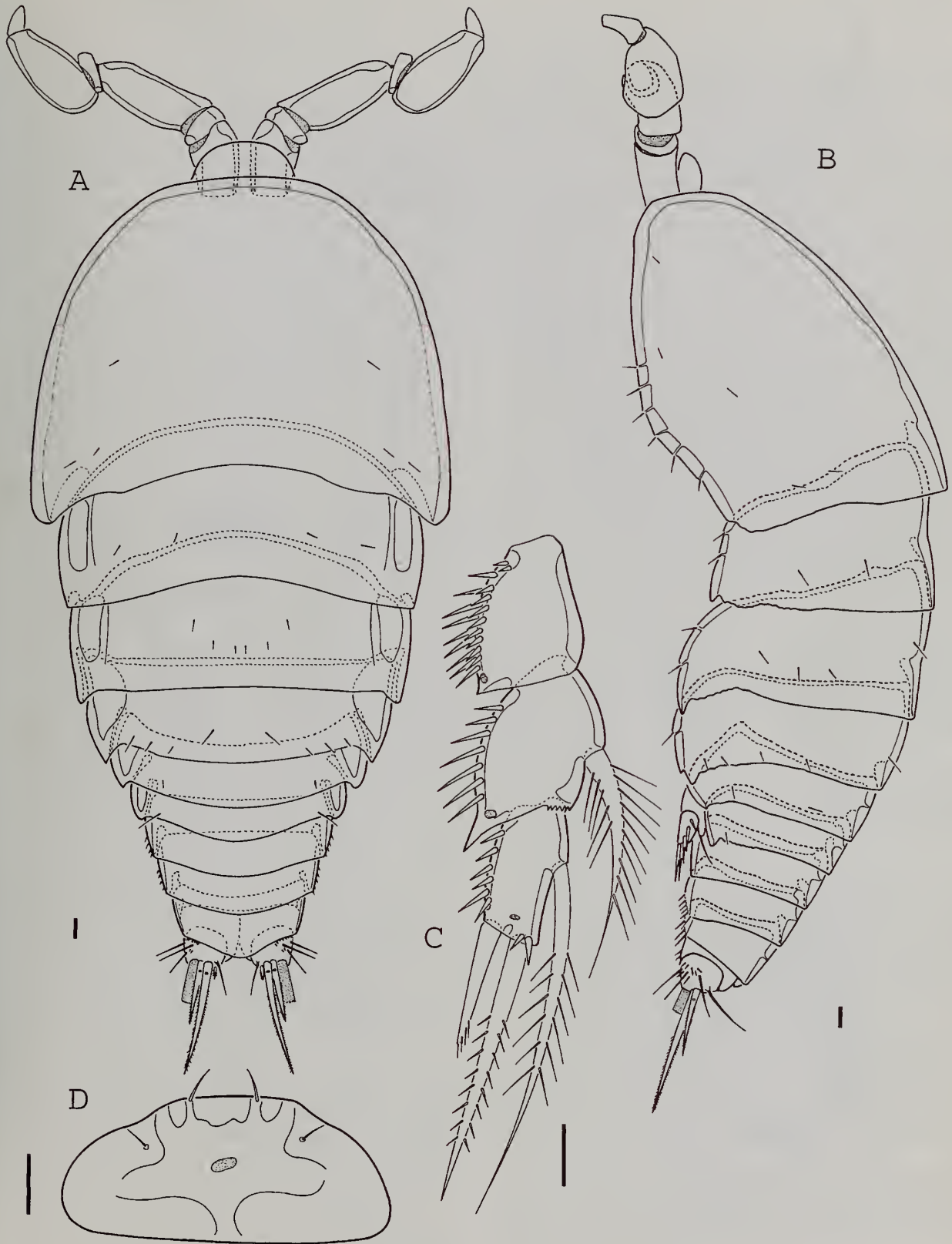


Fig. 17 *Neozausodes shulenbergeri* sp. nov. (♂). A, Habitus, dorsal view; B, habitus, lateral view; C, P2 endopod; D, rostrum. Scale bars = 10  $\mu$ m.

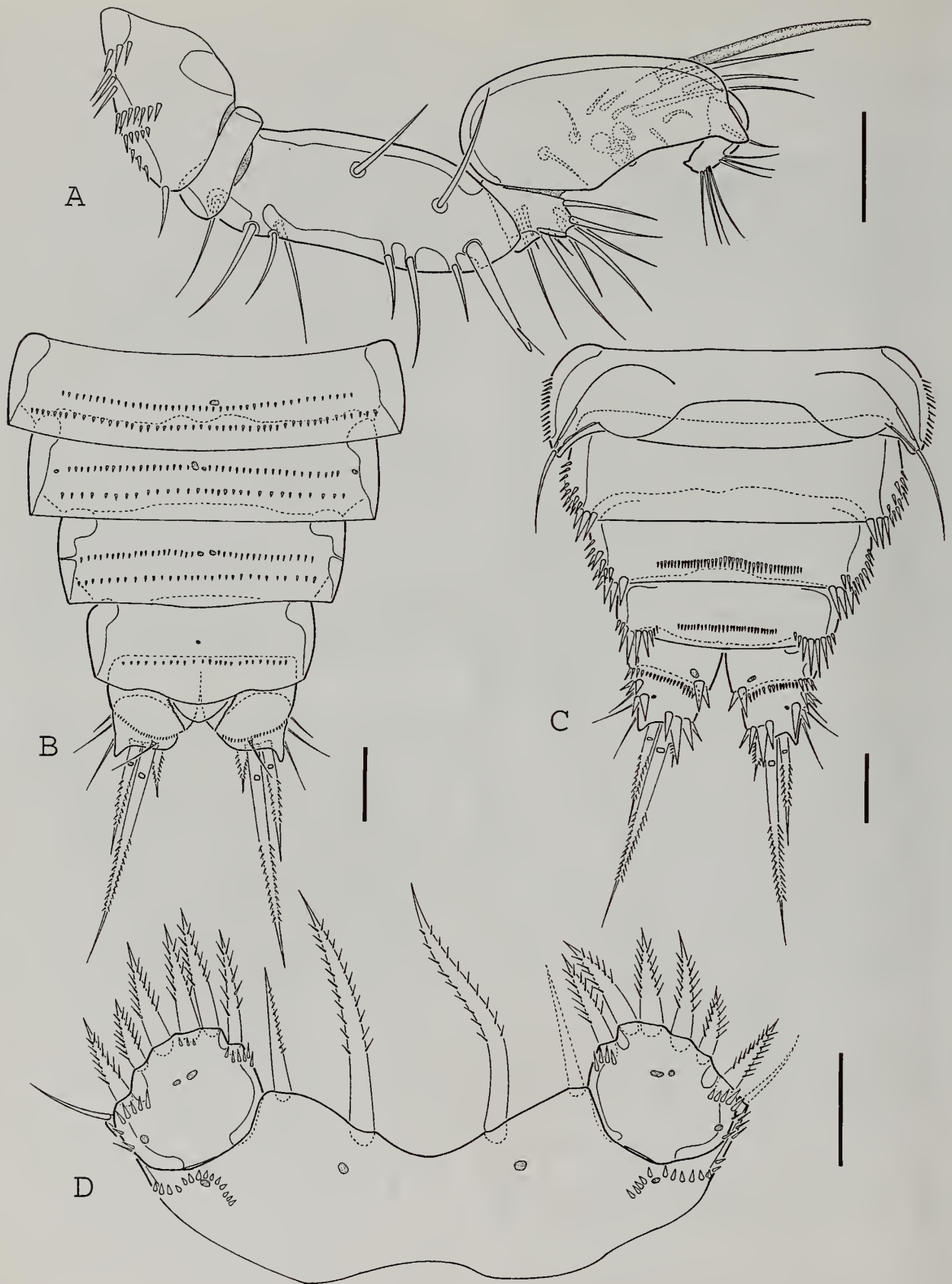


Fig. 18 *Neozausodes shulenbergeri* sp. nov. (♂). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view; D, P5. Scale bars = 20  $\mu$ m.

National Museum of Natural History (Smithsonian Institution, Washington, D.C.): additional paratypes represented by 3 ♀ and 2 ♂ in alcohol (USNM 288452–453) and 1 ♀ and 1 ♂ on slides (USNM 2888450–451).

**DESCRIPTION.** All illustrations are from paratypes except 19A–B which are from the holotype.

**FEMALE.** Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 288  $\mu\text{m}$  ( $\bar{x}$  = 283  $\mu\text{m}$ ,  $n$  = 4); without rostrum and caudal rami: 257  $\mu\text{m}$  ( $\bar{x}$  = 246  $\mu\text{m}$ ,  $n$  = 4). Body (Figs 19A–B, 20B–C) dorsoventrally flattened. Greatest width: 144  $\mu\text{m}$  ( $\bar{x}$  = 158  $\mu\text{m}$ ,  $n$  = 4) near posterior margin of cephalosome. Sensillae present on cephalothorax, pedigerous somites and first, third, fourth, and sixth urosomites (not all shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of thoracic somites thickly chitinized laterally. Free thoracic somites and urosomites 1–5 with fine spinular rows dorsally and dorsolaterally; urosomite 5 with ventral spinular row; anal somite with spinular rows ventrally and laterally on the posterior margin. Lateral margins of first and second free thoracic somites with 3 sensillae; third free thoracic somite with 2 sensillae. Ventral posterolateral corners of urosomites 3–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is exposed in dorsal and ventral aspects; with two ventral pores near posterior margin; anal operculum and pronounced pseudoperculum present. Caudal rami (Figs 19A–B, 20B–C) slightly wider than long, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string extending posteriorly from each caudal ramus present in some specimens.

Rostrum (Fig. 19C) prominent, lateral margins roughly parallel to each other, defined at base; with two short sensillae anteriorly and one sensilla near each mediolateral margin; with middorsal pore.

Antennule (Fig. 20A) 8-segmented; segments 1 and 2 longest; first segment widest with spinules; fourth segment with an aesthetasc (50  $\mu\text{m}$  long); apical acrothek probably consisting of 2 setae and 1 aesthetasc, however, we were unable to distinguish which elements were setae and which was an aesthetasc; with setal formula 1–[1], 2–[10], 3–[9], 4–[4 + (1 + ae)], 5–[2], 6–[4], 7–[4], 8–[4 + acrothek].

Antenna (Fig. 21A). Coxa short and unornamented; allobasis with spinular row, abexopodal seta, and surface suture marking original segment boundary between basis and first endopod segment; free endopod 1-segmented; lateral armature consisting of 1 long and 3 short setae; distal armature comprising 1 seta, 1 curved spine, and 4 geniculate spines, one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with spinules and hyaline surface frill as indicated in Fig. 21A; exopod 2-segmented, exp-1 with 1 lateral seta and 1 bipinnate distal seta and exp-2 with 2 distal setae.

Labrum well developed, not medially incised.

Mandible (Fig. 21B). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod with 2 lateral setae and 6 apical setae; exopod with 3 lateral setae, 3 distal setae, and spinular rows subdistally and along outer margin.

Maxillule (Fig. 21C). Praecoxa with spinular row along outer edge and with arthrite bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 5 setae; basal endite with 6 setae; endopod with 3 distal setae; exopod with 1 inner seta and 3 distal setae.

Maxilla (Fig. 21E). Syncoxa with 3 endites; praecoxal endite with 4 setae; coxal endites each with 2 bare setae and 1 pinnate seta; allobasis with claw, 1 pinnate and 2 bare setae; endopod 1-segmented with 5 bare setae.

Maxilliped (Fig. 21D). Syncoxa with a bipinnate seta and numerous spinular rows as indicated in Fig. 21D; basis with a row of fine spinules and seta at distal palmar margin; endopod represented by acutely recurved claw with a proximal accessory seta.

P1 (Fig. 22C). Rami prehensile; coxa with spinular row along outer margin and pore at inner distal corner; basis with bipinnate seta proximal to mid-point of outer margin and spine at inner distal corner; spinular rows present along inner and outer margins, and around articulation with endopod; with pore near outer seta. Exopod 3-segmented, 1.1 times as long as endopod (excluding apical elements); exp-1 with subdistal bipinnate seta and spinular rows along outer margin; exp-2 elongate, 1.9 times as long as exp-1, with slender inner seta distally and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate with subdistal pore; enp-2 0.3 times as long as enp-1, bearing geniculate spine, claw, and short, slender inner seta distally, with distal fan of fine spinules.

P2–P4 (Figs 22A–B, 23C) with 3-segmented exopods and 3- (P2–P3) or 2-segmented (P4) endopods. Coxae with spinular rows at outer distal corner of P2 and P4. Bases with outer bipinnate spine (P2) or bare seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P3 enp-3 and P4 exp-2–3 and enp-2. Pores present as illustrated (Figs 22A–B, 23C). Seta and spine formula of P2–P4 as in Table 1.

P5 (Figs 23A–B) not fused medially. Baseoendopod with anterior surface and marginal spinular rows; with 1 short, bare and 4 long, bipinnate inner setae; outer basal seta slender and arising from cylindrical process. Exopod 1.9 times as long as wide (excluding distal spines) with numerous anterior, posterior, and marginal spinular rows; with 1 inner, 1 apical and 3 outer pinnate spines; posterior surface with pore.

Genital double-somite (Figs 20B–C) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 3 naked setae.

**MALE.** Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 225  $\mu\text{m}$  ( $\bar{x}$  = 235  $\mu\text{m}$ ,  $n$  = 4); without rostrum and caudal rami: 194  $\mu\text{m}$  ( $\bar{x}$  = 202  $\mu\text{m}$ ,  $n$  = 4). Body width: 119  $\mu\text{m}$  ( $\bar{x}$  = 126  $\mu\text{m}$ ,  $n$  = 4). Not all sensillae shown in habitus views (Figs 24A–B). Sexual dimorphism in body size. rostrum (Fig. 24C), antennule, P2 endopod, P3 enp-2, P4 exp-3, P5, P6, and urosome segmentation (Figs 25B–C).

Antennule (Fig. 25A) 6-segmented, chirocer; aesthetasc-bearing segment not conspicuously swollen; segment 3 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; segment 5 with aesthetasc (30  $\mu\text{m}$  long); with armature formula 1–[1], 2–[1], 3–[9], 4–[9], 5–[8 + (1 + ae)], 6–[4 + acrothek].

P2 (Fig. 22D) as in ♀ except for endopod. Enp-1 with outer row of spinules. Enp-2 with outer distal corner extending to approximately one third the length of enp-3; outer margin spinulose; inner margin with subdistal stout pinnate seta. Enp-3 with spinulose outer margin, distal spinous apophysis, and 3 inner setae.

P3 (Fig. 22E) enp-2 with outer distal corner produced into apophysis.

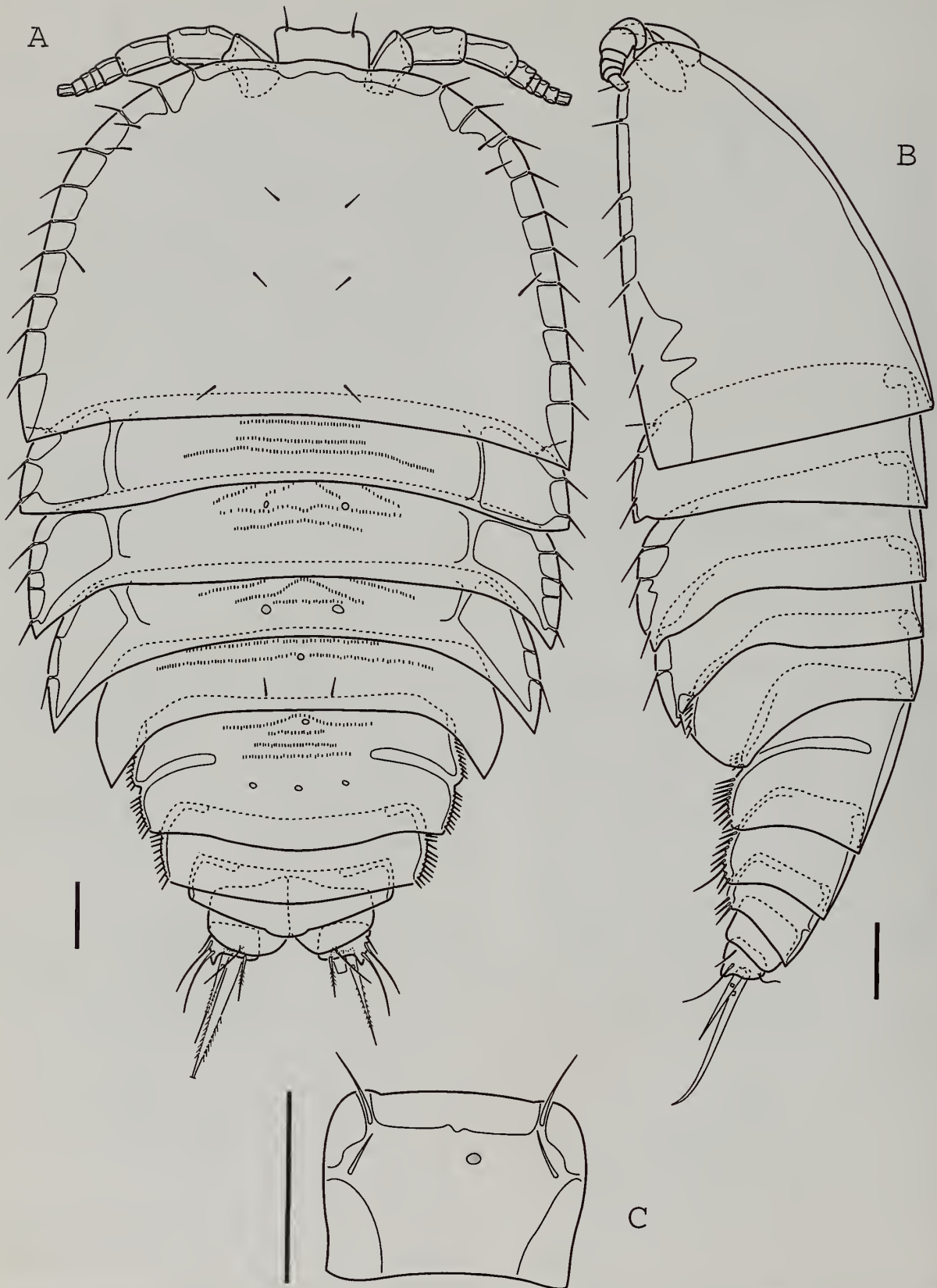
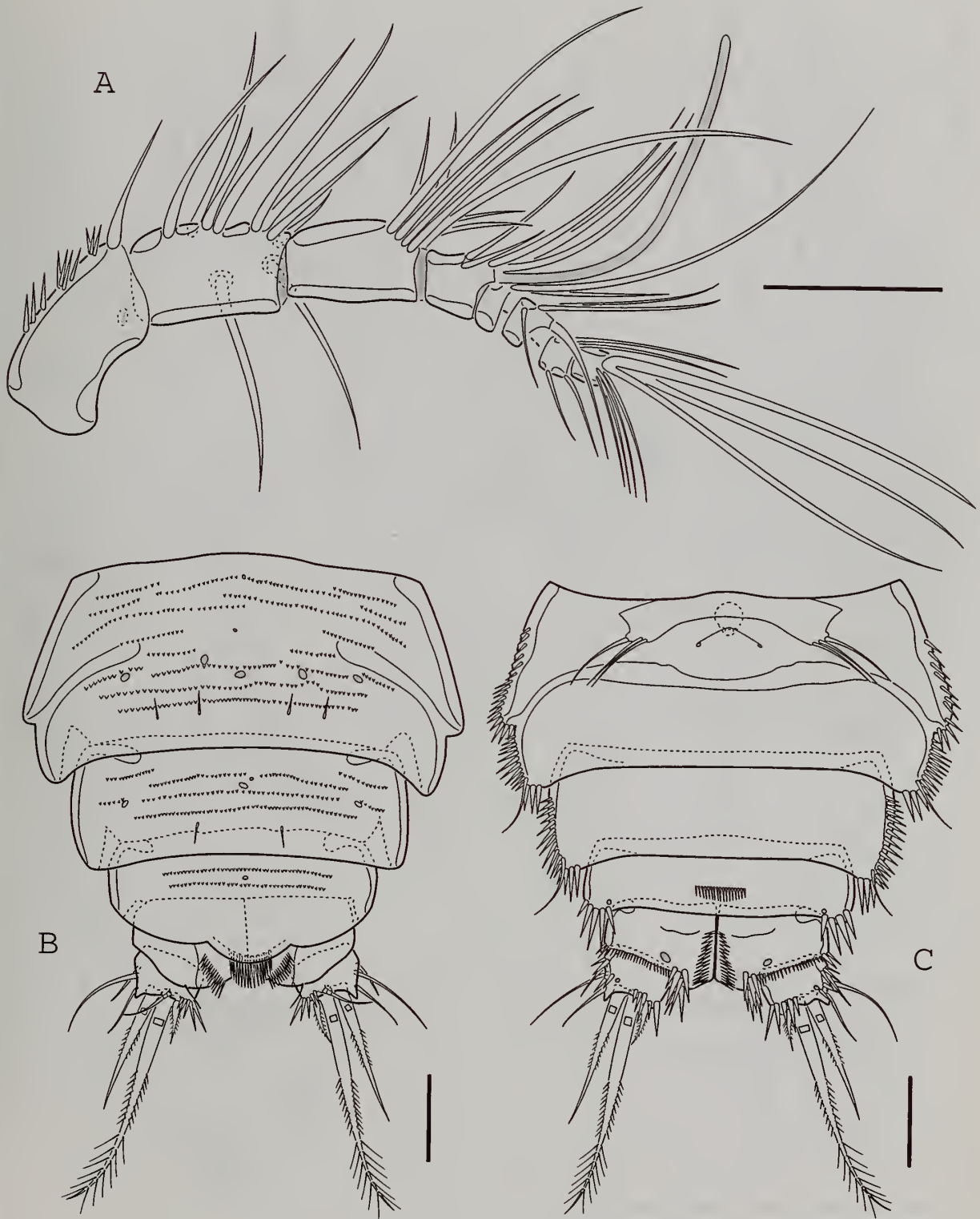


Fig. 19 *Mucropedia cookorum* sp. nov. (♀). A, habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars = 20  $\mu$ m.



**Fig. 20** *Mucropedia cookorum* sp. nov. (♀). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20  $\mu$ m.

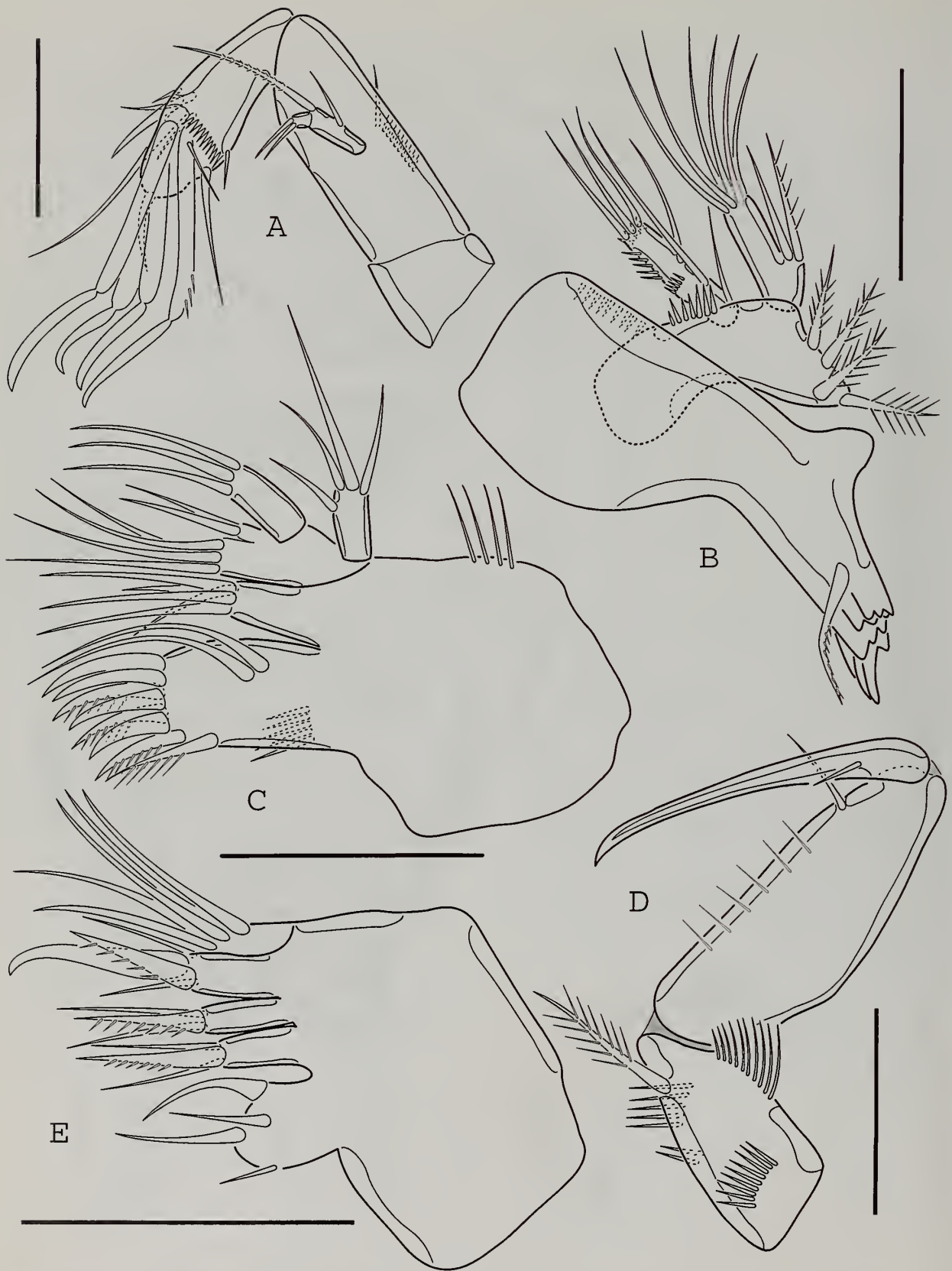


Fig. 21 *Mucropedia cookorum* sp. nov. (♀). A, Antenna; B, mandible; C, maxillule; D, maxiliped; E, maxilla. Scale bars = 20  $\mu$ m.

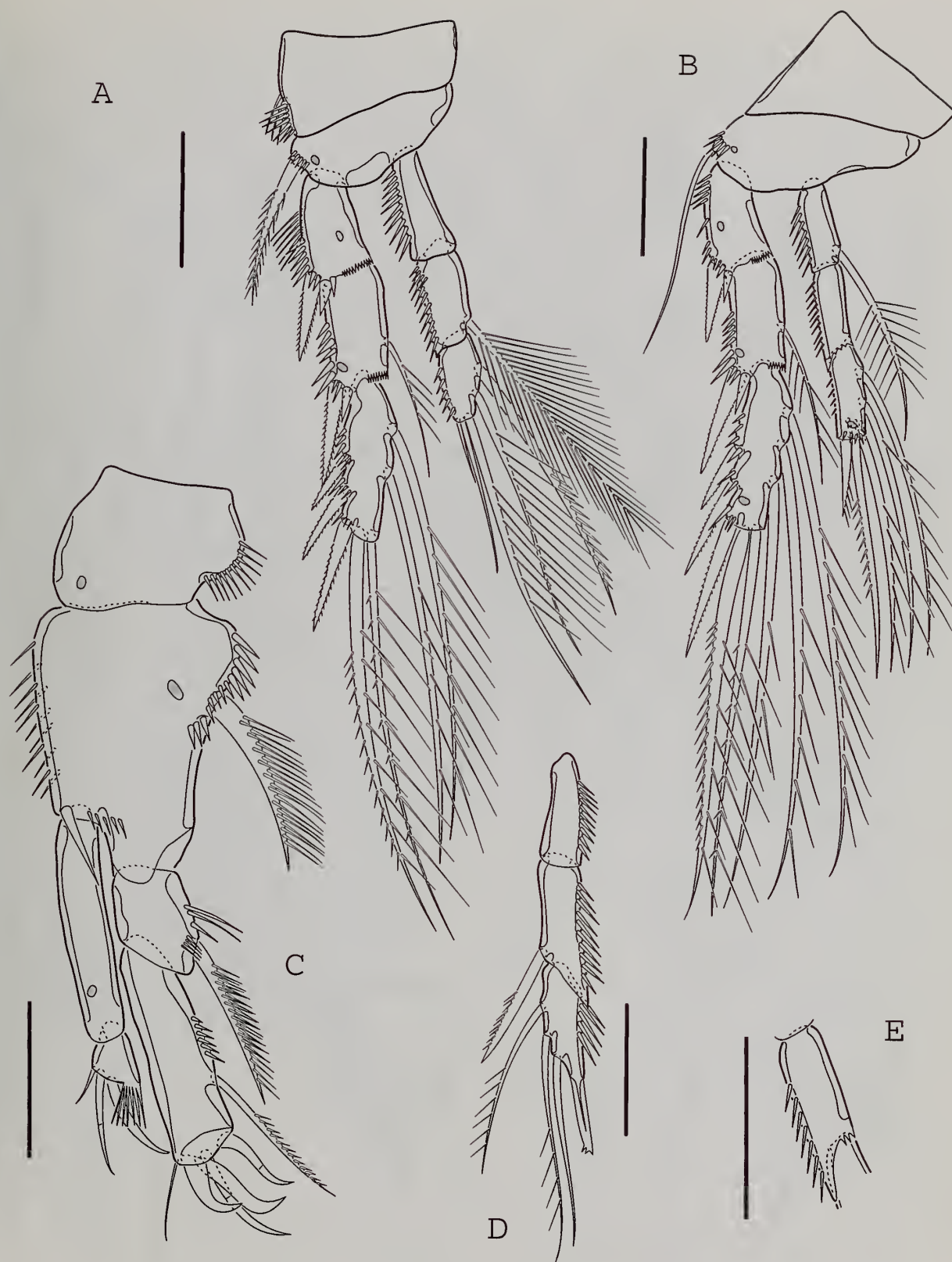


Fig. 22 *Mucropedia cookorum* sp. nov. A, ♀P2; B, ♀P3; C, ♀P1; D, ♂P2 endopod; E, ♂P3 endopod, second segment. Scale bars = 20 μm.

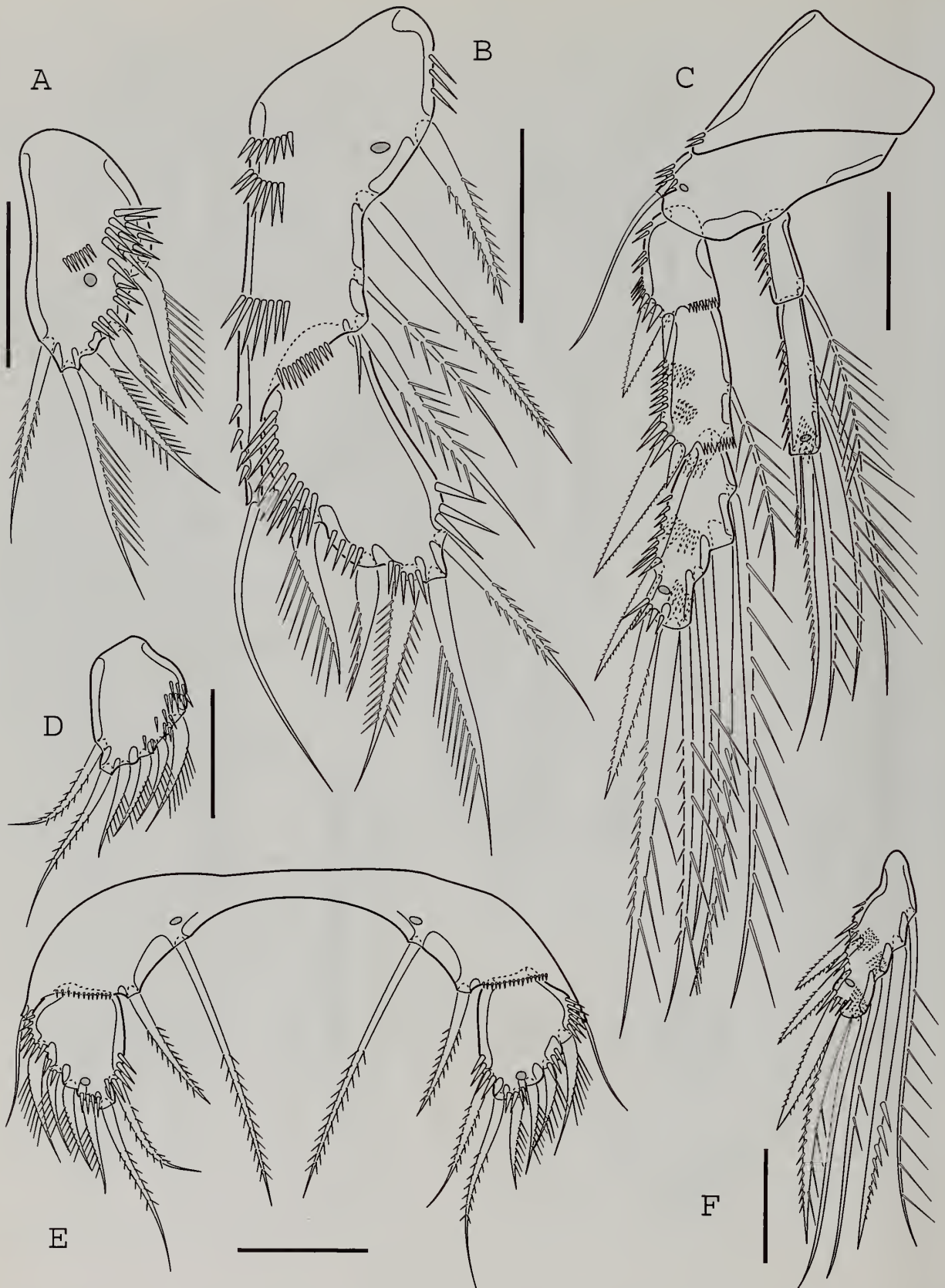


Fig. 23 *Mucropedia cookorum* sp. nov. A, ♀ P5 exopod, posterior; B, ♀ P5, anterior; C, ♀ P4; D, ♂ P5 exopod, posterior; E, ♂ P5, anterior; F, ♂ P4 exopod, third segment. Scale bars = 20 µm.



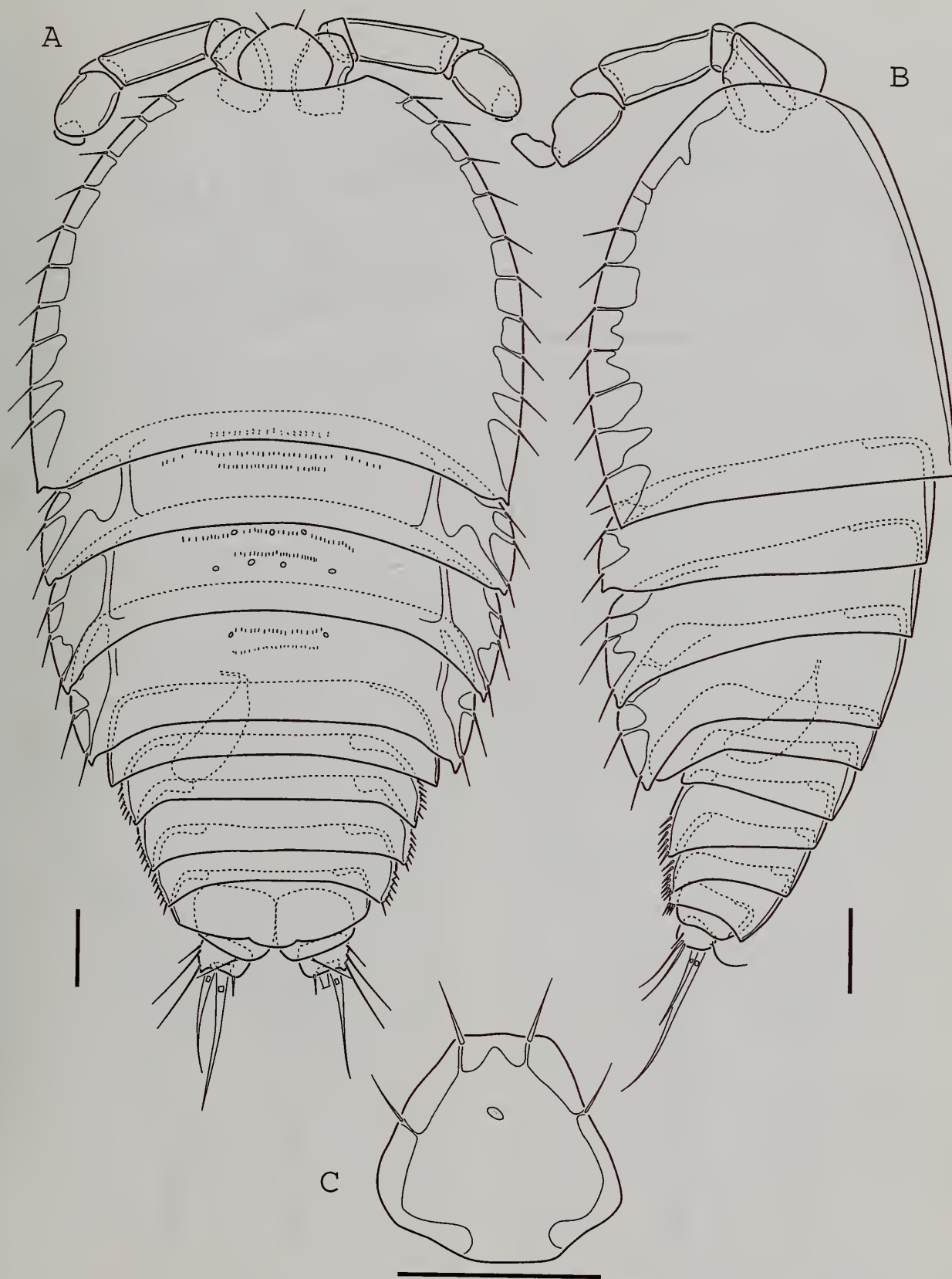


Fig. 24 *Mucropedia cookorum* sp. nov. (♂). A, Habitus, dorsal view; B, habitus, lateral view; C, rostrum. Scale bars = 20  $\mu$ m.

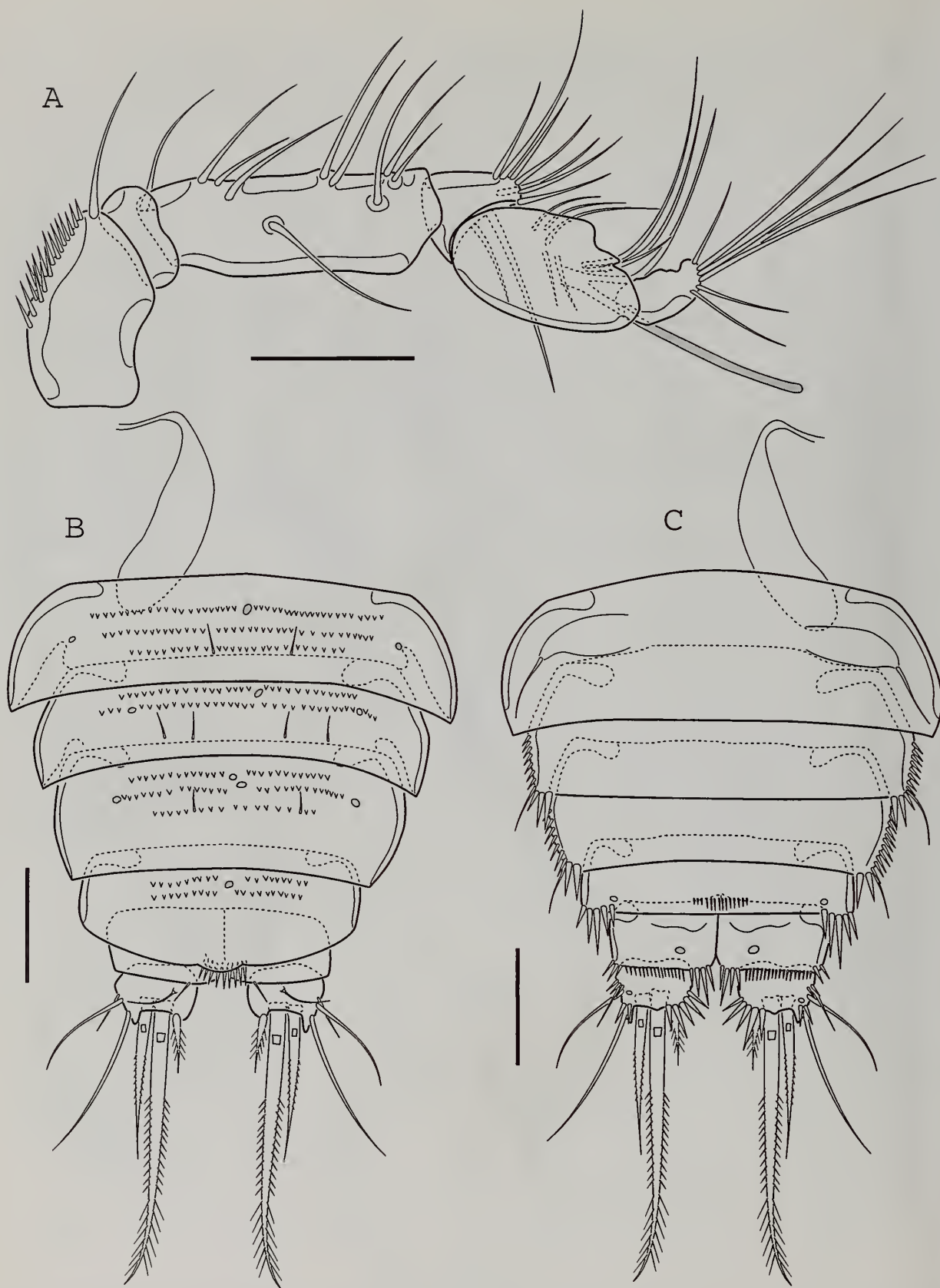


Fig. 25 *Mucropedia cookorum* sp. nov. (♂). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20  $\mu$ m.

P4 (Fig. 23F) exp-3 with 3 outer bipinnate spines.

P5 (Figs 25D–E) baseoendopods fused medially forming transversely elongate plate; each side with 2 bipinnate setae, slender outer basal seta arising from cylindrical process, and spinules around articulation with exopod. Exopod 1.2 times as long as wide (excluding setae), with an additional pinnate seta along the outer margin not found in ♀, and with fewer spinular rows.

P6 (Fig. 25C) symmetrical; with distal seta; located more laterally than in ♀.

**ETYMOLOGY.** Named in memory of Roy Cook and in honour of Jessie Cook, the first author's grandparents.

***Mucropedia kirstenae* sp. nov.**

**TYPE LOCALITY.** Gulf of Mexico: 29°40.63'N, 84°22.80'W, northern Gulf of Mexico, 18 m depth, unvegetated medium sand; see Thistle *et al.* (1995) for additional description.

**MATERIAL EXAMINED.**

The Natural History Museum: holotype ♀ in alcohol (BMNH 1999.208); allotypic paratype ♂ in alcohol (BMNH 1999.209); other paratypes are 1 ♀ and 1 ♂ in ethanol (BMNH 1999.210–211) and 2 ♀ ♀ and 2 ♂ ♂ on slides (BMNH 1999.212–215).

National Museum of Natural History (Smithsonian Institution, Washington, D.C.): additional paratypes represented by 2 ♀ ♀ and 2 ♂ ♂ in alcohol (USNM 288456–457) and 1 ♀ and 1 ♂ on slides (USNM 288454–455).

**DESCRIPTION.** All illustrations are from paratypes except Figs 26A–B, which are from the holotype.

**FEMALE.** Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 340 μm ( $\bar{x}$  = 320 μm,  $n$  = 4); without rostrum and caudal rami: 295 μm ( $\bar{x}$  = 276 μm,  $n$  = 4). Body (Figs 26A–B, 27B–C) dorsoventrally flattened. Greatest width: 153 μm ( $\bar{x}$  = 156 μm,  $n$  = 4) near posterior margin of cephalosome. Sensillae present on cephalothorax, pedigerous somites, and third, fourth, and sixth urosomites (not all shown). Ventrolateral margin of cephalic shield with sensillae. Epimera of pedigerous somites thickly chitinized laterally. Free thoracic somites and urosomites 1–5 with fine spinular rows dorsally and dorsolaterally; penultimate somite with ventral spinular row; anal somite with spinular rows ventrally and laterally on the posterior margin. Lateral margins of first and second pedigerous somites with 3 sensillae; third one with 2 sensillae. Ventral posterolateral corners of urosomites 3–5 and lateral margins of urosomites 1–4 with spinules. Genital double-somite with continuous chitinous internal rib ventrolaterally and ventrally (but not dorsally). Anal somite cleft medially; anus located terminally, triradiate, bordered by incised frill that is exposed in dorsal and ventral aspects; with two ventral pores near posterior margin; anal operculum and pronounced pseudoperculum present. Caudal rami (Figs 26A–B, 27B–C) approximately wider than long, with 7 setae: setae I–III bare, setae IV–V bipinnate, seta VI bipinnate, dorsal seta (VII) carried on a biarticulate socle. Gelatinous string extending posteriorly from each caudal ramus not observed in specimens.

Rostrum (Fig. 26C) prominent, lateral margins roughly parallel to each other, defined at base; with two short sensillae anteriorly and one sensilla near each mediolateral margin; with middorsal pore.

Antennule (Fig. 27A) 8-segmented; segments 1 and 2 longest; first segment widest with spinules; segment 4 with aesthetasc (60 μm long); setal formula: 1–[1], 2–[10], 3–[9], 4–[4 + (1 + ae)], 5–[2], 6–[4], 7–[4], 8–[5 + acrothek]; apical acrothek consisting of 2 setae and 1 aesthetasc.

Antenna (Fig. 28A). Coxa short and unornamented; allobasis

with spinular row, abexopodal seta, and incomplete surface suture marking original segment boundary between basis and first endopod segment; free endopod 1-segmented; lateral armature consisting of 1 long and 3 short setae; distal armature comprising 1 seta, 1 spine, and 4 geniculate spines, one of which bearing spinules proximal to geniculation and fused at base to a slender seta; with hyaline surface frill as indicated in Fig. 28A; exopod 2-segmented, exp-1 with 1 lateral seta and 1 bipinnate distal seta and exp-2 with 2 distal setae.

Labrum well developed, not medially incised.

Mandible (Fig. 28B). Gnathobase with pinnate seta at dorsal corner; coxa with proximal row of spinules; palp biramous, comprising basis and 1-segmented exopod and endopod; basis produced transversely, with proximal spinular row and 4 bipinnate setae; endopod with 2 lateral setae and 6 apical setae; exopod with 3 lateral setae, 3 distal setae, and spinular rows subdistally and along outer margin.

Maxillule (Fig. 28C). Praecoxa with spinular row along outer edge and with arthritis bearing 8 spines around distal margin, 2 anterior surface setae, and posterior spinular row; coxal endite with 5 setae; basal endite with 6 setae; endopod with 3 distal setae; exopod with 1 inner seta and 3 distal setae.

Maxilla (Fig. 28E). Syncoxa with 3 endites; praecoxal endite with 1 pinnate and 3 bare setae; proximal coxal endite with 1 bare seta and 2 pinnate setae; distal coxal endite with 2 bare setae and 1 pinnate seta; allobasis with claw, 1 pinnate and 2 bare setae; endopod 1-segmented with 5 bare setae.

Maxilliped (Fig. 28D). Syncoxa with a bipinnate seta and numerous spinular rows as indicated in Fig. 28D; basis with a row of fine spinules and seta along palmar margin; endopod represented by acutely recurved claw with a proximal accessory seta.

P1 (Fig. 29E). Rami prehensile; coxa with spinular row along outer margin and pore at inner distal corner; basis with bipinnate seta near mid-point of outer margin and spine at inner distal corner; spinular rows present along inner and outer margins, and around articulation with endopod; with pore near outer seta. Exopod 3-segmented, 0.9 times as long as endopod (excluding apical elements); exp-1 with subdistal bipinnate seta and spinular rows along outer margin; exp-2 elongate, 2.3 times as long as exp-1, with slender inner seta distally and outer margin spinular row extending to insertion of subdistal pinnate seta; exp-3 vestigial, largely incorporated into exp-2, with 2 geniculate spines and 2 claws. Endopod 2-segmented; enp-1 elongate with subdistal pore; enp-2 0.3 times as long as enp-1, bearing geniculate spine, claw, and short, slender inner seta distally, with distal fan of fine spinules.

P2–P4 (Figs 29B–C, 30A) with 3-segmented rami. Coxae with spinular rows at outer distal corner of P2 and P4 and pore at inner distal corner of P3 and P4. Bases with outer bipinnate spine (P2) or bare seta (P3–P4), and spinules plus a pore at outer distal corner. Endopods distinctly shorter than exopods. Spinular rows present on posterior surface of P2 enp-3, P3 enp-3 and P4 exp-2–3 and enp-3. Pores present as illustrated (Figs 29B–C, 30A). Seta and spine formula of P2–P4 as in Table 1.

P5 (Figs 30B–C) not fused medially. Baseoendopod with anterior surface and marginal spinular rows; with 4 long, bipinnate and 1 short, bare inner setae; outer basal seta slender and arising from cylindrical process. Exopod 1.9 times as long as wide (excluding distal spines) with numerous anterior, posterior and marginal spinular rows, with 1 inner, 1 apical and 3 outer pinnate spines; posterior surface with pore.

Genital double somite (Figs 27B–C) wider than long. Genital field located far anteriorly. Copulatory pore large, midventral; leading via short copulatory duct to single median seminal receptacle. Gonopores paired, closed off by opercula derived from vestigial sixth legs bearing 3 naked setae.

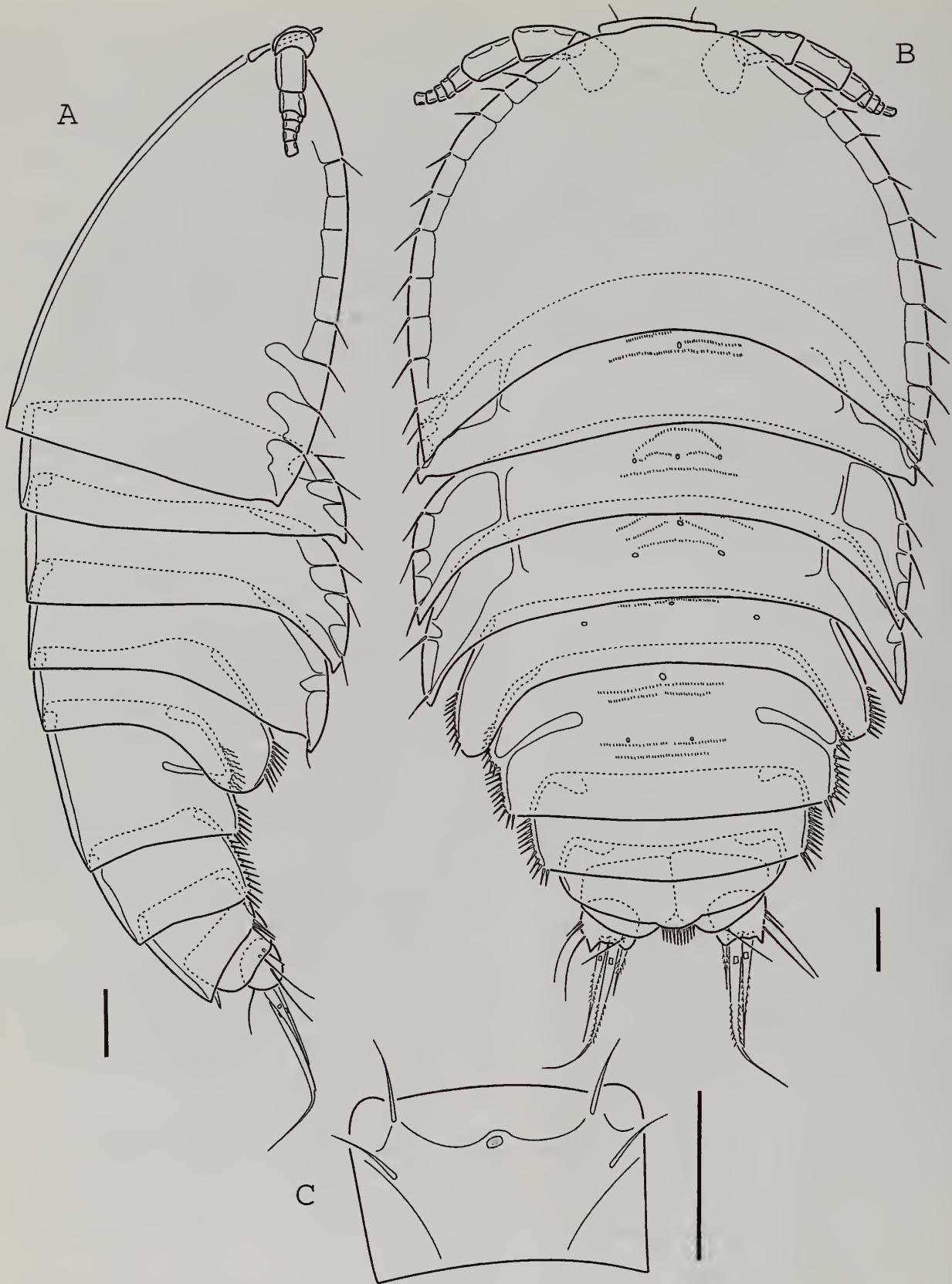


Fig. 26 *Mucropedia kirstenae* sp. nov. (♀). A, Habitus, lateral view; B, habitus, dorsal view; C, rostrum. Scale bars = 20  $\mu$ m.

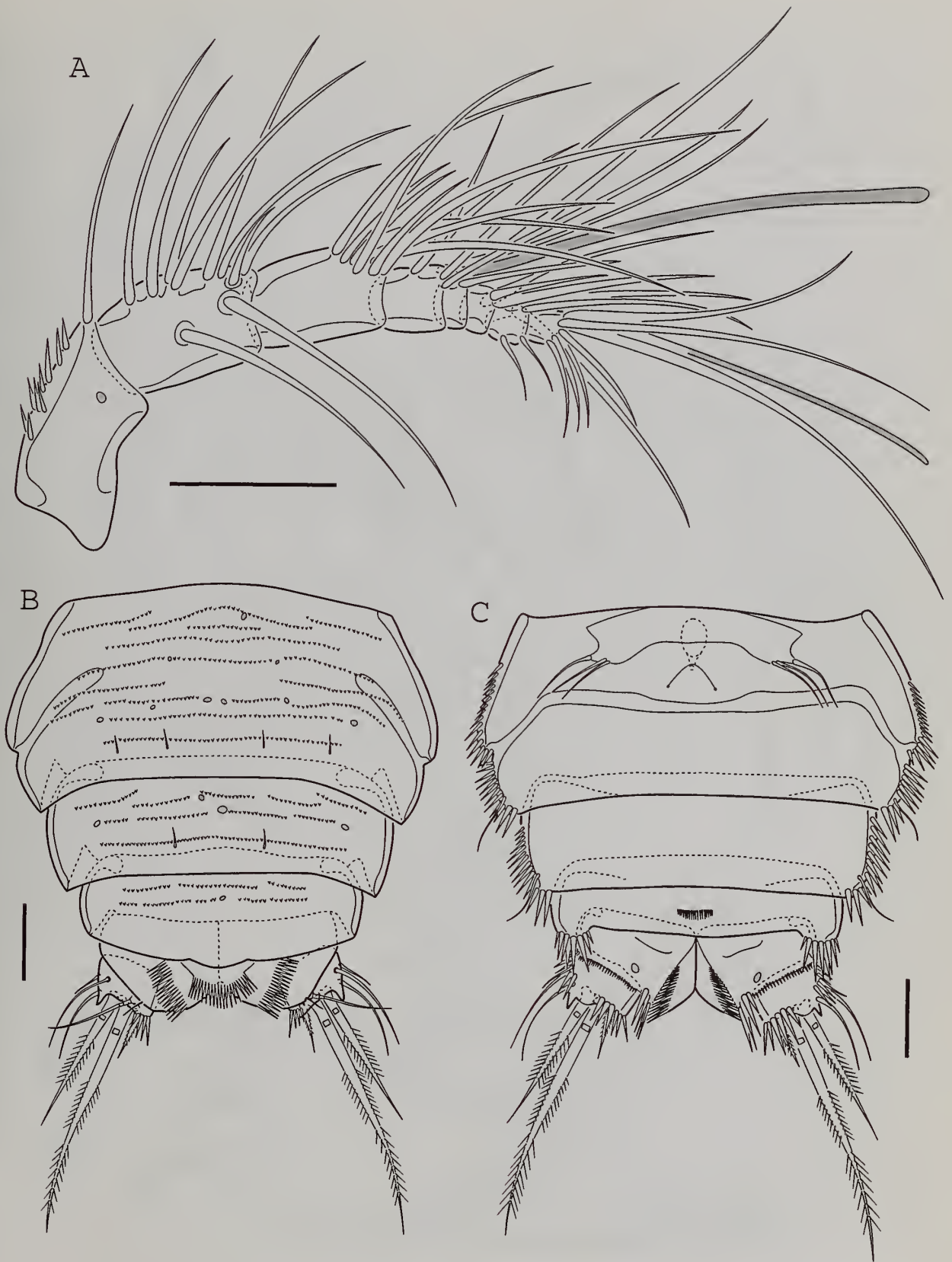


Fig. 27 *Mucropedia kirstenae* sp. nov. (♀). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20  $\mu$ m.

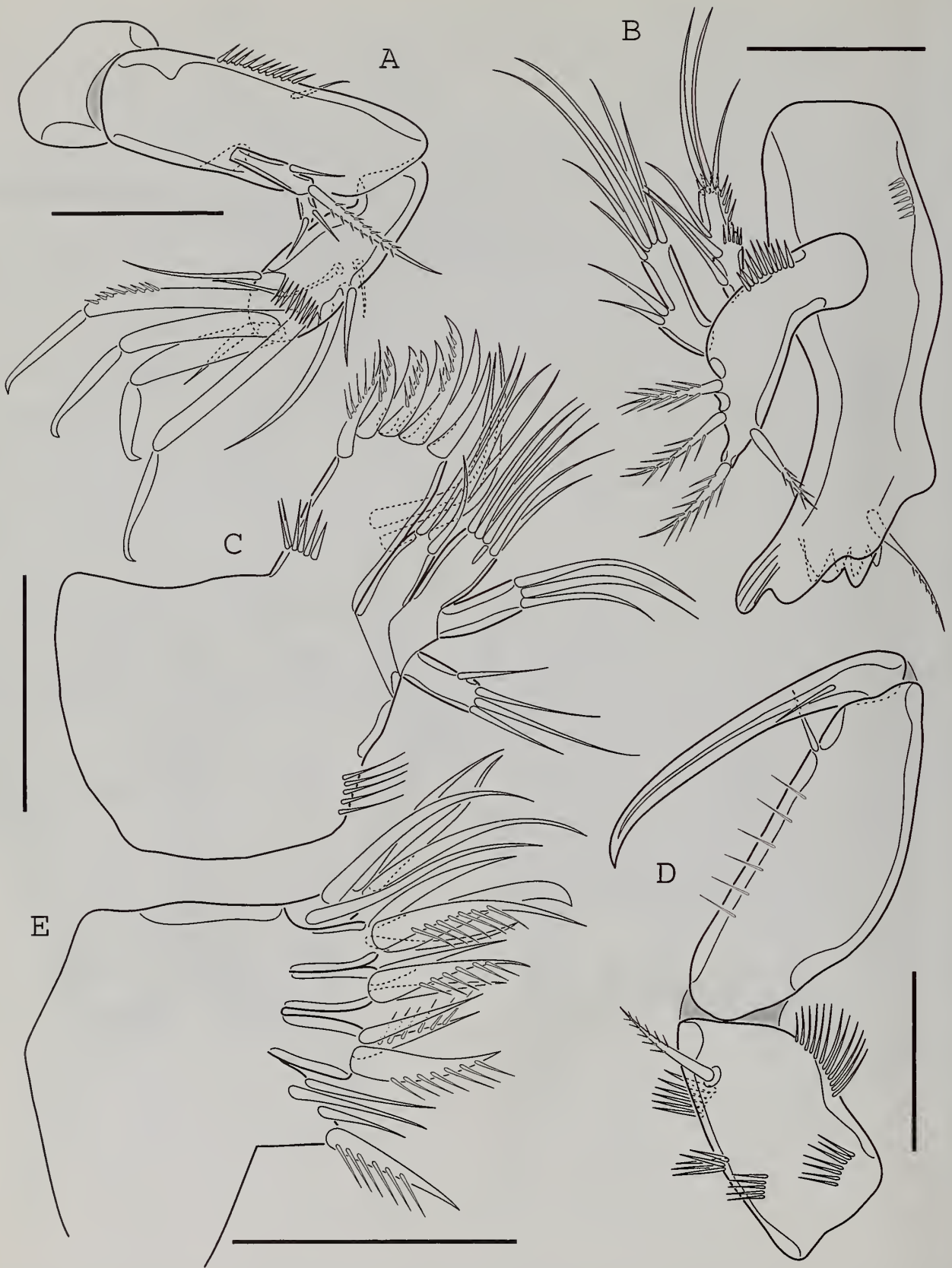


Fig. 28 *Mucropedia kirstenae* sp. nov. (♀). A, Antenna; B, mandible; C, maxillule; D, maxilliped; E, maxilla. Scale bars = 20  $\mu$ m.



Fig. 29 *Mucropedia kirstenae* sp. nov. A, ♂P2 endopod; B, ♀P2; C, ♀P3; D, ♂P3 endopod, second segment; E, P1. Scale bars = 20  $\mu$ m.



Fig. 30 *Mucropedia kirstenae* sp. nov. A, ♀ P4; B, ♀ P5 exopod, posterior view; C, ♀ P5, anterior view; D, ♂ P4 exopod, third segment; E, ♂ P5 exopod, posterior view; F, ♂ P5, anterior view. Scale bars = 20  $\mu$ m.



MALE. Body length: measured from anterior margin of rostrum to posterior margin of caudal rami: 253  $\mu\text{m}$  ( $\bar{x}$  = 249  $\mu\text{m}$ ,  $n$  = 4); without rostrum and caudal rami: 220  $\mu\text{m}$  ( $\bar{x}$  = 217  $\mu\text{m}$ ,  $n$  = 4). Body width: 131  $\mu\text{m}$  ( $\bar{x}$  = 134  $\mu\text{m}$ ,  $n$  = 4). Not all sensillae shown in habitus views (Figs 31A–B). Sexual dimorphism in body size, rostrum (Fig. 31C), antennule, P2 endopod, P3 endopod, P4 exp-3, P5, P6, and urosome segmentation (Figs 32B–C).

Antennule (Fig. 32A) 6-segmented, chirocer; aesthetasc-bearing segment not conspicuously swollen; segment 3 longest; with geniculation between segments 5 and 6. First segment with several spinular rows along anterior margin; segment 5 with aesthetasc (50  $\mu\text{m}$  long); with armature formula 1–[1], 2–[1], 3–[9], 4–[9], 5–[8 + (1 + ae)], 6–[7].

P2 (Fig. 29A) as in ♀ except for endopod. Enp-1 with outer row of spinules and anterior pore. Enp-2 with outer distal corner extending approximately one third the length of enp-3; outer margin spinulose; inner margin with subdistal thick pinnate seta. Enp-3 with spinulose outer margin, distal spinous apophysis, and 3 inner setae.

P3 (Fig. 29D) enp-2 with outer distal corner produced into apophysis; enp-3 without pore and posterior spinules found in ♀.

P4 (Fig. 30D) exp-3 with 3 outer bipinnate spines.

P5 (Figs 30E–F) baseoendopods fused medially forming transversely elongate plate; each side with 2 bipinnate setae, slender outer basal seta arising from cylindrical process, and spinules around articulation with exopod. Exopod 1.1 times as long as wide (excluding setae), with an additional pinnate seta along the outer margin not found in ♀, and with fewer spinular rows.

P6 (Fig. 32C) symmetrical; with distal seta; located more laterally than in ♀.

ETYMOLOGY. Named for Kirsten Lambshead.

#### NOTES.

*M. kirstenae* can be readily distinguished from *M. cookorum* by the segmentation of the P4 endopod (3-segmented in *M. kirstenae*, 2-segmented in *M. cookorum*). Both species are extremely close otherwise and additional differences should be sought at the level of setal lengths and segmental proportions. It is the consistent nature of these differences rather than their magnitude that convinced us of the distinctiveness and co-occurrence of two species. The existence of sibling species is a well known phenomenon in the family Harpacticidae and makes accurate identification onerous. Soyer *et al.* (1987) demonstrated the presence of sibling species of the genus *Tigriopus* on the Kerguelen and Crozet Islands. Huys *et al.* (1996) recently pointed out that *Harpacticus obscurus* T. Scott, *H. giesbrechti* Klie and *H. littoralis* Sars are extremely difficult to separate and identification is often based on setal lengths and ornamentation, pore patterns and position of spinule rows.

Genus *Archizausodes* gen. nov.

DIAGNOSIS. Harpacticidae. Antennule ♀ 8-segmented, without pinnate or plumose setae on segments 1–6; without strong, modified spines on segments 3–5 or enlarged pectinate or pinnate spines on segment 6. Antennule ♂ without modified spines on segment 3. Antennary exopod 2-segmented, with armature formula [2, 2]. Maxilla with 4 spines/setae on praecoxal endite. P2–P3 endopods 3-segmented, P4 endopod 2-segmented. P2 ♀ enp-3 with 2 inner setae. P3 ♀ enp-2 with inner seta. P4 exp-3 with 3 outer spines in both sexes. P4 enp-2 with 2 inner setae in both sexes. P2 ♂ enp-2 without distinct apophysis, inner seta not modified; enp-3 with 1 apical seta (inner one lost), outer spine fused to segment. P3 ♂ enp-2 outer distal corner not attenuated.

Swimming leg setal formula:

	exopod	endopod
P2	0.1.223	0.1.221 [♀] 0.1.211 [♂]
P3	0.1.323	1.1.221
P4	0.1.323	1.221

P5 exopod elongate-oval in both sexes. P5 endopodal lobe ♀ not developed; distal 3 inner setae rudimentary.

Sexual dimorphism in rostrum, antennule, P2 endopod, P5, P6, genital segmentation and size.

TYPE SPECIES. *Zausodes biarticulatus* Itô, 1979 = *Archizausodes biarticulatus* (Itô, 1979) comb. nov.

OTHER SPECIES. None.

ETYMOLOGY. The generic name is derived from the Greek prefix *archi-*, meaning first, and alludes to the primitive position of the genus. Gender: masculine.

*Archizausodes biarticulatus* (Itô, 1979) comb. nov.

TYPE LOCALITY. Chichi-jima Island, Bonin Islands; shallow water off Miyanojima; coarse sand with broken shells and corals.

#### NOTES.

Additional autapomorphies for this genus include the elongate proximal exopod segment of P1, the transversely prolonged basis of P4, and the reduction of particular setae on the exopod and baseoendopod of ♀ P5. *A. biarticulatus* shows some similarities with *Z. cinctus* (see below).

## PHYLOGENY

### Selection of outgroup

Lang (1944, 1948) divided the Harpacticidae in two subfamilies, Harpacticellinae and Zausodiinae, the names of which were later corrected by Vervoort (1964) as Harpacticinae and Zausodinae, respectively. The Zausodinae was proposed to accommodate *Zaus*, *Zausodes* and *Zausopsis*, all of which have a strongly dorso-ventrally depressed, more or less shield-shaped body with completely developed pleurotergites on the pedigerous somites. The Harpacticinae included *Harpacticus*, *Tigriopus*, *Harpacticella* and *Perissocope* which according to Lang (1944, 1948) have a body which is 'normal, elongate and not shield-shaped'. Two more genera, *Discoharpacticus* Noodt and *Paratigriopus* Itô have been added to the latter subfamily since (Noodt, 1954; Itô, 1969).

Lang (1948: 355) remarked that *Zausodes* showed a certain resemblance with *Perissocope* in the reduced swimming leg armature but nevertheless assigned more weight to the body form, favouring a relationship with *Zaus* and *Zausopsis*. Since *Zausodes* has a short P1 exp-1, a well developed maxilliped and 2 setae on the ♂ P5 baseoendopod he was of the opinion that the genus had diverged early in the evolution of the Zausodinae. On the other hand he expressed some doubts as to the relationships of *Perissocope* since males were as yet unknown.

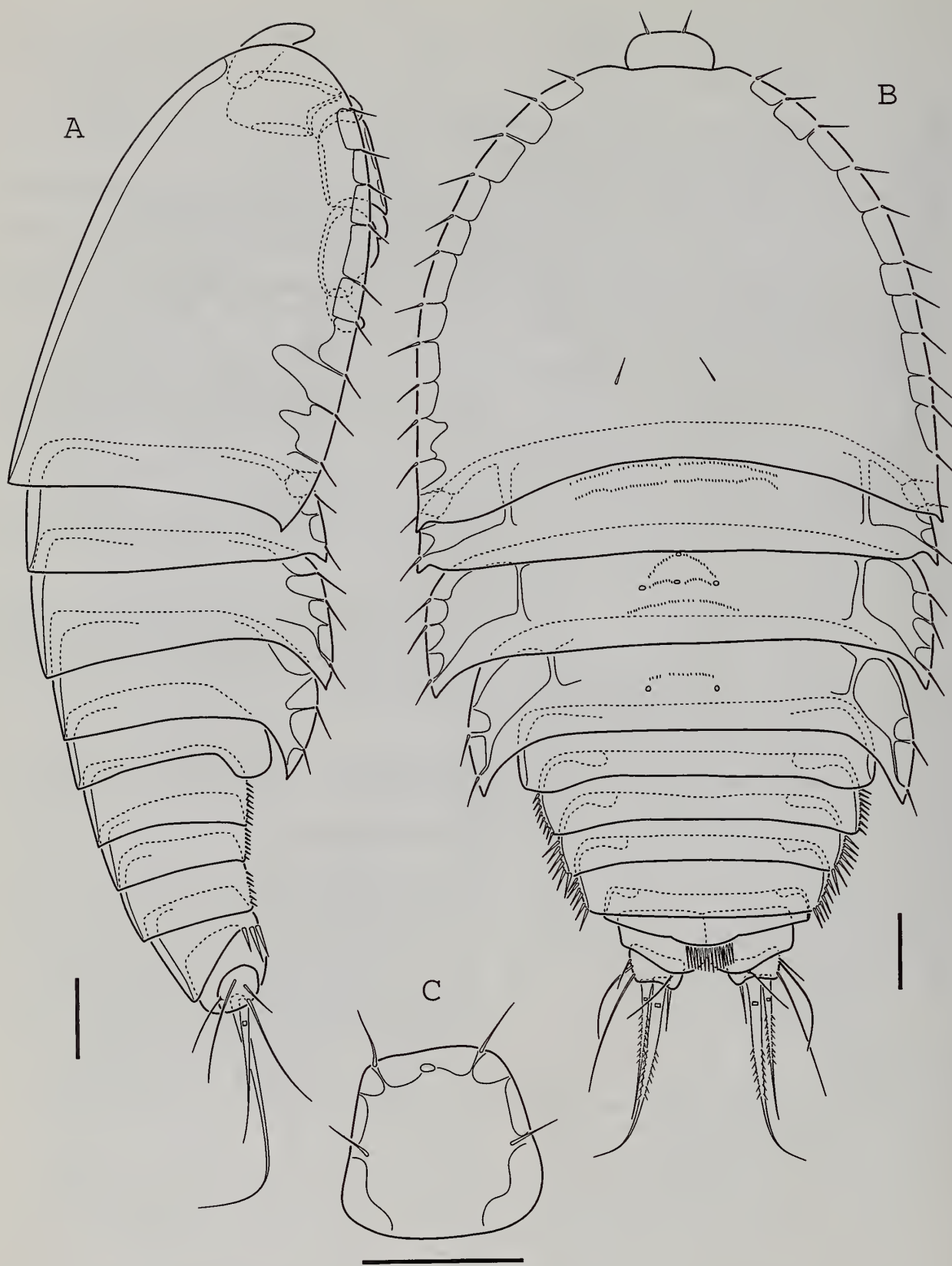


Fig. 31 *Mucropedia kirstenae* sp. nov. (♂). A, Habitus, lateral view; B, habitus, dorsal view; C, rostrum. Scale bars = 20  $\mu$ m.

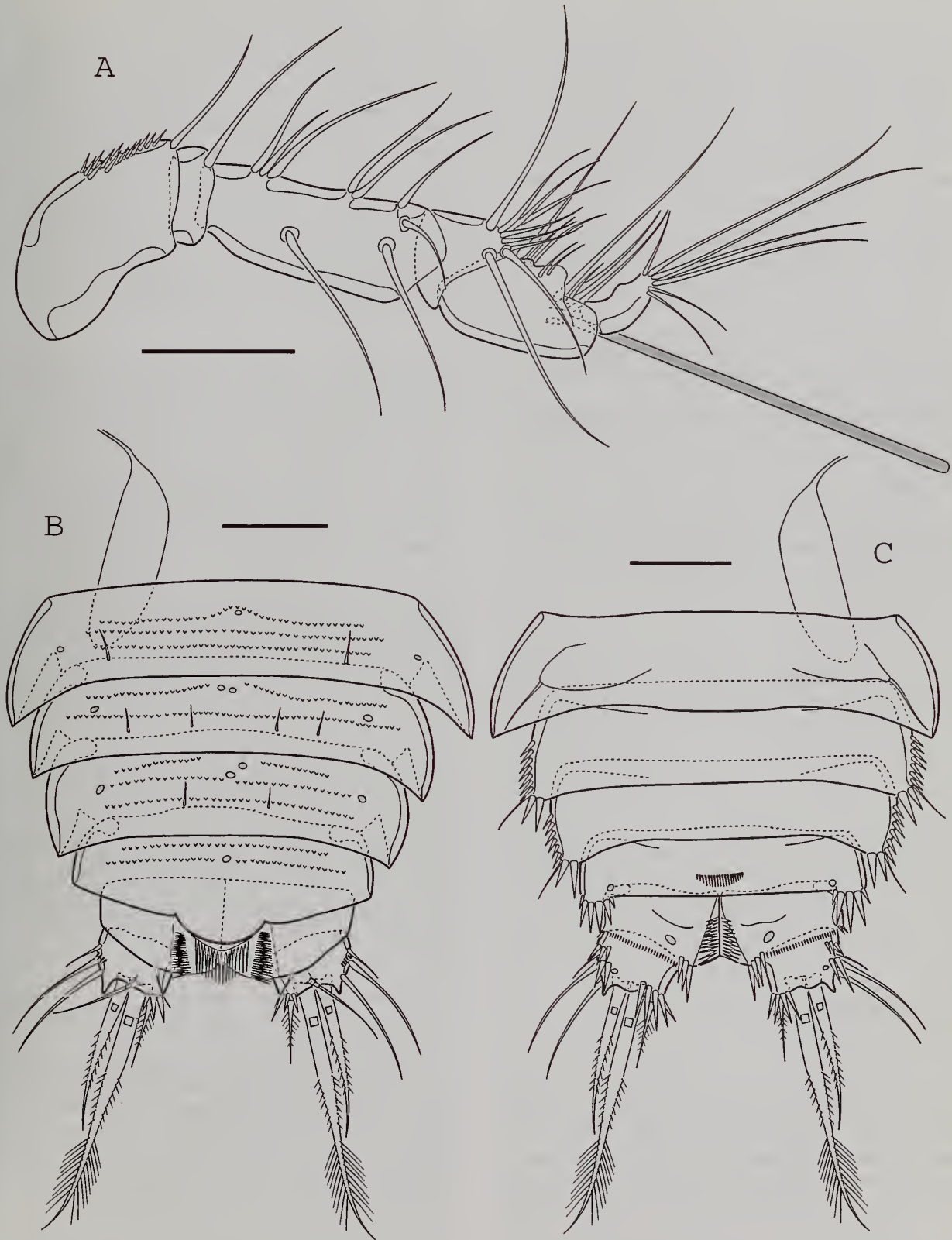


Fig. 32 *Mucropedia kirstenae* sp. nov. (♂). A, Antennule; B, urosome (excluding P5-bearing somite), dorsal view; C, urosome (excluding P5-bearing somite), ventral view. Scale bars = 20  $\mu$ m.

A first indication of the artificiality of Lang's subdivision was given by Itô (1979) who noted the similarity between the shape of the P1 exopod of *Z. biarticulatus* and that of the genus *Perissocope*. Itô did not assign his species to *Perissocope* because it lacked the proximally-born inner seta on P1 enp-1 distinctive of this genus. Watkins (1987) remarked that *Zausodes* and *Perissocope* are more closely related morphologically, ecologically and zoogeographically than either is to any other genus of the Harpacticidae. He suggested that the similar body shape between *Zausodes* and the other Zausodinae was a product of convergent evolution, particularly as the various body somites contribute differently to the overall teardrop shape, and similar convergences are found in *Harpacticus compressus* Frost, *Discoharpacticus mirabilis* Noodt and *Perissocope biarticulatus* Watkins.

Preliminary phylogenetic analysis (Huys, unpubl.) supports a robust sistergroup relationship between *Perissocope* and *Zausodes* sensu lato on the basis of the following synapomorphies:

1. strong sexual dimorphism in the shape of the rostrum;
2. antennule ♀ with fused segments 7 and 8 (representing ancestral segments XXIV and XXV) forming compound double segment (see below: character 1);
3. armature of P1 exp-3 consisting of 2–3 simple (unhinged) and 2 geniculate (hinged) claws (see below: character 8); confirmed by re-examination of the type material of *P. adistaltus* Wells (BNHM 1967.7.11.5–6);
4. sexual dimorphism of P2 involving the loss of the inner distal seta of enp-3 in the male; this seta is generally reduced in length in other harpacticid genera such as *Harpacticus*, *Tigriopus* and *Paratigriopus* but is completely absent in *Zausodes* sensu lato and *Perissocope*.

With the recent description of *P. biarticulatus* by Watkins (1987) the absence of the inner seta on P2–P4 exp-1 can no longer be regarded as a synapomorphy linking *Perissocope* and *Zausodes*. The adhesive mucus strings produced by the caudal rami and the associated glands were first described for *Z. sextus* and *Z. septimus* by Lang (1965) and subsequently also reported for species of *Perissocope* by Watkins (1987). This character is not unique to these two genera since a similar mucus apparatus has also been recorded in other representatives of the Harpacticidae (Watkins, 1987) and even outside this family (Huys, 1990).

Although the *Zaus-Zausopsis* clade is undoubtedly monophyletic, recognizing it as a distinct subfamily Zausodinae would relegate the Harpacticinae to a taxon of paraphyletic status. We recommend therefore to abandon Lang's (1944, 1948) subfamilial classification until a comprehensive phylogenetic analysis of the family is completed.

## Morphological characters

### (1) Segmentation ♀ antennule

The female antennule is primitively 9-segmented in the Harpacticidae with segments 7 and 8 representing ancestral segments XXIV and XXV, respectively. The homology of these segments is established by their posterior setae (Huys & Boxshall, 1991). This ancestral condition is found in the genera *Harpacticus*, *Zaus*, *Discoharpacticus*, *Tigriopus* and *Paratigriopus*. Within the former *Zausodes* complex the number of antennular segments ranges between 6 and 8. The 8-segmented state is derived by fusion of segments 7 and 8, forming a double segment in *Z. arenicolus*, *Z. septimus*, *A. biarticulatus* and the two species of *Mucropedia*. The origin of this compound segment is unequivocally established by the presence of

2 posterior setae. Comparison of ontogenetic studies of harpacticid genera possessing 9-segmented antennules such as *Tigriopus* (Itô, 1970) and *Harpacticus* (Itô, 1971, 1976; Itô & Fukuchi, 1978) indicates that the double segment is not the result of a failure in the separation of segments 7 and 8 at an earlier stage in ontogeny since both these segments are already expressed at copepodid I. The double segment is also found in all other *Zausodes* species (Table 1) in which the antennule is only 7- or 6-segmented. It is regarded here as a synapomorphy linking *Perissocope* and the *Zausodes* complex.

A further derived state is found in the 3 Brazilian species (Jakobi, 1954), *N. sextus*, *N. schulenbergeri* and *N. areolatus* in which a triple segment is formed by incorporation of segment 6 into the double segment, producing a 7-segmented (or 6-segmented in *N. areolatus*) antennule. This condition has independently evolved in the genus *Perissocope* (Wells, 1968). Our study has revealed a 6-segmented antennule in *N. areolatus* which represents an autapomorphy for this species. It has originated through fusion of segment 5 to the aesthetasc-bearing segment 4.

### (2) Proximal elements ♀ antennule

The armature elements on the ♀ antennule are typically setiform in the great majority of the genera in the Harpacticidae. In some species of *Zausodes* sensu lato particular elements on the proximal segments are modified into stout, rigid spines which typically bear a subapical flagellum (Figs 8A; 14A). The position and number of these spines is identical in all species for which they have been recorded, i.e. two on segment 3 and one on segments 4 and 5 each. Two spines are found on segment 4 in *N. areolatus* as a result of secondary segmental fusion.

### (3) Distal elements ♀ antennule

Some species of *Zausodes* sensu lato possess two large, conspicuous spines on segment 6 (or the homologous portion of segment 5 in the 6-segmented antennule of *N. areolatus*). These spines are typically unilaterally pinnate or pectinate (Figs 8A; 14A) and easy to discern without dissection. They are not found on the male antennules.

### (4) Setal ornamentation ♀ antennule

Species of *Perissocope* and *Zausodes* sensu lato typically have antennular setae which lack any form of ornamentation. Outgroup comparison with other harpacticid genera such as *Zaus* (Itô, 1980) and *Harpacticus* (e.g. Itô, 1976) suggests that this is the ancestral condition. In the type species *Z. arenicolus* (Fig. 2B) and *Z. septimus* (Lang, 1965; Mielke, 1990) the four proximal segments of the ♀ antennule bear pinnate setae, the plumosity being much more expressed in the latter. This modification is regarded here as apomorphic.

### (5) Segmentation antennary exopod

Within the Harpacticidae the antennary exopod is 3-segmented only in *Tigriopus* and some species of *Perissocope*. Comparison of setation patterns indicates that the 2-segmented condition is derived by fusion of the middle and distal exopod segments. This segmentation is found in most harpacticid genera such as *Harpacticus*, *Zaus*, *Zausopsis* and *Harpacticella*, and in three species of the former *Zausodes* complex (*biarticulatus*, *kirstenae*, *cookorum*). All other *Zausodes* species show the further derived 1-segmented state (Table 1), being the most reduced condition within the family.

### (6) Armature antennary exopod

The maximum setation is found in *Harpacticus*, *Zaus* and *Zausopsis* which possess 2 lateral setae on exp-1 and 2 lateral plus 2 apical

**Table 1** Segmentation of ♀ antennule (A1) and antennary exopod (A2), armature formula of antennary exopod and swimming legs P2–P4 in *Perissocope* (2 species) and 12 species of the *Zausodes* complex. The swimming leg armature formulae of *Z. cinctus* Krishnaswamy and *P. adialstus* Wells have been corrected (see text).

	Segmentation		A2	P2	Armature				
	A1	A2			P2	P3	P4		
<i>arenicolus</i>	8	1	2	0.1.223	0.1.221	0.1.323	1.0.221	0.1.323	1.0.121
<i>areolatus</i>	6	1	2	0.1.223	0.1.221	0.1.323	1.221	0.1.323	1.121
<i>biarticulatus</i>	8	2	(2+2)	0.1.223	0.1.221	0.1.323	1.1.221	0.1.323	1.221
<i>cinctus</i>	7	1	2	0.1.223	0.1.221	0.1.323	1.1.221	0.1.323	1.1.221
<i>cookorum</i> [♀]	8	2	(2+2)	0.1.223	0.1.221	0.1.323	1.0.221	0.1.322	1.221
	[♂]							0.1.323	
<i>kirstenae</i> [♀]	8	2	(2+2)	0.1.223	0.1.221	0.1.323	1.0.221	0.1.322	1.0.221
	[♂]							0.1.323	
<i>limigenus</i>	7	1	2	0.1.223	0.1.121	0.1.323	1.0.221	0.1.323	1.121
<i>paranaguaensis</i>	7	1	2	0.1.223	0.1.120	0.1.323	1.0.221	0.1.323	1.121
<i>septimus</i>	8	1	2	0.1.223	0.1.221	0.1.323	1.0.221	0.1.323	1.121
<i>sextus</i>	7	1	2	0.1.223	0.1.221	0.1.323	1.0.221	0.1.323	1.121
<i>shulenbergeri</i>	7	1	2	0.1.223	0.1.121	0.1.323	1.0.221	0.1.323	1.121
<i>stammeri</i>	7	1	2	0.1.223	0.1.121	0.1.323	1.0.221	0.1.323	1.121
<i>Perissocope</i>									
<i>adiastaltus</i>	7	3	(2+0+3)	0.1.223*	0.1.221	0.1.323	1.1.321	0.1.323	1.1.121
<i>biarticulatus</i>	8	3	(1+0+3)	1.1.223	0.1.221	1.1.323	1.1.321	1.1.322	1.1.221

\* Wells (1968) figured P2 exp-3 with formula 323; this is clearly based on an aberrant specimen since no extant harpacticoid has more than 7 elements on this segment (Huys & Boxshall, 1991; also confirmed by re-examination of other type material).

setae on exp-2. Comparison with the 3-segmented exopod in *Tigriopus* suggests that the proximal lateral seta on exp-2 in these genera originates from the incorporated middle segment and therefore the ancestral setal formula must have been [2,1,3]. In *Perissocope* the lateral seta on exp-2 is lost resulting in a [2,0,3] formula in *P. adialstus* Wells or [1,0,3] in *P. biarticulatus* Watkins. Further setal reduction has occurred in the *Zausodes* complex where only 2 setae are retained on the distal segment in the most primitive species (*biarticulatus*, *kirstenae*, *cookorum*), or secondarily, the exopod became an unsegmented bisetose ramus (all other species).

#### (7) Armature praecoxal endite maxilla

Some species of *Perissocope* have 5 elements on the praecoxal endite of the maxilla (Huys *et al.*, 1996; Fig. 106F) which is the highest number recorded in any member of the Harpacticidae. This number is reduced to four (state 1) or three setae (state 2) in the *Zausodes* complex. Itô (1979) recorded variability in the maxilla of *Z. biarticulatus* and regarded the 3-setae condition as the typical one. The 'atypical' maxilla illustrated in his Fig. 3-1 shows 4 elements arranged in the same pattern as found in *Z. arenicolus* (Fig. 3B) and *Z. septimus* (Mielke, 1990: Abb. 3A). On the basis of this similarity we have scored state 1 for *Z. biarticulatus*. Lang (1965) showed only 2 setae on this endite but we suspect that the third one was overlooked and have given this species a score 2 accordingly (Table 3).

#### (8) Armature P1 exp-3

The distal exopod segment of P1 is small or vestigial in the Harpacticidae and typically embedded in the distal margin of the middle elongate segment. Huys *et al.* (1996) described the basic armature of this segment as four unhinged claws, 1 hinged claw and a seta, but careful re-examination of a range of genera revealed that the seta in reality belongs to the middle exopod segment. This seta is often small (e.g. Fig. 5C) and sited at the distal inner corner of exp-2. Huys *et al.*'s misconception stems from observations of *Harpacticus* and *Zaus* in which the distal segment is largely incorporated in the middle one. In other genera such as *Harpacticella* and *Tigriopus* the distal segment is well delimited showing the real

origin of the inner seta (Itô, 1970, 1977; Itô & Kikuchi, 1977). Both *Perissocope* and the *Zausodes* complex deviate from the normal armature pattern by the presence of two hinged (geniculate) claws (see above). The modification of one of the simple claws into a second geniculate one is a synapomorphy for these taxa. Species of the *Zausodes* complex have lost one of the simple claws, retaining only four elements on exp-3 (2 geniculate and 2 simple claws).

#### (9) Armature P1 exp-1

Harpacticidae typically possess a well developed inner seta on the proximal endopod segment of P1. The exceptions to this rule are the species belonging to the *Zausodes* complex which have secondarily lost this seta.

#### (10) Armature P2 exp-3

Most Harpacticidae have 2 inner setae on the distal endopod segment of P2. Some species within the *Zausodes* complex possess only 1 seta on this segment (Fig. 15A; Table 1). This reduction has evolved convergently in other genera such as *Harpacticus* (e.g. *H. compsonyx*) and *Tigriopus*.

#### (11) Armature P3 exp-2

The inner seta on the middle endopod segment of P3 is present in most harpacticid genera, including *Perissocope*. Within the *Zausodes* complex, however, this seta is commonly lost and is retained only in *Z. biarticulatus* (and the imperfectly described *Z. cinctus* – see below).

#### (12) Armature P3 exp-3

Species of *Perissocope* and most other genera of the family possess 3 inner setae on the distal endopod segment of P3. Various reductions occur in the more advanced genera *Tigriopus*, *Paratigriopus* and *Discoharpacticus*. All species of the *Zausodes* complex invariably have 2 inner setae on this segment.

#### (13) Armature P4 exp-3

Sexual dimorphism in the number of armature elements on the P4 exopod is extremely rare within the Harpacticoida. In some species

**Table 2** Characters used in phylogenetic analysis. Apomorphic character states are referred to in square brackets. Characters 5–7 are multistate characters.

1	Antennule ♀ 8-segmented [7-segmented, segments 6 and 7 fused]
2	Antennule ♀ with only setiform elements on segments 3, 4 and 5 [segment 3 with 2 and segments 4–5 with 1 strong, modified spine]
3	Antennule ♀ segment 6 (or homologous portion in 6- or 7-segmented antennule) without enlarged spines [with 2 enlarged pectinate or pinnate spines]
4	Antennule ♀ with all elements naked (except for pinnate spines referred to in character 3) [with pinnate or plumose setae on segments 1–6]
5	Antennary exopod 3-segmented [state 1: 2-segmented; state 2: 1-segmented]
6	Antennary exopod with total of 5 setae (2 on exp-1, 3 on exp-3; exopod 3-segmented) [state 1: 2 on exp-1, 2 on exp-2 and exopod 2-segmented; state 2: total of 2 setae on single segment]
7	Maxilla with 5 setae on praecoxal endite [state 1: 4 setae; state 2: 3 setae]
8	P1 exp-3 with 2 geniculate (hinged) and 3 simple claws [with 2 geniculate and 2 simple claws]
9	P1 enp-1 with long inner seta [without]
10	P2 enp-3 with 2 inner setae [with 1 inner seta]
11	P3 enp-2 with inner seta [without]
12	P3 enp-3 with 3 inner setae [with 2 inner setae]
13	P4 exp-3 with 3 outer spines in ♀ [with 2 outer spines in ♀, 3 in ♂]
14	P4 endopod 3-segmented [2-segmented; enp-2 and -3 fused]
15	P4 enp-2 (or homologous portion in 2-segmented endopod) with inner seta [without inner seta]
16	P4 enp-3 (or homologous portion in 2-segmented endopod) with 2 inner setae [with 1 inner seta]
17	P5 exopod oval or elongate in both sexes [round]
18	P5 ♀ endopodal lobe expressed [completely lost]
19	P5 ♀ endopodal lobe inner seta not distinctly shorter than other endopodal elements [rudimentary]
20	P5 ♀ endopodal lobe 3rd and 4th setae well developed [much shorter than others]
21	Antennule ♂ segment 3 without transformed elements [with modified spine]
22	P2 enp-2 ♂ with apophysis [secondarily lost]
23	P2 enp-2 ♂ inner element setiform, not sexually dimorphic [modified into stout spine, distinctly shorter than in ♀]
24	P2 enp-3 outer spine articulating with segment [fused to segment]
25	P3 enp-2 ♂ outer distal corner not attenuated [attenuated]

**Table 3** Character data matrix. Characters listed in Table 2 are scored using the multistate system: 0 = ancestral (plesiomorphic) state, 1 = derived (apomorphic) state, 2 = further derived state, ? = missing data, indicating that the character state is either unknown or unconfirmed.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>arenicolus</i>	0	0	0	1	2	2	1	1	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0
<i>areolatus</i>	1	1	1	0	2	2	2	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	0
<i>biarticulatus</i>	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	0	0	1	0	1	0
<i>cookorum</i>	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1
<i>kirstenae</i>	0	0	0	0	1	1	1	1	1	0	1	1	1	0	1	0	0	1	1	0	0	1	1	1	1
<i>limigenus</i>	1	1	1	?	2	2	?	1	1	1	1	1	0	1	1	1	1	0	0	0	?	?	?	?	?
<i>paranaguensis</i>	1	1	1	?	2	2	?	1	1	1	1	1	0	1	1	1	1	0	0	0	?	?	?	?	?
<i>septimus</i>	0	0	0	1	2	2	1	1	1	0	1	1	0	1	1	1	0	0	0	1	0	1	0	0	0
<i>sextus</i>	1	1	1	0	2	2	2	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	0
<i>shulenbergeri</i>	1	1	1	0	2	2	2	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1	0	0	0
<i>stammeri</i>	1	1	1	?	2	2	?	1	1	1	1	1	0	1	1	1	1	0	0	0	?	?	?	?	?
<i>PERISSOCOPE</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>cinctus</i>	1	0	0	0	2	2	?	1	1	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?

of the Thompsonulidae (Huys & Gee, 1990) and Tetragonicipitidae (Kunz, 1984) sexual dimorphism involves the loss of elements in the male, whereas in species of *Huntemannia* Poppe an increase in the number of elements has been reported (Wilson, 1958; Geddes, 1968b). Two new species from the Gulf of Mexico (*kirstenae*, *cookorum*) show 2 outer spines on the distal exopod segment of P4 in the female and a supernumerary spine in the male. All other species of the *Zausodes* complex possess 3 spines in both sexes.

#### (14) Segmentation P4 endopod

Only three species of the *Zausodes* complex (i.e. *arenicolus*, *kirstenae* and *cinctus*) have retained the 3-segmented condition of the P4 endopod. In all other species the middle and distal segments have failed to separate, resulting in a 2-segmented ramus. Lang (1965) refused to split up *Zausodes* on the basis of P4 endopod segmentation since for many other characters close congruence was found between species with different segmentation. Lang assumed that the 2-

segmented state had arisen convergently and pointed out that the original division of the distal segment in *Z. sextus* is still indicated by a dentiform notch along the outer margin. An incomplete surface suture was also found in *Z. areolatus* (Fig. 11C), suggesting that the P4 endopod segmentation is probably an evolutionary labile character.

#### (15) Armature P4 enp-2

Most harpacticid genera displaying a 3-segmented P4 endopod possess an inner seta on the middle segment. This seta has been lost in the *Zausodes* complex (except *Z. cinctus*), including the two species in which the middle segment is still separated (*kirstenae*, *arenicolus*).

#### (16) Armature P4 enp-3

The maximum number of inner setae on the distal (enp-3) endopod segment of P4 in any species of the Harpacticidae is two. This number is found in most members of the family, including some (but

not all) species of *Perissocope* such as *P. biarticulatus*. Within the *Zausodes* complex 2 setae are found in only four species (Table 1), however in both *biarticulatus* and *cookorum* the distal segment represents the fused enp-2 and -3, obscuring the origin of the proximal inner seta. Comparison with the closely related *kirstenae*, in which all segments are expressed, suggests that both inner setae are derived from enp-3.

(17) *Shape P5 exopod of both sexes*

The P5 exopod is usually oval or elongate in both sexes. In one species group of the *Zausodes* complex the exopod is distinctly round (e.g. Figs 15D, 18D) which by outgroup comparison with *Perissocope* and other genera is regarded here as the apomorphic condition.

(18) *Shape P5 ♀ endopodal lobe*

The endopodal lobe is well developed in the majority of female harpacticids, including most members of the *Zausodes* complex. In four species (*biarticulatus*, *kirstenae*, *cookorum*, *cinctus*) the whole baseoendopod is modified, forming a transversely elongated plate, and the endopodal lobe is no longer expressed (Figs 23B; 30C).

(19–20) *Armature P5 ♀ endopodal lobe*

Species belonging to *Perissocope* and the *Zausodes* complex typically have 5 well developed setae on the P5 endopodal lobe of the female. In some species of the latter particular elements have undergone secondary reduction in size. In the *cookorum-kirstenae-biarticulatus* group the innermost seta is rudimentary and sited at the extreme distal corner near the articulation with the exopod (Figs 23B, 30C; character 19 in Table 3). Further reduction has occurred in *biarticulatus* where the three innermost setae are completely vestigial (Itô, 1979). In the type species *Z. arenicolus* the 3rd and 4th setae (counted from the innermost according to Huys *et al.* (1996)) are very reduced and the innermost one is well developed. This reduction is treated separately as character 20 in Table 3 and scored as state 1 in both *arenicolus* and *septimus*. In the latter one of the smaller setae is lost, retaining only 4 elements on the endopodal lobe (Lang, 1965; Mielke, 1990). The reduction of setae 3 and 4 in *biarticulatus* is regarded here as a further derived state of character 19 and not as the apomorphic state of character 20.

(21) *Armature antennule ♂*

Male antennules in the Harpacticidae are of the subchirocer or chirocer type. Armature elements are typically modified on the segments located either side of the geniculation. In one group of the *Zausodes* complex the male antennule also possesses a modified element on segment 3. It is represented by a strong spine which is situated dorsally near the distal margin of the segment (Figs 12F, 18A).

(22–23) *Modification P2 enp-2 ♂*

The male P2 endopod is of high significance in understanding the phylogeny of the Harpacticidae (Itô, 1984). Many genera possess an outer spinous apophysis on the middle endopod segment which attains its maximum size in *Harpacticus* and *Discoharpacticus*. Analysis of the phylogenetic relationships within the family (Huys, unpubl.) suggests that this apophysis has become gradually smaller during harpacticid evolution and was lost independently in *Paratigriopus*, *Harpacticella* and *Zaus-Zausopsis*. A similar regressive evolution has also been documented in the Paranannopidae for a similar apophysis on the male P2 endopod (e.g. Gee & Huys, 1991; Huys & Gee, 1993, 1996). Within the *Perissocope-Zausodes* lineage the apophysis is clearly in a state of reduction. The genus

*Perissocope* combines both species with a slender apophysis (*P. biarticulatus*, *P. exiguus*, *P. bayeri*) and species without such an uncinate process (*P. adialtustus*). Within the former *Zausodes* complex only the type species *Z. arenicolus* possesses a short spinous outgrowth on P2 enp-2 (Fig. 7E) whereas all other species have lost the apophysis completely (Figs 12D, 17C, 22D).

In both *kirstenae* and *cookorum* the inner element of P2 enp-2 is sexually dimorphic, being setiform in the ♀ and modified into a short stout spine in the ♂ (character 23 in Table 3; Figs 22D, 29A).

(24) *Modification P2 enp-3 ♂*

The outer spine on the distal endopod segment of the male P2 is frequently modified in the Harpacticidae. In male *Harpacticus* the outer spine is usually lost at the final moult or not formed at all in any male copepodid instar (Itô, 1984). In some species such as *H. furcatus* Lang the outer spine is represented by a rudimentary setule (Itô & Fukuchi, 1978). In other genera such as *Tigriopus*, *Paratigriopus* and *Zaus* the outer spine is not sexually dimorphic and articulating with the segment. A different modification is found in male *Perissocope* where the outer spine is completely integrated into the distal segment, forming a long, slender apophysis (e.g. Vervoort, 1964; Pallares, 1975; Watkins, 1987; Wells, 1968). A similar apophysis was found by Itô (1979) in *Z. biarticulatus* and in two new species (*kirstenae*, *cookorum*) described here. In the latter the apophysis is represented by a spinous process which is minutely pectinate at the inner subapical margin and about equal in length to the outer spine in the female (Figs 22D, 29A).

(25) *Modification P3 enp-2 ♂*

Distinct sexual dimorphism on the P3 endopod is rare in the Harpacticidae. Differences in surface ornamentation between the sexes are occasionally found in *Harpacticus* (Itô, 1976; Itô & Fukuchi, 1978) and in species of the *Zausodes* complex (*shulenbergi*, *kirstenae*), however, these have not been included in the analysis. A more pronounced modification involves the formation of a mucroniform process at the outer distal corner of the middle segment. This is found in the genus *Perissocope* and in two closely related species of the *Zausodes* complex (*kirstenae*, *cookorum*) (Figs 22E, 29D).

## Data matrix and analysis

In order to resolve the relationships within the *Zausodes* complex the analysis was executed at the species level. The characters used in the analysis of phylogenetic relationships between *Perissocope* and the 12 species of the *Zausodes* complex are listed in Table 2. The character states are explained inside square brackets using the multistate system: 0 = the ancestral state, 1 = the derived state, 2 = a further derived state. The scores for each character and taxon are compiled in matrix format in Table 3. A question mark indicates missing data, either because the appendage or structure is unknown in that species (certain sexually dimorphic characters could not be scored because only one sex is known) or because it was impossible to score the character accurately due to the lack of detail in the original descriptions (cf. Jakobi, 1954). *Z. cinctus* Krishnaswamy was excluded from the analysis. Its status is discussed below.

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## RESULTS AND DISCUSSION

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Two most parsimonious trees were obtained with tree-length 36 and consistency index 0.778 (Fig. 33). Both trees differ only in the position of *Z. septimus* which in tree A forms a monophyletic group

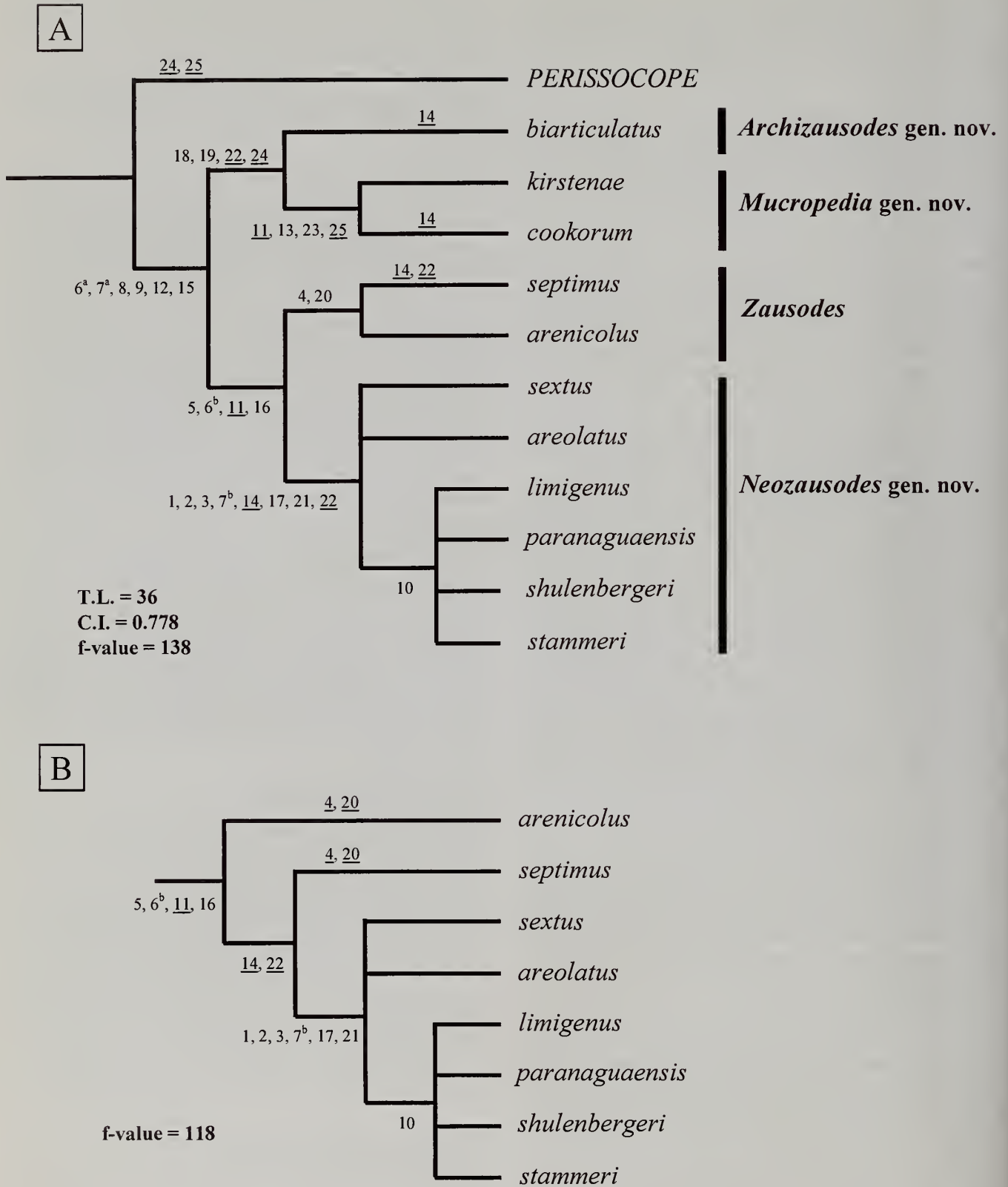


Fig. 33 Optimal trees depicting relationships between species of the *Zausodes* complex and the genus *Perissocope*. Numbers refer to apomorphic states of characters listed in Table 2 [underlined numbers refer to convergences, superscript letters indicate multistate characters]. T.L. = tree-length; C.I. = consistency index.



with *Z. arenicolus*, whereas in tree B it occupies a transitional position between the type species and the other *Zausodes* species. Tree B has a lower *f*-value (118) than tree A (138), however, we have selected the latter as the optimal one on account of the lower number of convergences. In tree A *Z. septimus* and *Z. arenicolus* are clustered on the basis of two apomorphies which are unique to these two species (characters 4 and 20). This grouping is at the expense of introducing convergences for characters 14 and 22, however, both these characters already show convergence in other clades (Fig. 33A) and are known to be evolutionary labile. The justification for grouping *Z. septimus* with the other *Zausodes* species in tree B is based solely on the convergent evolution of characters 14 and 22, thereby causing additional homoplasies for characters 4 and 20.

The monophyly of the *Zausodes* complex and its sistergroup relationship to *Perissocope* are confirmed. The complex is divided in two lineages by a strongly supported basal dichotomy and each lineage is composed of two clades.

The *biarticulatus-kirstenae-cookorum* lineage is supported by leg 5 characters such as the loss of the endopodal lobe and the reduction of the innermost seta of the baseoendopod. Additional apomorphies are the modification of the distal outer spine on the male P2 endopod and the sexual dimorphism on the P3 endopod. A peculiar character shared by these species (but not used in the analysis) is the presence of a well developed hyaline frill on the distal endopod segment of P1. Under the traditional light microscope this frill resembles a tuft or fan of spinules sited at the distal outer corner of enp-2 (Figs 22C, 29E). All three species have retained the primitive segmentation and setation of the antennary exopod. Within this lineage *Z. biarticulatus* occupies the most primitive position since it is the only species which has retained the inner seta on P3 enp-2. The other species (*cookorum*, *kirstenae*) are clustered on the basis of their unique sexual dimorphism on the P2 endopod, P3 endopod and P4 exopod.

The monophyly of the second lineage which includes all other species is supported by the 1-segmented antennary exopod bearing only 2 setae and the reduced armature on the P4 endopod. A basal dichotomy divides the lineage into two distinct clades, the *arenicolus*-clade and the *sextus*-clade. The former accommodates the type species and *Z. septimus* and is characterized by the presence of ornate setae on the ♀ antennule and by the reduction of particular setae on the ♀ P5 baseoendopod. Both species have retained primitive antennule characters such as the 8-segmented condition in the ♀ and the complete absence of modified elements in both sexes. The *sextus*-clade, encompassing 6 closely related species, is extremely well supported but largely unresolved. This is partly due to the deficient descriptions of the Brazilian species (*limigenus*, *stammeri*, *paranaguaensis*) for which it has proven impossible to score all characters (Table 3). The clade is defined by the 7 (or 6 in *areolatus*)-segmented ♀ antennule, the presence of modified spines in both proximal and distal regions of the ♀ antennule and on segment 3 of the ♂ antennule, the reduced armature on the maxillary praecoxal endite and the round shape of the P5 exopod in both sexes. A subgroup, combining *shulenbergi* and Jakobi's (1954) species, can be recognized within this clade and is characterized by the presence of only 1 inner seta on P2 enp-3.

Itô (1979) already remarked that *Z. biarticulatus* occupied a separate taxonomic position within *Zausodes* and highlighted particular similarities with the genus *Perissocope*. Lang (1965) on the other hand favoured a subdivision of the genus *Zausodes* but was reluctant to do so on the basis of P4 endopod segmentation. Our analysis has revealed marked intrageneric differences in the sexual dimorphism of all three swimming legs (P2–P4), the setation and

armature of the antennary exopod, and the form and modification of antennular elements in both sexes. Such variability has not been recorded for any of the other 8 genera in the family, suggesting that the *Zausodes* complex combines distinct lineages which – in accord with the generic concept currently applied in the Harpacticidae – would deserve generic status. The genus *Zausodes* is therefore redefined to include only *Z. arenicolus* and *Z. septimus*, and three new genera (*Archizausodes* gen. nov., *Mucropedia* gen. nov. and *Neozausodes* gen. nov.) are proposed, reflecting the basic topology illustrated in Fig. 33A.

### Status of *Zausodes cinctus* Krishnaswamy, 1954

The taxonomic position of this species from off the Madras coast (India) is enigmatic since Krishnaswamy's (1954) description is erroneous in many aspects. We attempted but were unable to obtain the type specimens from the Zoological Survey of India in Calcutta. The strongly elongated P5 exopod is unique within *Zausodes* sensu lato and leaves little doubt that *Z. cinctus* is a distinct species. However, the numerous deficiencies in the original figures make it impossible to allocate this species to one of the four genera recognized herein. For example, Krishnaswamy (1954) claims that the P1 exopod is only 2-segmented and sexually dimorphic, the male having only 2 claws and 1 seta on the distal segment and no outer seta (corresponding to exp-2). The endopod of this leg is reminiscent of the laophontid type, bearing only one strong claw on the distal segment. There is no doubt that the author has overlooked elements on both rami and that his report of sexual dimorphism is based on this oversight. Similarly, there is considerable confusion over the armature formula of the endopods of P2–P4. According to Krishnaswamy the distal endopod segment of P2–P4 has 1 terminal and 3 inner setae which Lang (1965) translates as a [211] formula, implying that an outer spine is present. The latter is invariably short in Harpacticidae, however, Krishnaswamy's figures show only a long plumose seta which is outwardly directed. We speculate that this unusual orientation of the outer apical seta (perhaps as a result of imperfect mounting) has obscured the outer spine (cf. Itô's (1979) drawings of *A. biarticulatus*) and that the armature formula of P2–P4 enp-3 is more likely [221] as in *Archizausodes* and *Mucropedia*. If this assumption is correct then *Z. cinctus* displays the most primitive swimming leg armature within *Zausodes* sensu lato since no other species possesses an inner seta on P4 enp-2 (and *A. biarticulatus* being the only other species to exhibit an inner seta on P3 enp-2). In this context we point out the possible homology between the latter seta and the proximal inner seta of P4 enp-2 in *A. biarticulatus* which we – by reference to the 1.0.221 pattern in closely related *M. kirstenae* (Table 1) – have interpreted as originating from enp-3.

Another remarkable feature is the presence of only 4 elements on the ♀ P5 exopod. Krishnaswamy's illustration shows a distinct gap between the proximal and distal outer spine which corresponds with the position of the vestigial seta on the P5 of *A. biarticulatus* (cf. Itô, 1979: Fig. 5–1). It is conceivable that a similarly reduced seta is present in *Z. cinctus*. Both species, coincidentally the only Asian representatives of the *Zausodes* complex, also share the absence of the endopodal lobe and show a similar arrangement of the endopodal setae (with *Z. cinctus* having an additional long seta).

The male P2 endopod of *Z. cinctus* was neither described nor illustrated by Krishnaswamy (1954). Sexual dimorphism in the P2 endopod is always present in the *Zausodes* complex, so it is conceivable that it was overlooked. Pending the re-examination of Krishnaswamy's types or topotype material we rank *Z. cinctus* as *species incertae sedis* in the Harpacticidae.

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