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A revision of Thompsonulidae Lang, 1944 (Copepoda: Harpacticoida)

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The harpacticoid copepod subfamily Thompsonulinae Lang, 1944, formerly recognized as belonging to the family Tachidiidae (Lang, 1948) is raised to family rank and redefined to include only the genera *Thompsonula* T. Scott and ***Caribbula* gen. nov.** *Thompsonula hyaenae* (I. C. Thompson) and *T. curticauda* (Wilson) are redescribed and refigured. Re-examination of the original material showed that Wilson's *Rathbunula agilis* is synonymous with *T. curticauda* and not with *T. hyaenae*, as suggested by Lang (1948). It is now clear that the two species of *Thompsonula* have distinct distributions, *T. curticauda* being confined to the North American continent and *T. hyaenae* to western Europe and the Mediterranean. The genus *Caribbula* is established to accommodate the type species, *T. hyaenae elongata* (Gee) and ***C. fleegeri* sp. nov.** which are described and figured. The genus *Caribbula* is distinguished from *Thompsonua*, primarily by the unique sexual dimorphism on the exopod of P4 and, at present, is known only from the eastern seaboard of the United States and Gulf of Mexico. The genera *Danielssenia*, *Psammis*, *Paradanielssenia*, *Micropsammis* and *Leptotachidia* are tentatively assigned to the family Paranannopidae Por.

KEY WORDS:—Crustacea – Copepoda – Harpacticoida – Thompsonulidae – *Thompsonula* – ***Caribbula* gen. nov.**

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INTRODUCTION

I. C. Thompson (1889) described *Jonesiella hyaenae* from material dredged in Port Erin Bay, Isle of Man, during the fifth cruise of the steamer *Hyaenae*. Despite the fact that this animal had a three-segmented endopod on the first swimming leg, he assigned it to Brady's (1880) genus *Jonesiella*, preferring to alter slightly an existing genus rather than create a new one. The discrepancies in the first swimming leg (and antenna) were recognized by T. Scott (1893) and he later (1905) removed *J. hyaenae* from *Jonesiella* and placed it in a new genus *Thompsonula*. *Jonesiella* turned out to be a dubious genus: Sars (1898) relegated it to a junior synonym of *Danielssenia* Boeck, 1872 by synonymizing Brady's (1880) species *J. spinulosa* with *D. typica* and allocating *J. fusiformis* to the same genus. However, Shen & Bai (1956) regarded *D. typica* and *D. fusiformis* as conspecific and this was confirmed recently by Gee (1988a). Apparently overlooking Sars' (1898) account, T. & A. Scott (1901) added a third species, *J. brucei*, to *Jonesiella* but this was rightly transferred to the diosaccid genus *Pseudomesochra* T. Scott 1902 by Lang (1935).

Monard (1927) modified and elaborated Sars' (1930–1921) system of higher taxa and, for the first time, included the genus *Thompsonula* in the family Tachidiidae. Sars' concept of the Tachidiidae was also largely adopted by Gurney (1932), except that he removed the genus *Robertsonia* to the Diosaccidae and synonymized *R. aculeifera* Klie, 1913, with *T. hyaenae*. At the same time C. B. Wilson (1932) added two new genera, *Rathbunula* and *Echinocornus*, to the Tachidiidae but did not discuss their undeniable affinities with *Thompsonula*. This is surprising since the latter genus was included in Wilson's generic key (p. 582) and even keyed out in the same couplet (173) with *Rathbunula*.

In his outstanding monograph, Lang (1948) revised the family Tachidiidae and recognized it as consisting of three sub-families, Microarthidioninae Lang (=Tachidiinae Boeck), Euterpininae Brian and Thompsonulinae Lang, the latter being established to accommodate the type genus *Thompsonula* and the genera *Danielssenia* Boeck and *Psammis* Sars. He relegated both Wilson's genera to synonyms of *Thompsonula* but recognized *T. curticauda* as the second species in the genus. He also thought that *Psammis* and *Danielssenia* were more closely related to each other than to *Thompsonula* or any other tachidiid.

Since the publication of Lang's monograph, three new genera have been added to the Thompsonulinae (*Paradanielssenia* Soyer, *Leptotachidia* Becker, *Micropsammis* Mielke) but none of them are closely related to *Thompsonula*. The isolated position of the latter led Huys (in press) to suggest that the subfamily might not be a natural unit as he failed to recognize any synapomorphies between *Thompsonula* and the other genera of the subfamily. In this paper we raise Thompsonulinae Lang to full family rank, redefine it to include only the type genus *Thompsonula* and a second ***Caribbula* gen. nov.,** and justify the validity of this action. The status and relationships of the other genera will be dealt with in further papers but here they are tentatively assigned to the family Paranannopidae Por.

MATERIAL AND METHODS

Before dissection, the habitus was drawn and body length measurements made from a whole specimen mounted in lactophenol. Specimens were then dissected in lactic acid, the parts mounted in lactophenol and the preparations sealed with glyceel. All drawings of these specimens were prepared using a camera lucida on a Leitz Dialux 20 interference microscope.

Whole specimens of both sexes of *Thompsonula hyaenae* from the Belgian coast were examined with a JEOL JSM-840 scanning electron microscope. They were prepared by dehydration through graded ethanol, critical-point dried, mounted on stubs and sputter-coated with gold.

In this paper the terminology of Lang (1948, 1965) is adopted except that: (1) following Mielke (1984), the terms pars incisiva, pars molaris and lacinia mobilis are omitted in the description of the mandibular gnathobase; (2) the terminology applied to the segments of the mandible and maxilliped follows that of Boxshall (1985: 341–345); and (3) the terminology for caudal ramus structure follows that of Huys (1988). Abbreviations used in the text and figures are: P1–P6 for swimming legs 1–6; exopod (endopod)-1 (-2, -3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the base of the rostrum to the posterior margin of the anal somite.

SYSTEMATICS

Thompsonulidae Lang, 1944

Synonyms. Thompsonulinae Lang, 1944 (part).

Diagnosis. Body shape ranging from sub-cylindrical to fusiform, without marked distinction between prosome and urosome. P1-bearing somite fused with cephalothorax. Dorsal surface of prosome with numerous sensillae interspersed with mucous pores. Female genital double-somite always with lateral and ventral, and sometimes with dorsal, internal chitinous ridge; genital field with separate gonopores, minute copulatory pore and paired, well-developed seminal receptacles. Urosomites with continuous dorsal and ventral row of spinules. Anal somite not markedly notched in middle of posteror border; dorsal anal operculum with spinulose border; pseudoperculum absent. Caudal rami broader than long, with seven setae; terminal setae (IV, V) strongly developed and spinulose; seta I very small. Rostrum very large and defined at base, rounded anteriorly, with two lateral sensillae.

Antennule in female five- or six-segmented, in male six- or seven-segmented, sub-chirocer. In both sexes, short and stout, recurved with numerous strongly pinnate spines, a tube pore on segments I and II and two aesthetascs.

Antenna with well-developed coxa. Allobasis with strong abexopodal pinnate spine and three-segmented exopod, with two setae on proximal, one on middle and three spines and a seta (sometimes tubular) on distal segment. Endopod one-segmented with seven distal and four sub-distal elements.

Labrum spinulose. Mandible with two well-developed setae, confluent at base, at dorsal corner of gnathobase. Palp well developed. Basis with four setae. Endopod one-segmented with two lateral setae and seven terminal setae (all fused at base). Exopod usually one-, sometimes two-segmented.

Maxillule with precoxal arthrite defined at base and with 11 distal elements

and two surface setae. Coxal epidodite represented by one plumose seta, endite cylindrical with five setae. Baso-endites fused, with eight distal elements of which two are geniculate. Endopod and exopod one-segmented, each with four setae.

Maxilla with three endites on syncoxa, proximal endite short with two spines, middle and distal endites each with three spines. Baso-endite produced terminally into a strong claw, bearing a geniculate spine and two setae. Endopod indistinctly segmented with seven setae of which three are geniculate.

Maxilliped prehensile. Syncoxa with three pinnate spines and one seta. Basis elongate with two setae on inner margin. Endopod slender, one-segmented with terminal claw and four or five accessory setae.

P1-P4 with intercoxal sclerites well developed and unarmed. Rami three-segmented with endopod longer than exopod. Outer margin of each ramus with large spinules. Outer spines of exopod strongly pinnate. P1 unmodified; coxa and basis fused near inner margin; basis with strong, pinnate, recurved, ventrally directed inner spine; setal formula as in Table 1.

TABLE 1. Setal formulae

	Exopod	Endopod
P1	0.1.022	1.1.121
P2	1.1.223	1.1.221
P3	1.1.223	1.1.321
P4	1.1.323	1.1.221

P5 with outer lobe of baseoendopod well developed, exopod separate and no intercoxal sclerite. In female, baseoendopods not fused medially, endopodal lobe well developed with five setae; exopod (partly overlain by baseoendopod) with six setae. In male, baseoendopods fused medially, endopodal lobe somewhat reduced with two setae; exopod with five setae. P6 in female represented by one well-developed plumose seta and a minute spine. In male, one member (right or left) fused to somite wall, opposite member articulating at base and closing off gonopore; each bearing three setae.

Female with one egg sac, male with one spermatophore. Sexual dimorphism in antennule, P5, P6, genital segmentation and sometimes in P4 (loss of inner proximal seta on exopod-3).

Habitat. Marine sediments.

Type genus. Thompsonula T. Scott 1905. Other genera: ***Caribbula* gen. nov.**

Genus *Thompsonula* T. Scott, 1905

Synonyms. Robertsonia (part.) sensu Klie, 1913; *Rathbunula* C. B. Wilson, 1932. *Echinocornus* C. B. Wilson, 1932.

Diagnosis. Thompsonulidae. Body markedly fusiform, widest in region of second free-prosomite. Cephalic shield narrow anteriorly bearing large, recurved rostrum, 2.3 times longer than maximum width and reaching at least to distal margin of second segment of antennule. Female genital double-somite without dorsal suture; genital field with almost circular seminal receptacles, posterior borders of which partially surround copulatory pore. Urosomites with denticulate hyaline frill and continuous aventral spinule row on penultimate urosomite. Antennule in female five or six-segmented, proximal segment

distinctly longer than wide; in male six-segmented (resulting from fusion of segments III and IV). Allobasis of antenna with short abexopodal seta reaching only to proximal third of endopod. Proximal endite of maxilla cylindrical, with terminal setae lying on top of one another. Outer seta of P1 basis plumose in mid-region with flagellate tip. Coxa of P2-P4 with spinule row associated with tube pore composed only of short spinnules, no corresponding spinule row on posterior face. Basis of P2 with naked outer seta. No sexual dimorphism in swimming legs. P5 with endopodal lobe of baseoendopod tapering only slightly and broadly rounded at distal margin; exopod almost circular with distal margin not reaching distal margin of endopodal lobe.

Type species. Thompsonula hyaenae (I. C. Thompson, 1889) (by monotypy). Other species *T. curticauda* (C. B. Wilson, 1932).

Thompsonula hyaenae (I. C. Thompson, 1889)

(Figs 1–12)

Synonyms. Jonesiella hyaenae I. C. Thompson, 1889).

Material examined

1. British Museum (Natural History). I. C. Thompson collection: 1951.8.10.650, one female, dissected, labelled *Jonesiella hyena*: Port Erin, Isle of Man, 4–6 fathoms; 1959.2.9.111, one female whole mount, labelled *Jonesiella hyaena*: Port Erin, Isle of Man, dredged at 4 fathoms on 19.06.1892; 1959.2.9.112, one male whole mount labelled *Jonesiella hyaena*: Morecombe, in stomach of plaice in 1893.

Norman collection: 1911.11.8, M.2302 two females, whole mounted, labelled *Jonesiella hyena* (but of *Halectinosoma*): Port Erin, Isle of Man, (leg. I. C. Thompson in 1889); 1911.11.8.43566.585, 20 females and three males, spirit preserved in vial labelled *Thompsonula hyaenae*: Whitsand Bay Cornwall (leg. Norman & T. Scott on 31.8.1903); 1911.11.8.43586.587, two females, spirit preserved in vial labelled *Jonesiella hyaenae*: On *Zostera* in St. Mary's Harbour, Scilly Isles (leg. Norman & T. Scott, 1903); 1911.11.8.43588.590. Three females, spirit preserved in vial labelled *Jonesiella hyaenae*. Firth of Forth (leg. T. Scott in 1903).

2. Naturhistoriska Riksmuseet, Stockholm. 78. one male, spirit preserved. Cuxhaven, depth 10 m (leg. A. Remane on 22.7.1912), det. K. Lang.

3. From Dr R. Hamond. Two females and one male (formalin preserved), from off Calais, leg. May/June 1987.

4. From Dr J.-Y. Bodiou. Four females (formalin preserved), from off Banyuls-sur-Mer, France.

5. Ten females and six males from north of mouth of Westerscheldt estuary, 51°28′25″N 03°28′10″E, (leg. R. Huys 7.9.1983), depth 5.4 m, 99.75% sand of median grain size 0.223 mm.

6. Two females from Vlakte van de Raan, SW of Dutch Delta region (leg. R. Huys, 6.11.1984), depth 6.4 m, 99.24% sand of median grain size 0.203 mm.

7. Eight males and 34 females from off Goeree coast in front of former Haringvliet estuary (leg. R. Huys 12.10.1984), depth 7.2 m, 98.34% sand of median grain size 0.186 mm.

8. Two females off coast of Voorne, Dutch Delta region (leg. R. Huys 12.11.1984), depth 5.3 m, 96.35% sand of median grain size 0.168 mm.

Description of female

Body (Figs 1, 10). Heavily sclerotized, markedly fusiform in shape and no clear distinction between prosome and urosome; length 597–637 μm (mean 610 μm, n=5); maximum width at second free prosomite and tapering symmetrically anteriorly and posteriorly; slightly dorso-ventrally flattened. Cephalothorax equal in length to free prosomites, posterior border of cephalic shield smooth but dorsal and lateral surface with many sensillae and mucous pores. Free prosomites with sensillae and patches of tubercles on dorsal surface (Fig. 1); posterior margins of prosomites smooth, except for a small row of spinules on the postero-lateral border of last prosomite (Fig. 1A). All urosomites (except anal) with a dorso-lateral row of spinules near posterior border, a few sensory setules on dorsal and ventral surfaces and minutely denticulate hyaline frills (Figs 2C, D). Genital double-somite with lateral and ventral chitinous ridge; with dorso-lateral row of spinules medially and a ventral row on posterior border (Figs 1, 2D, 10D). Genital field (Figs 2A, D) with minute copulatory pore closely associated with large, paired, sub-circular seminal receptacles and separate gonopores; vestigial P6 with a row of stout spinules, one plumose seta and a minute spine just inside gonopore opening. Ventral row of spinules on posterior border of antepenultimate urosomite composed of groups of large and small spinules and that on penultimate segment of small spinules only (Fig. 2D). Anal somite only slightly divided posteriorly with row of large spinules dorso-laterally and small spinules ventrally around base of caudal rami. Dorsal anal operculum semi-circular with spinulose posterior border (Figs 2B, 10B, F). Caudal rami (Figs 2B–D, 6B) twice as broad as long with rows of spinules on inner and outer lateral posterior borders; seta I very small with filamentous tip and setae II coarsely spinulose; seta III smooth and seta VI minutely bipinnate, both these setae moderately long, reaching to the spinulose region of seta IV (Fig 6B); setae IV and V well developed, tripinnate, with very strong spinules (Fig 6B) in distal portion; seta IV about half as long as seta V which is 33% of body length; seta VII triarticulate.

Rostrum (Figs 3A, 12D). Very large, slightly recurved, defined at base and rounded anteriorly; with pair of sensillae near lateral apical margins.

Antennule (Figs 3A, 10B, 12D). Short and stout, borne on a strongly developed pedestal; five-segmented. Segment I twice as long as any succeeding segment, bearing a bipinnate spinulose seta at outer distal corner and a well-developed tube pore at the proximal inner corner. Segment II with an outer distal expansion bearing a tube pore at base and two simple and one bipinnate spinulose setae distally; body of segment with two bipinnate spinulose setae and two simple setae on dorsal surface and three bipinnate spinulose setae on ventral surface. Segment III with aesthetasc; three long simple setae and one bipinnate spinulose seta on anterior expansion; a group of eight simple setae in middle of anterior margin; two very stoutly spinulose, bipinnate setae on distal margin. Segment IV with two simple setae on anterior margin; two stoutly spinulose bipinnate and two simple setae on distal margin; two finely spinulose multipinnate setae on posterior margin. Segment V with small aesthetasc distally; two finely spinulose multipinnate setae on proximal posterior margin and five other simple setae.

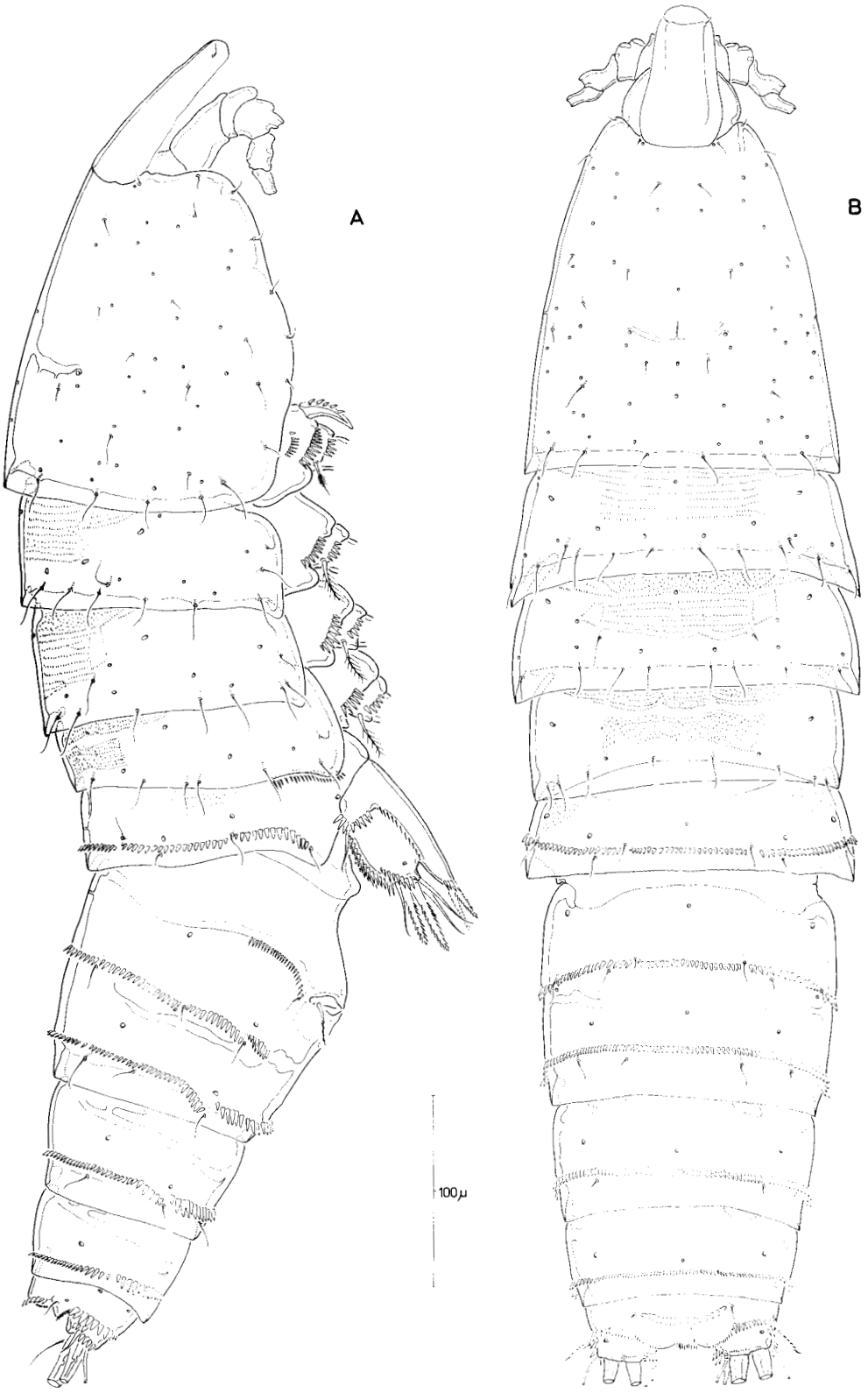


Figure 1. *Thompsonula hyaenae*. A, Habitus of female, lateral view. B, Habitus of female, dorsal view.

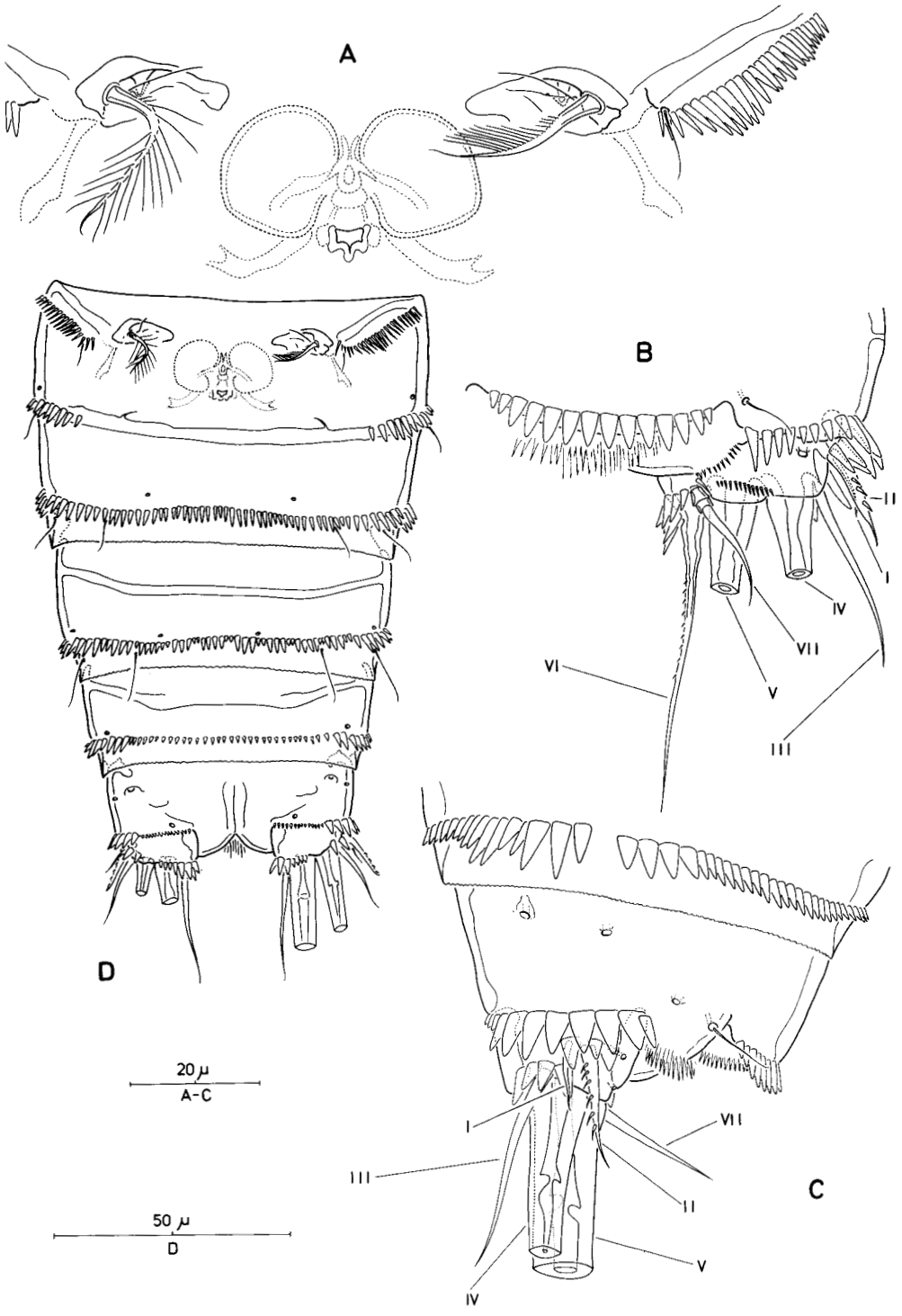


Figure 2. *Thompsonula hyaenae*. A, Genital complex with copulatory pore and P6. B, Anal operculum and caudal ramus, dorsal view. C, Anal somite and caudal ramus, lateral view. D, Urosome (excluding P5-bearing somite) of female, ventral view.

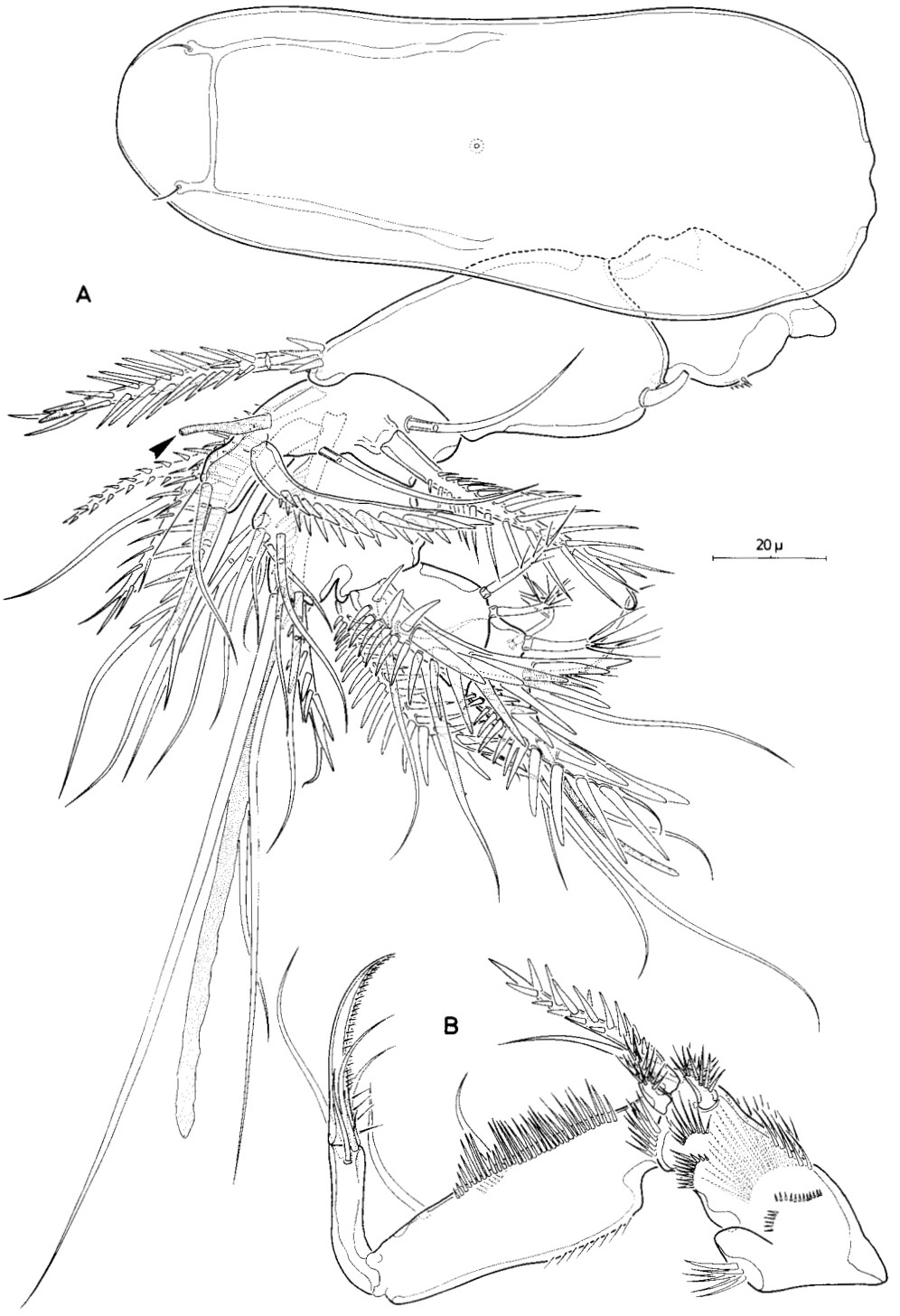


Figure 3. *Thompsonula hyaenae*. A, Rostrum and antennule of female (arrow indicating tube pore on segment II). B, Maxilliped.

Antenna (Figs 4A, 11A). Coxa well developed with row of setules on inner margin. Allobasis with strongly spinulose seta on outer margin. Exopod three-segmented; exopod-1 with one small and one larger, strongly spinulose setae; exopod-2 with one strongly spinulose seta; exopod-3 with a row of spinules and three large, strongly spinulose, bipinnate setae terminally and a long, characteristic, tube seta subterminally (Fig. 11B). Endopod one-segmented with two rows of very stout spinules on outer margin, a tube pore at outer distal corner and a small row of fine setules distally on inner margin; also bears, sub-distally, two stout, spinulose spines and two small, naked setae, fused at base and, on distal margin, a spine, four finely toothed geniculate setae, one naked seta and one long finely plumose unipinnate tube seta.

Mandible (Fig. 4B). Gnathobase with two well-developed pinnate setae at dorsal corner and two bicuspid and five unicuspid teeth on cutting edge. Basis elongate, about 2.4 times longer than wide, with two rows of setules distally on inner margin and four setae on distal margin, three bipinnate medially and one simple. Endopod one-segmented, about twice as long as exopod, with a row of spinules at base; two lateral and seven, simple terminal setae fused at base; a peculiar projection also borne sub-terminally. Exopod always one-segmented; with two lateral, simple, setae and one plumose and three simple setae (fused at base) terminally.

Maxillule (Fig. 4C). Precoxa with a row of spinules at outer corner. Arthrite of precoxa with row of spinules at defined base; distal border with ten stout elements of which the proximal three are spinulose; two surface setae. Coxal epipodite represented by one plumose seta (Fig. 11C) and coxal endite with six, minutely spinulose setae. Basal endite with eight setae on distal margin and a row of spinules sub-distally. Endopod one-segmented, with four simple, terminal setae and a lateral row of setules. Exopod one-segmented with four plumose setae and a row of setules on lateral margin.

Maxilla (Fig. 5A). Syncoxa with two rows of spinules on outer margin; three endites, inner one small with two pinnate setae, other two elongate with a row of setules, two pinnate spines and a simple seta. Basis extended into strong spinulose spine with a simple seta and a pinnate spine at base. Endopod unsegmented with three geniculate and five simple setae.

Maxilliped (Figs 3B & 11D). Prehensile but moderately slender. Coxa ornamented as in Fig. 3B; with one long and two short pinnate setae and one naked seta at distal inner corner. Basis 2.9 times longer than wide, with straight inner margin bearing two simple setae and a row of long slender spinules; a row of fine setules on outer margin. Endopod one-segmented, about five times longer than wide, with a finely toothed terminal, claw and five accessory setae.

PI (Fig. 6A). Intercoxal plate well developed, narrow, unadorned. Anterior face of coxa with two rows of coarse spinules near outer margin and a row of small spinules on median distal margin; posterior face with a small row of fine spinules near outer margin. Basis with an outer plumose seta and a very stout recurved spinulose inner spine; anterior face with a pore below exopod, a row of coarse spinules between exopod and outer seta, a row of spinules at base of endopod and another around base of inner spine. Both rami unmodified and three-segmented with one or more rows of coarse spinules around outer and distal margins of all segments; exopod-2, endopod-1 and endopod-2 with a pore on anterior face. Setal arrangement and ornamentation as in Fig. 6A but note inner seta of endopod-1 minutely pinnate over most of length.

Figure 4. *Thompsonula hyaenae*. A, Antenna (arrows indicating tubular setae). B, Mandible (arrows indicating setae of gnathobase and termino-lateral process of endopod). C, Maxillula (arrow indicating epipod).

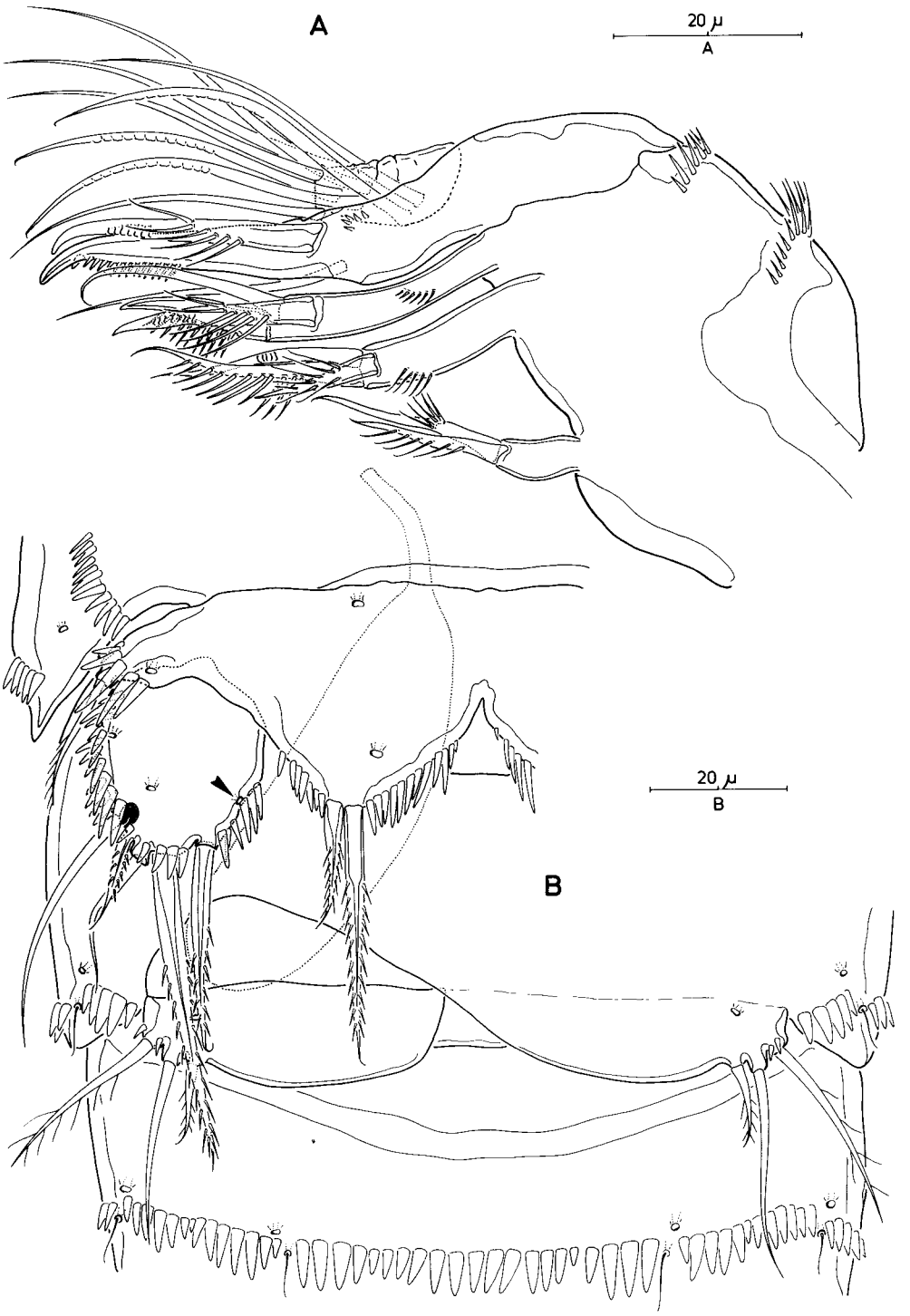


Figure 5. *Thompsonula hyaenae*. A, Maxilla. B, P5 and P6 of male (arrow indicating lateral tube pore on exopod).

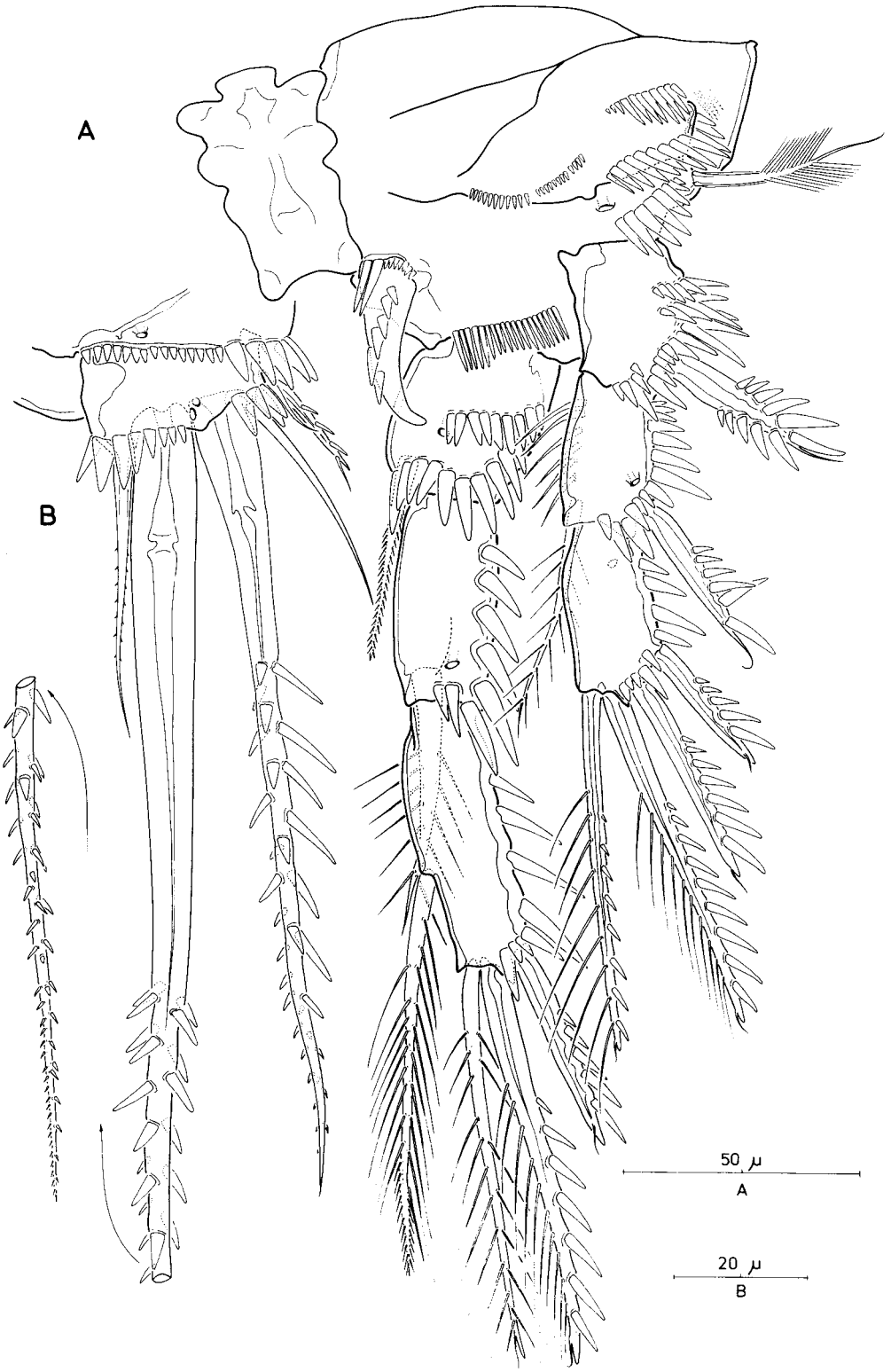


Figure 6. *Thompsonula hyaenae*. A, P1. B, Caudal ramus, ventral view.

P2-P4 (Figs 7, 8A). Intercoxal plate unadorned. Anterior face of coxa with a median row of spinules, a pore near inner margin and a row of coarse spinules at outer distal corner; posterior face with a row of spinules near proximal outer corner. Basis with a row of coarse spinules round base of small outer seta and another around base of endopod, each with an associated pore. All rami three-segmented with endopod longer than exopod; middle and distal segments of both rami with a pore near distal outer margin, exopod-1 without a pore and endopod-1 with two pores; setal arrangement and ornamentation as in Figs 7, 8A; distal inner seta of exopod-3 very small and implanted on posterior face rather than on margin (Figs 8A, C).

P5 (Figs 8B, 10E). Baseoendopod heavily adorned with many rows of strong spinules around inner, distal and outer margins of endopodal lobe and on outer peduncle; distal margin broadly rounded, bearing five heavily spinulose spines with filamentous tips, middle spine as long as baseoendopod; dorsal surface with a number of pores, one of which opens medially on the outer margin. Exopod only slightly longer than broad, not reaching distal margin of endopodal lobe, heavily spinulose on outer and distal margins; with six setae of which setae I, IV & V heavily spinulose and with filamentous tips, setae II & III slender and plumose and seta VI long, slender and smooth.

Description of male

Body. Length 575–595 μm (mean 586 μm, n=4). Otherwise as in female except genital somite not fused to third urosomite and spinules in ventral rows on urosomites more strongly developed and arranged in groups of varying spinule length.

Antennule (Figs 9, 12A–C). Mounted on a very small pedestal, six-segmented and sub-chirocer. Segment I with tube pore at posterior proximal corner, a few spinules and a stout bipinnate seta at anterior distal corner. Segment II with a peduncle at anterior distal corner bearing two stout bipinnate spinulose setae and four simple setae; four similar bipinnate setae borne on anterior margin and one simple and one bipinnate seta on both distal and posterior margins. Segment III small, with five simple setae on anterior margin and three stout bipinnate spinulose seta and one simple seta arising from dorsal face. Swollen segment IV (Fig. 9D) with spinules on anterior face (Fig. 12C); aesthetasc and a large simple seta fused at base and surrounded by five other simple setae in proximal part of segment; four stout bipinnate spinulose setae and two minute simple setae in middle region of segment and one simple seta distally. Segment V small with three claw-like projections on distal margin (Figs 9C & 12B). Segment VI small and tapering with a small aesthetasc and two setae on distal margin, two pairs of setae on anterior margin and one group of three and one group of two setae on posterior margin (Fig. 9B).

Mouth parts and P1-P4 with no sexual dimorphism.

P5 (Fig. 5B). Baseoendopods of each side fused in centre but endopodal lobes distinct, with two pores on outer surface, a row of stout spinules on distal margin which bears two pinnate setae of which inner over twice as long as outer; outer peduncle with a pore on outer surface and a row of spinules around base of seta on distal margin. Exopod almost circular with row of stout spinules around free margins and three pores on outer face; five setae on distal margin of which setae I

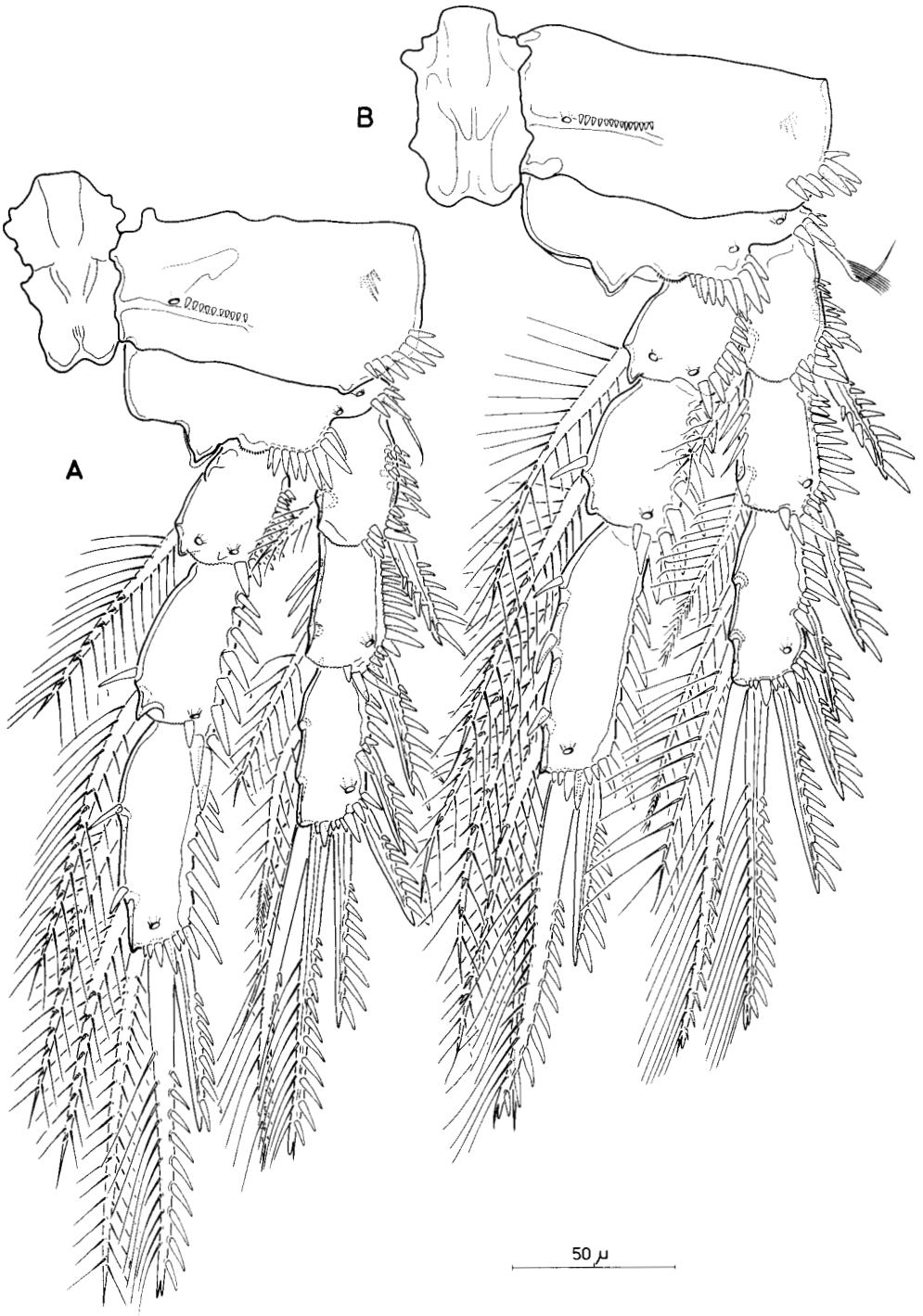


Figure 7. *Thompsonula hyaenae*. A, P2. B, P3.

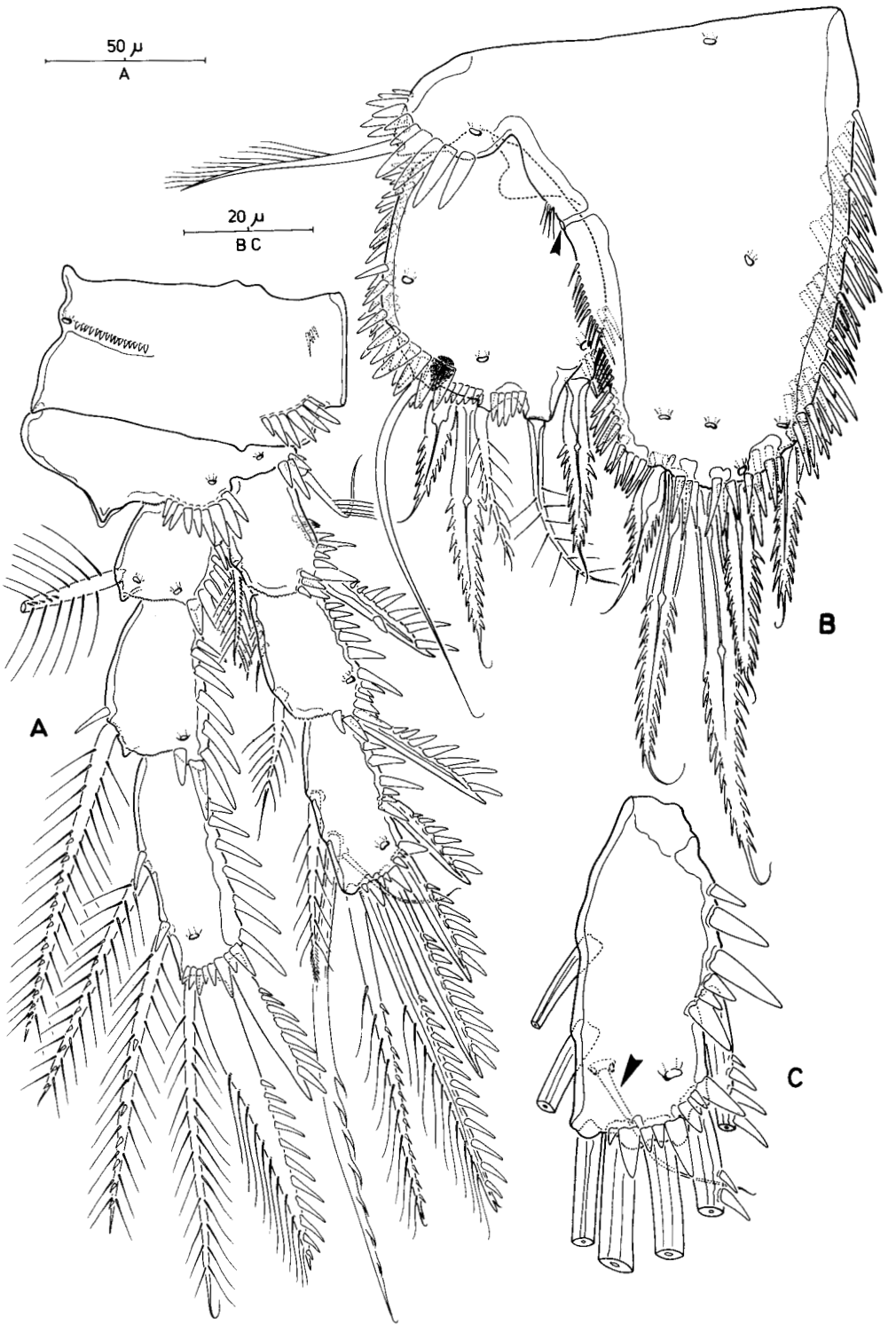


Figure 8. *Thompsonula hyaenae*. A, P4. B, P5 of female (arrow indicating lateral pore on baseoendopod). C, Distal exopod segment of P4 (arrow indicating surface standing seta), anterior view.

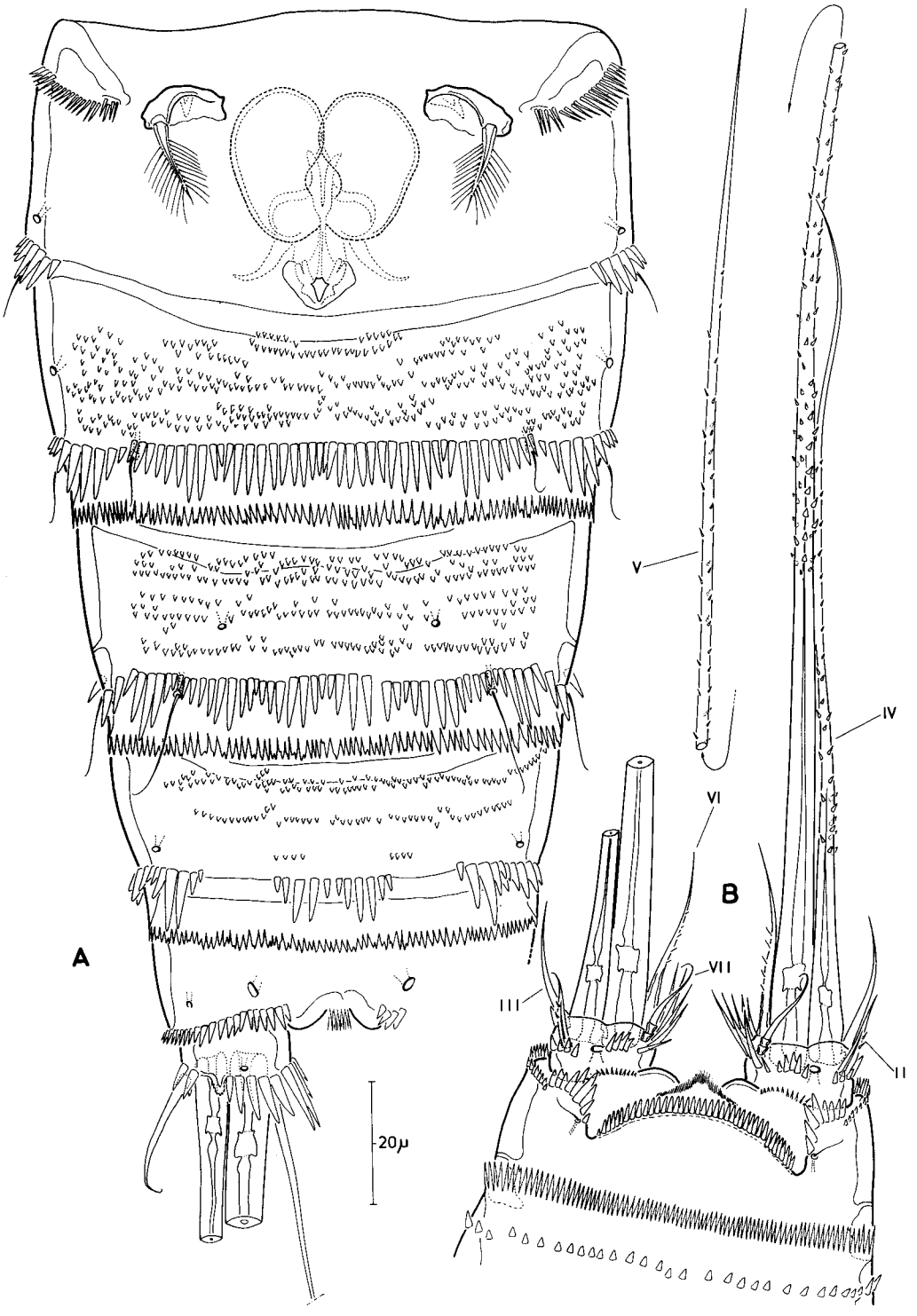


Figure 24. *Caribbula elongata*. A, Urosome (excluding P5-bearing somite) of female, ventral view. B, Anal somite and caudal ramus, dorsal view.

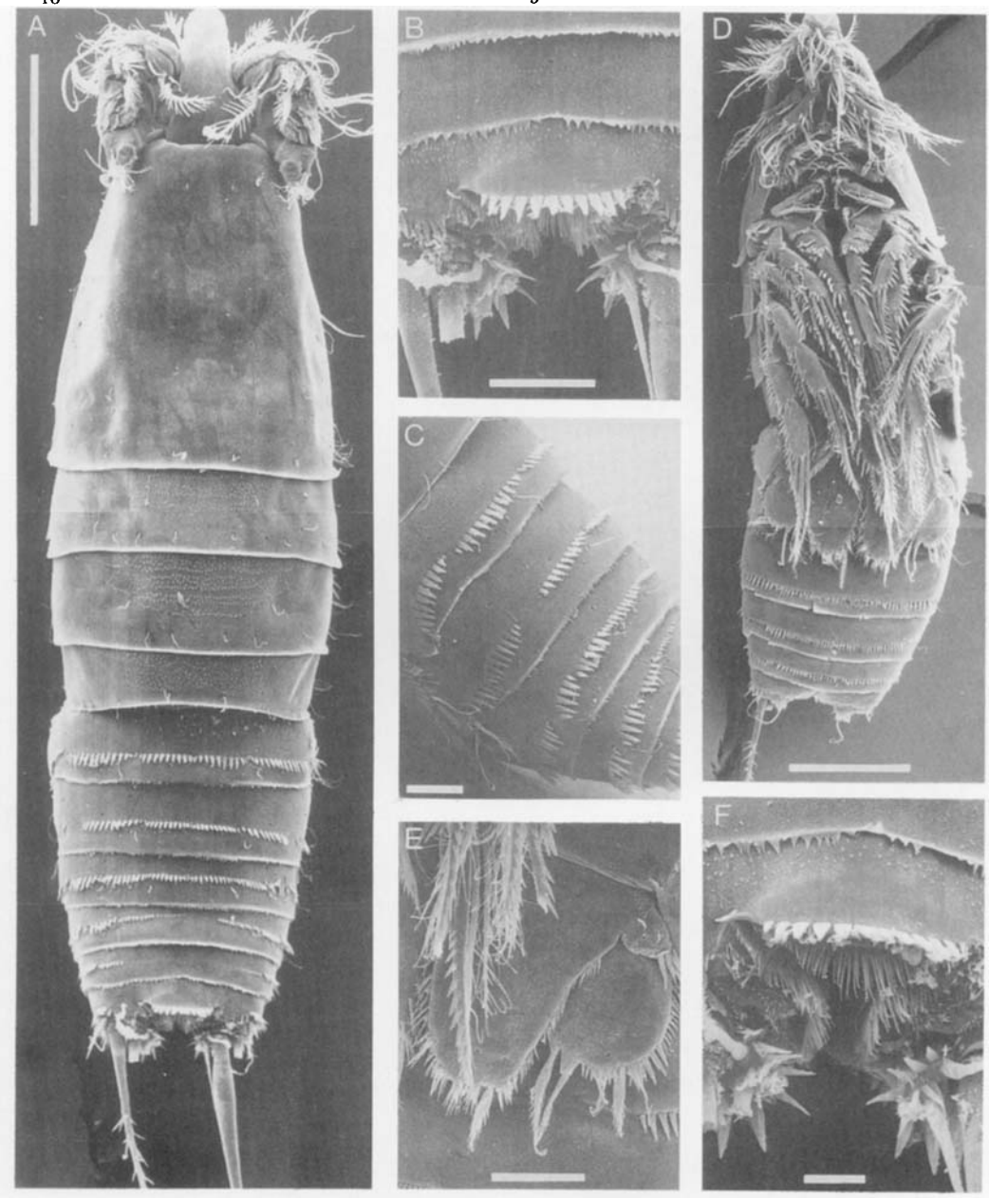


Figure 10. SEM of *Thompsonula hyaenae*. A, Habitus of male, dorsal view. B, Anal operculum. C, Anterior part of male urosome, lateral view. D, Habitus of female, ventral view. E, P5 of female. F, Operculum and anal somite, postero-dorsal view. Scale bars: A,D = 100 μm; B,C,E = 25 μm; F = 10 μm.

and II stout and bipinnate, seta III small and simple, seta IV very small and bipinnate, and seta V simple and as long as seta I.

P6 (Fig. 5B). One member fused to somite wall, other member articulating, both with smoothly rounded free margins and each bearing two bipinnate seta between which is a simple seta.

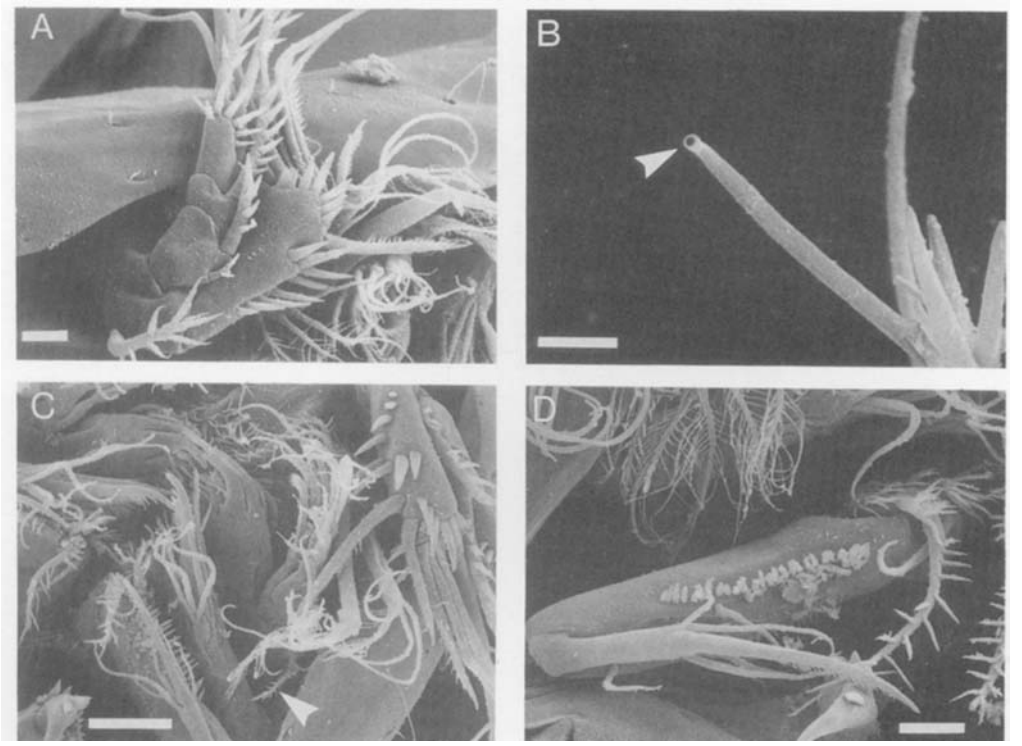


Figure 11. SEM of *Thompsonula hyaenae*. A, Antenna. B, Tubular seta on exopod of antenna. C, Mouthparts (arrow indicates epipodite seta of maxillula). D, Maxilliped, ventral view. Scale bars: A,D = 10 μm B = 5 μm; C = 20 μm.

Thompsonula curticauda (C. B. Wilson, 1932)

(Figs 13–18)

Synonyms. Rathbunula curticauda Wilson, 1932; *R. agilis* Wilson, 1932; *Echinocornus pectinatus* Wilson, 1932.

Material examined

1. National Museum of Natural History (Smithsonian Institution), Washington, D.C. NMNH 00063870, eight female, 41 male, four copepodite spirit preserved syntypes labelled *Rathbunula curticauda*: beach sand washings in Buzzards Bay, Woods Hole, Massachusetts (leg. C. B. Wilson 20.7.1927); NMNH 00063866, 33 female, 27 male, 11 copepodite spirit preserved syntypes labelled *Thompsonula agilis*: beach sand washings in Buzzards Bay, Woods Hole Massachusetts (leg. C. B. Wilson 25.7.1927); NMNH 00063886, 16 copepodite spirit preserved syntypes labelled *Echinocornus pectinatus*: beach sand washings on Nobska beach, Falmouth, Massachusetts (leg. C. B. Wilson 20.7.1927); NMNH 00368973, four female, spirit preserved, labelled *Thompsonula curticauda*: North Carolina continental shelf, depth 14–50 m (leg. B. C. Coull Feb/April 1969). [Note this vial also contained the types (three females, two males) of a new species *Caribbula fleegeri*].

2. British Museum (Natural History), London. 1948.9.10.34, three female, three male, spirit preserved, syntypes labelled *Rathbunula agilis*: beach sand

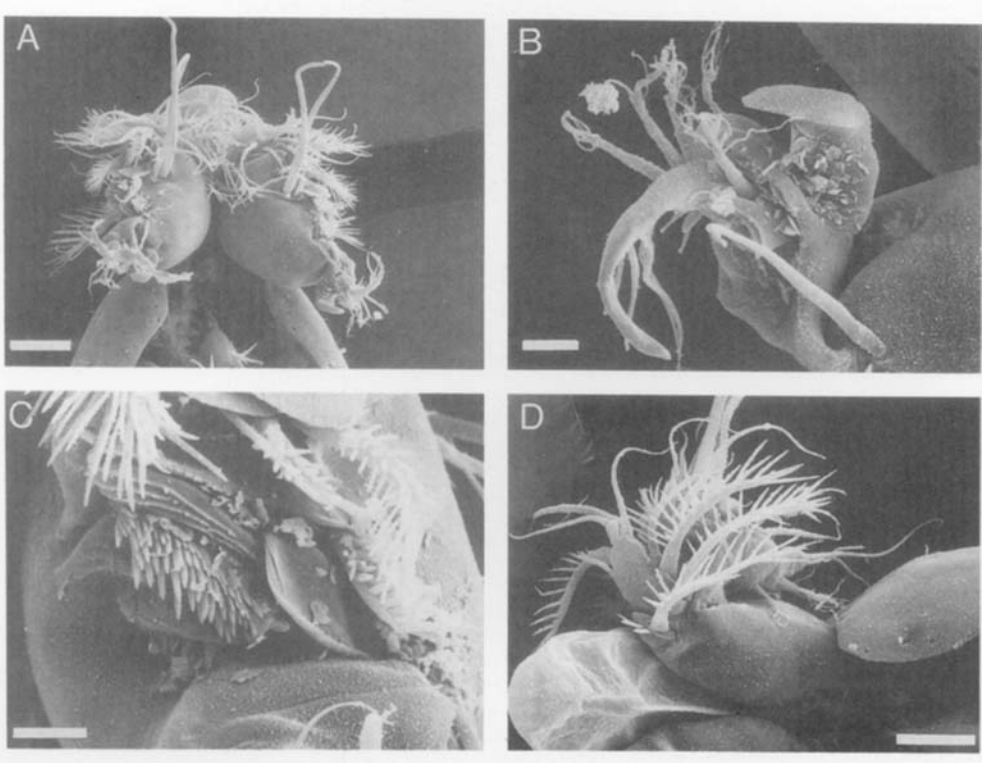


Figure 12. SEM of *Thompsonula hyaenae*. A, Antennulae of male, ventral view. B, Male antennula, segments V & VI, showing claw-like projection. C, Male antennula, segment IV showing details of inner surface. D, Rostrum and antennula of female, ventral view. Scale bars: A,C,D = 25 μm; B = 5 μm.

washings in Buzzards Bay, Woods Hole, Massachusetts (leg. C. B. Wilson 25.7.1927); 1948.9.10.35, two female, two male, spirit preserved, syntypes labelled *Rathbunula curticauda*: beach sand washings in Buzzards Bay, Woods Hole, Massachusetts (leg. C. B. Wilson 20.7.1927).

3. From Dr B. C. Coull. 11 females, nine males, seven juveniles (formalin preserved). Sandy site in North Inlet, South Carolina (identified as *T. hyaenae*).

Description of female

Confined to those features which differ from the type species.

Body (Fig. 13). Length 495–530 μm (mean 511 μm, n = 5). Genital field (Fig. 14A) with row of long, fine spinules associated with gonopores. Hyaline frill of urosomites (Figs 13, 14B, C) more coarsely denticulate than in type species. Seta V of caudal rami 75% of body length (Fig. 17A) and setae III and VI relatively short, not reaching half-way to the start of spinulation on seta IV.

Antennule (Fig. 17C). Six-segmented, small segment IV distinct from segment III (these two fused in type species); segment II without tube pore.

Antenna (Fig. 15C). Allobasis with short, spinulose abexopodal seta with a row of spinules at base.

Mandible (Figs 14D, E). Basis somewhat oval, only 1.7 times longer than broad. Endopod only 1.25 times longer than exopod and without sub-terminal projection character of type species. Exopod may be one or two-segmented but

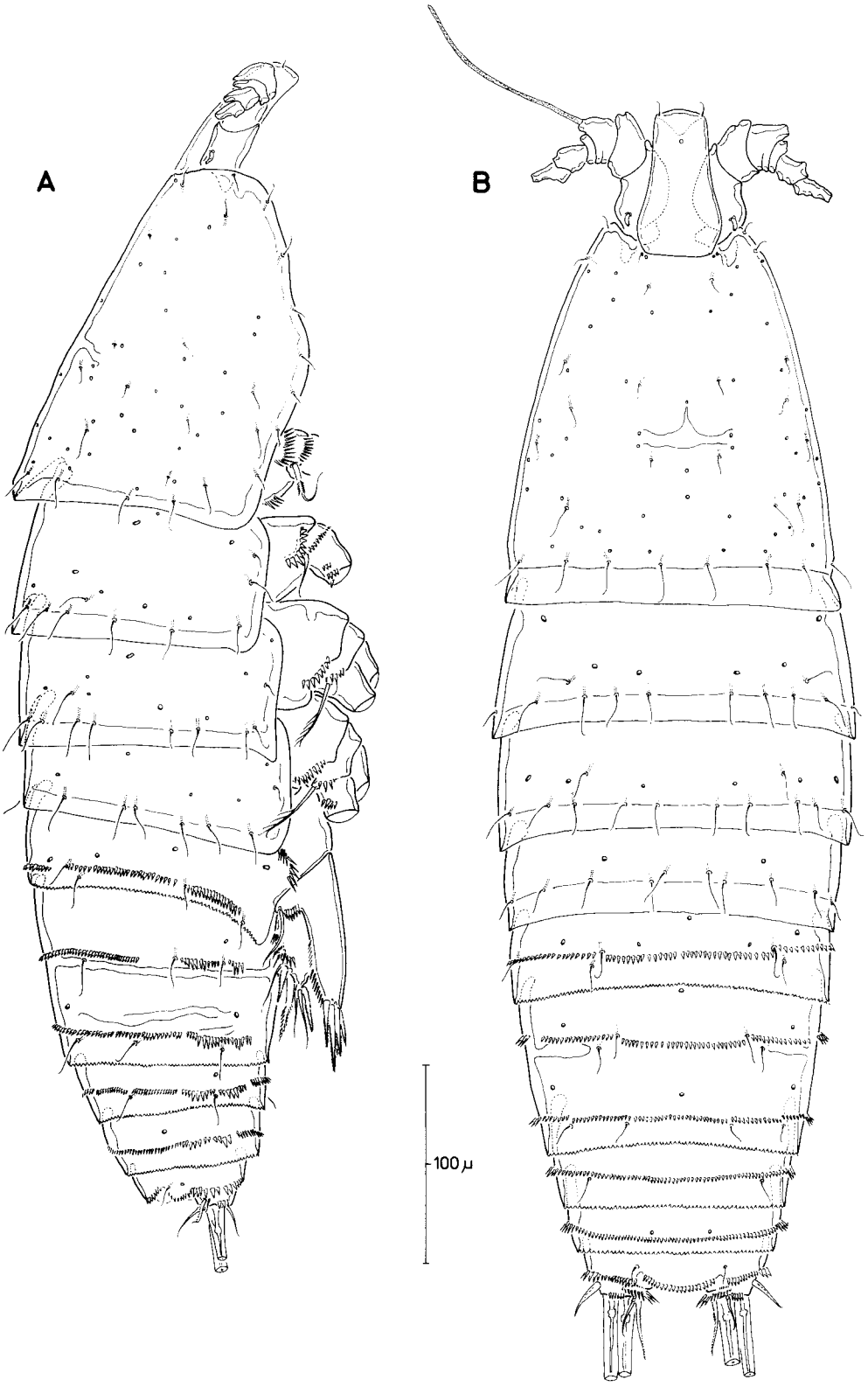


Figure 13. *Thompsonula curticauda*. A, Habitus of female, lateral view. B, Habitus of female, dorsal view.

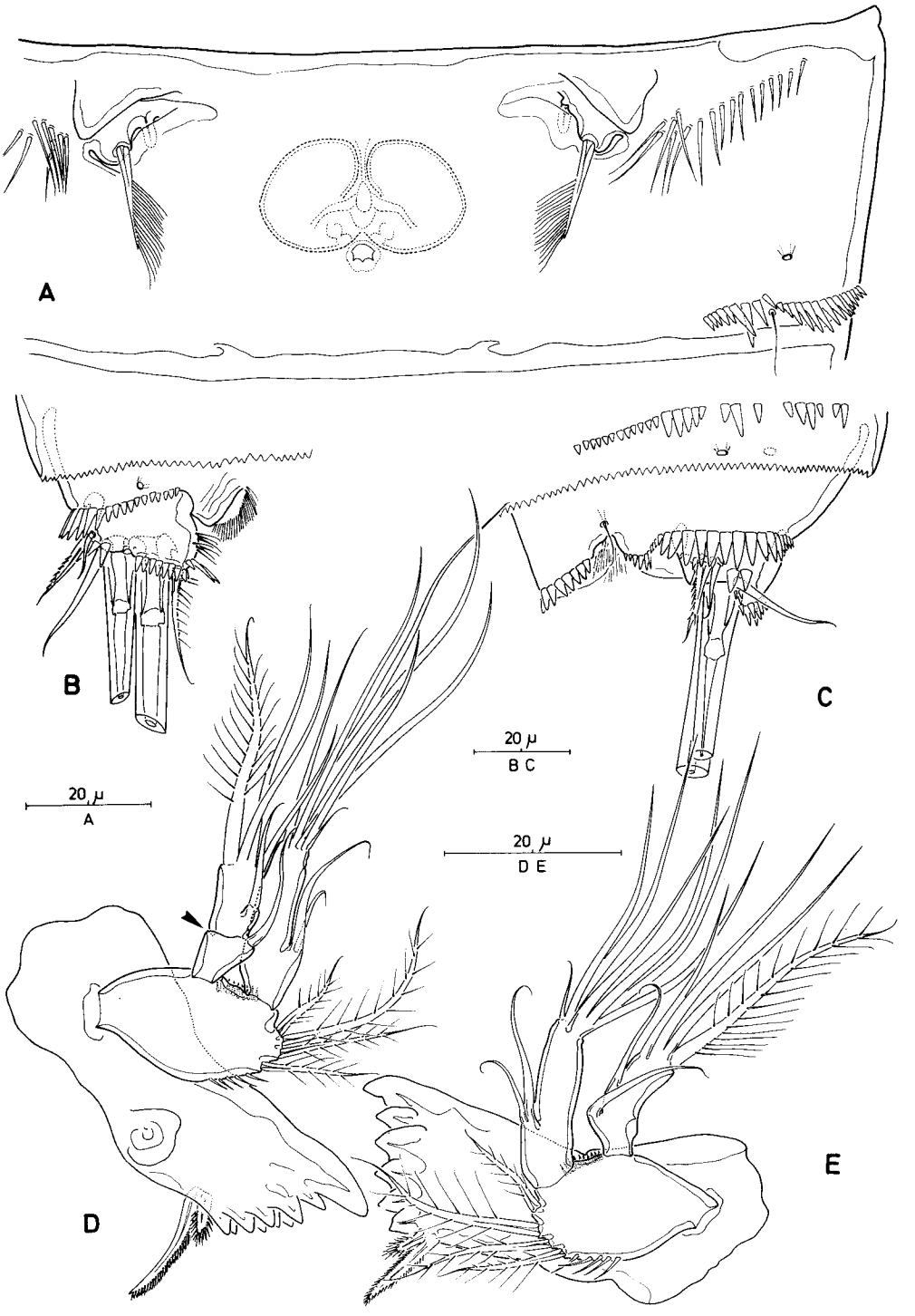


Figure 14. *Thompsonula curticauda*. A, Genital complex showing P6 and copulatory pore. B, Caudal ramus, ventral view. C, Anal somite and caudal ramus, lateral view. D, Mandible (arrow indicating 2-segmented endopod. E, Mandible of other specimen (atypical condition).

in one-segmented individuals still an indication of segmentation by a break in cuticle.

Maxilliped (Fig. 18D). Somewhat more robust that type species. Basis only 2.2 times as long as wide and endopod only three times as long as wide. All three pinnate spines on coxa sub-equal in length.

P1 (Fig. 15A). Median row of spinules on coxa and spinule row on distal median margin of basis composed of much finer, smaller spinules than in type species. Endopod-1 with sparsely plumose inner seta.

P2-P4 (Figs 15, 16). P2 basis (Fig. 15B) with a row of spinules on inner margin absent in type species. Endopod-1 of all limbs with only one pore on anterior face.

Description of male

Confined to those features different from the type species.

Body. Length 466–500 μm (mean 482 μm, n=4).

P5 (Fig. 18A). All spinules more delicate and fewer in number than in type species, particularly on inner margin of endopodal lobe. Terminal setae on endopodal lobe sub-equal and shorter than depth of baseoendopod.

P6 (Figs 18B, C). As in type species except that free margin of each member projects posteriorly forming a distinct hump.

***Caribbula* gen. nov.**

Diagnosis. Thompsonulidae. Body not markedly fusiform, widest at posterior margin of cephalothorax or first free-prosomite. Cephalothorax rounded anteriorly with prominent rostrum only 1.4 times as long as maximum width and reaching only just past distal border of proximal segment of antennule. Female genital double-somite with dorsal chitinous ridge; genital field with copulatory pore considerably posterior to seminal receptacles which are distinctly longer than wide. Hyaline frill of urosomites deeply divided; ventral spinule row on penultimate urosomite discontinuous. Antennule in female five-segmented, segment I not as long as wide; in male seven-segmented, as segments III and IV not fused. Allobasis of antenna with long abexopodal seta reaching almost to distal margin of endopod. Proximal endite of maxillary syncoxa distinctly bilobed with two setae set side by side. Outer basal seta on P1 basis spiniform and distally pinnate. Coxa of P2–P4 with row of spinules (associated with tube pore) composed of at least some long setules; a row of short spinules present on posterior face. Basis of P2 with pinnate outer spine. Sexual dimorphism in P4; in male only two inner setae on exopod-3 (proximal seta of female lost in male). Female P5 baseoendopod with endopodal lobe distinctly triangular and narrow at distal margin; exopod oval and extending at least to distal margin of endopodal lobe.

Type species: *Caribbula elongata* (Gee 1988) **comb. nov.** Other species ***C. fleegeri* sp. nov.**

Etymology. Named after the regional locality of the type species in the Caribbean Sea.

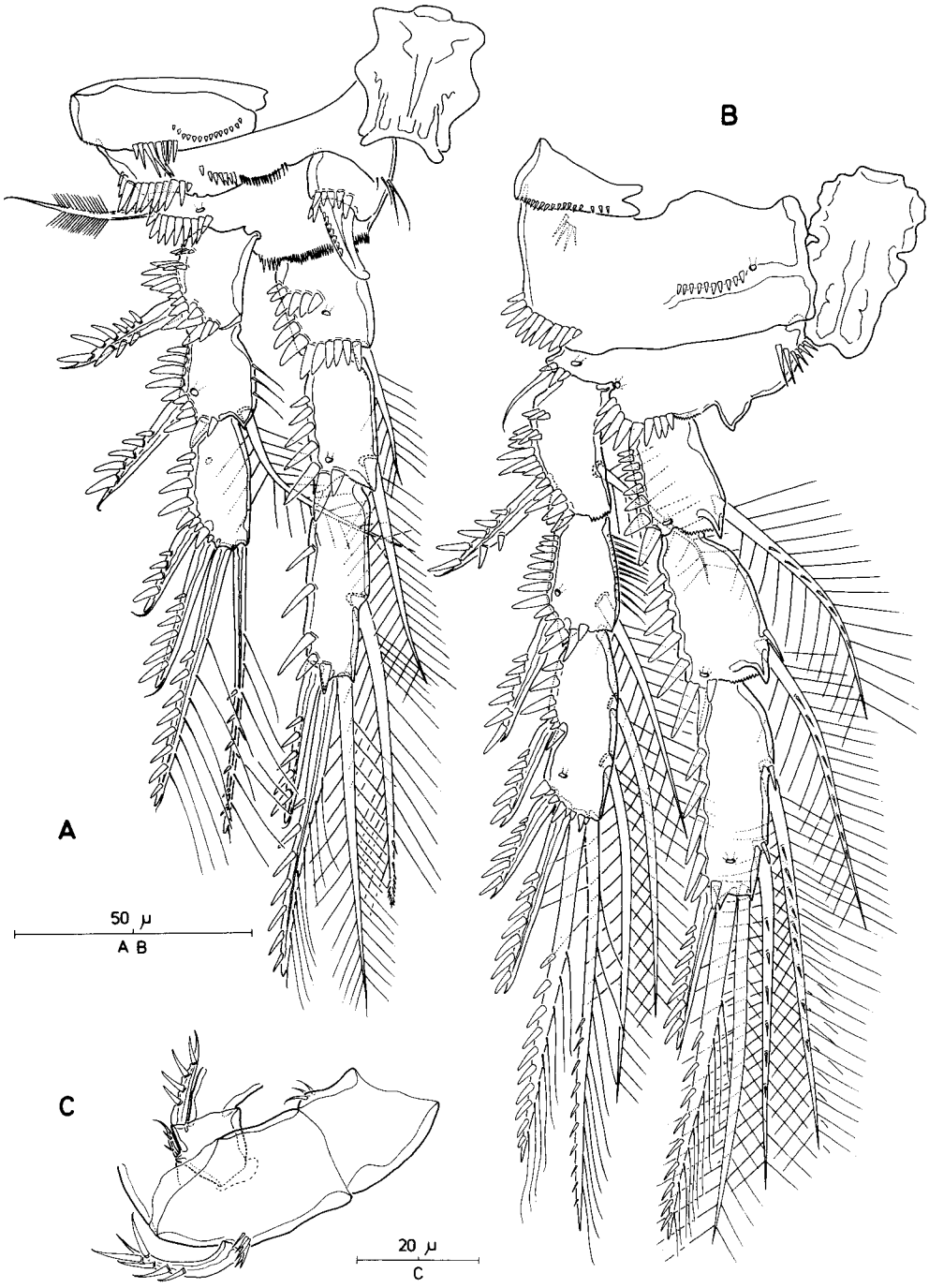


Figure 15. *Thompsonula curticauda*. A, P1. B, P2. C, Allobasis of antenna.

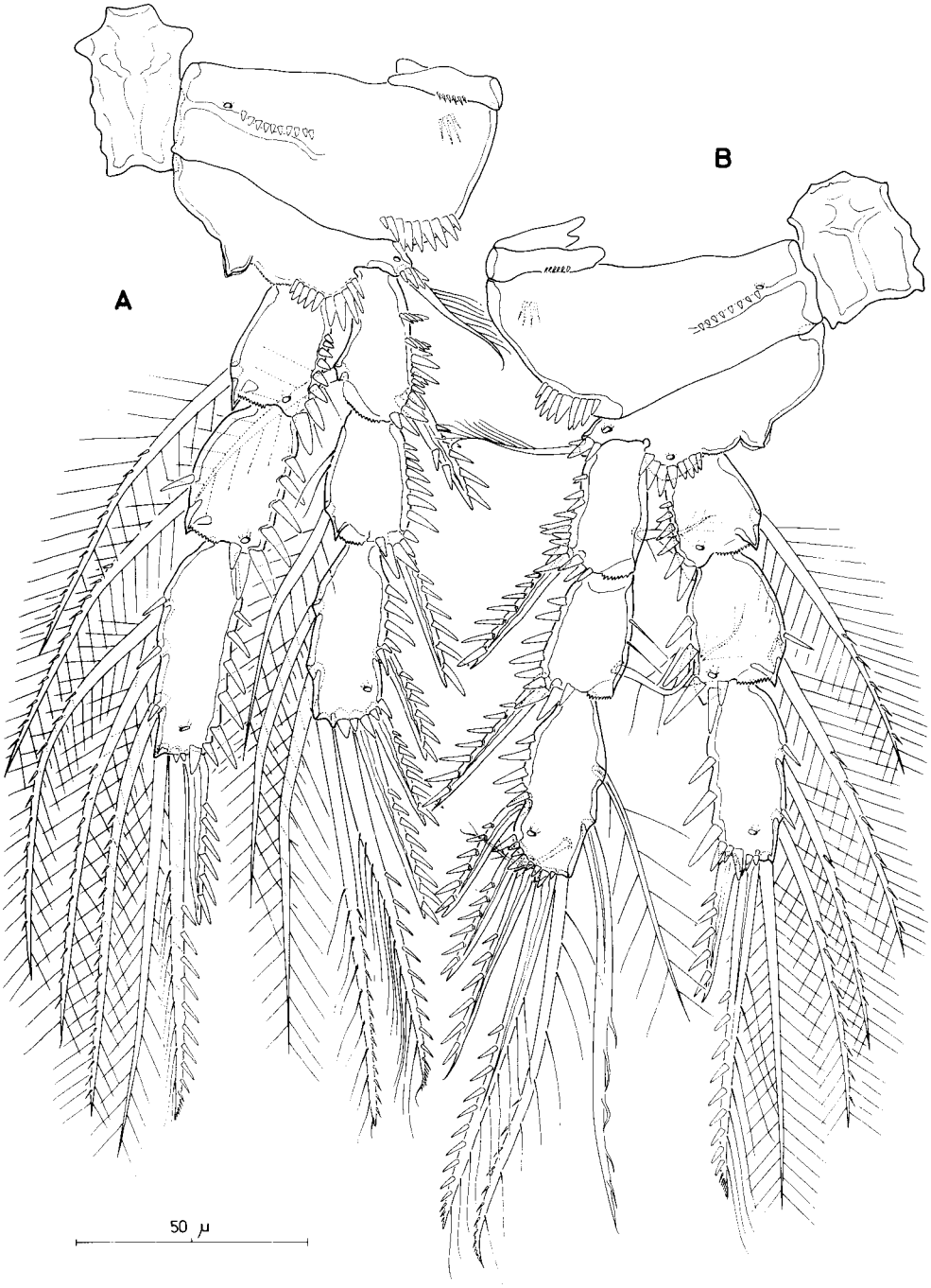


Figure 16. *Thompsonula curticauda*. A, P3. B, P4.

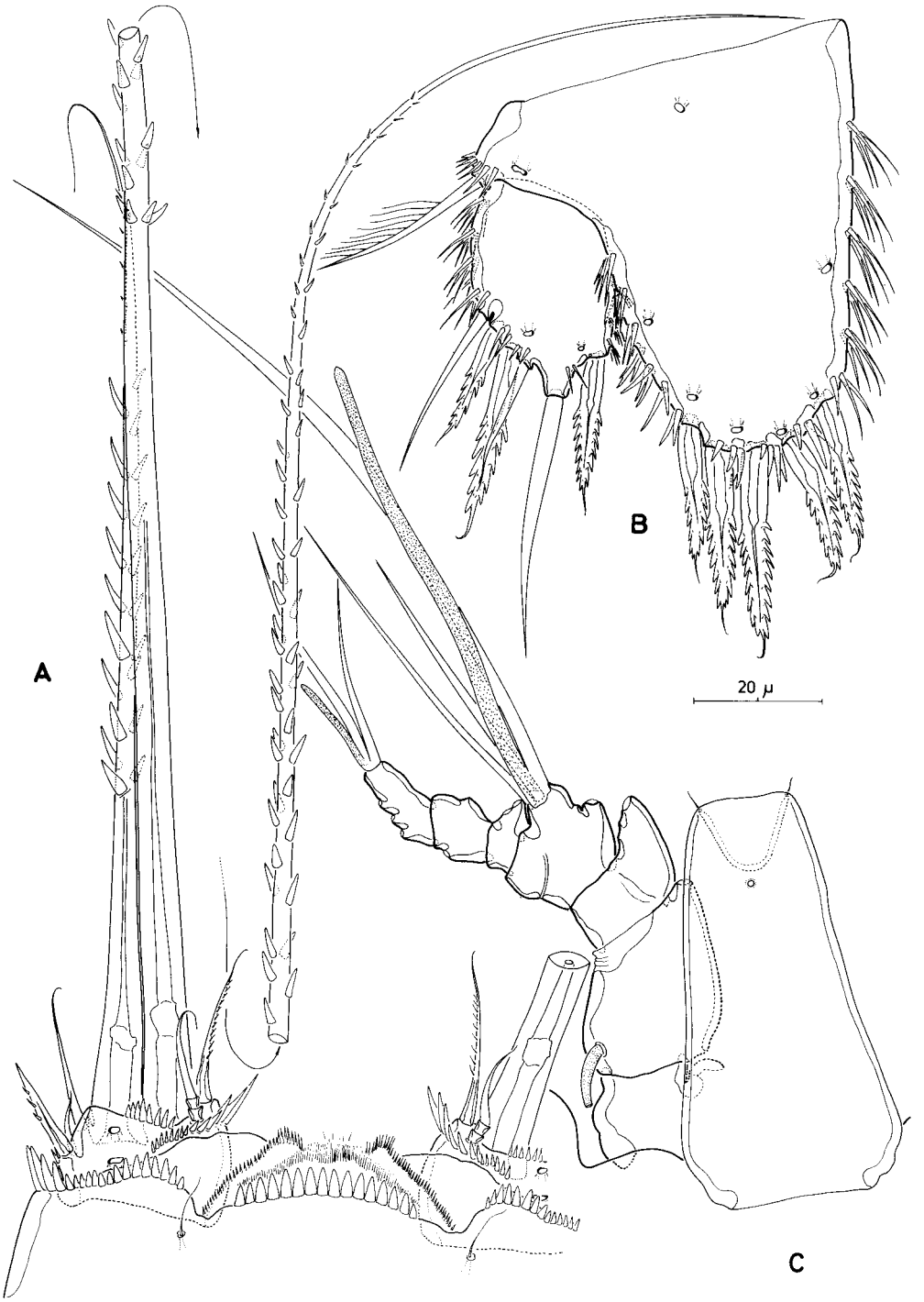


Figure 17. *Thompsonula curticauda*. A, Caudal ramus and anal operculum, dorsal view. B, Female P5. C, Rostrum and antennula of female.

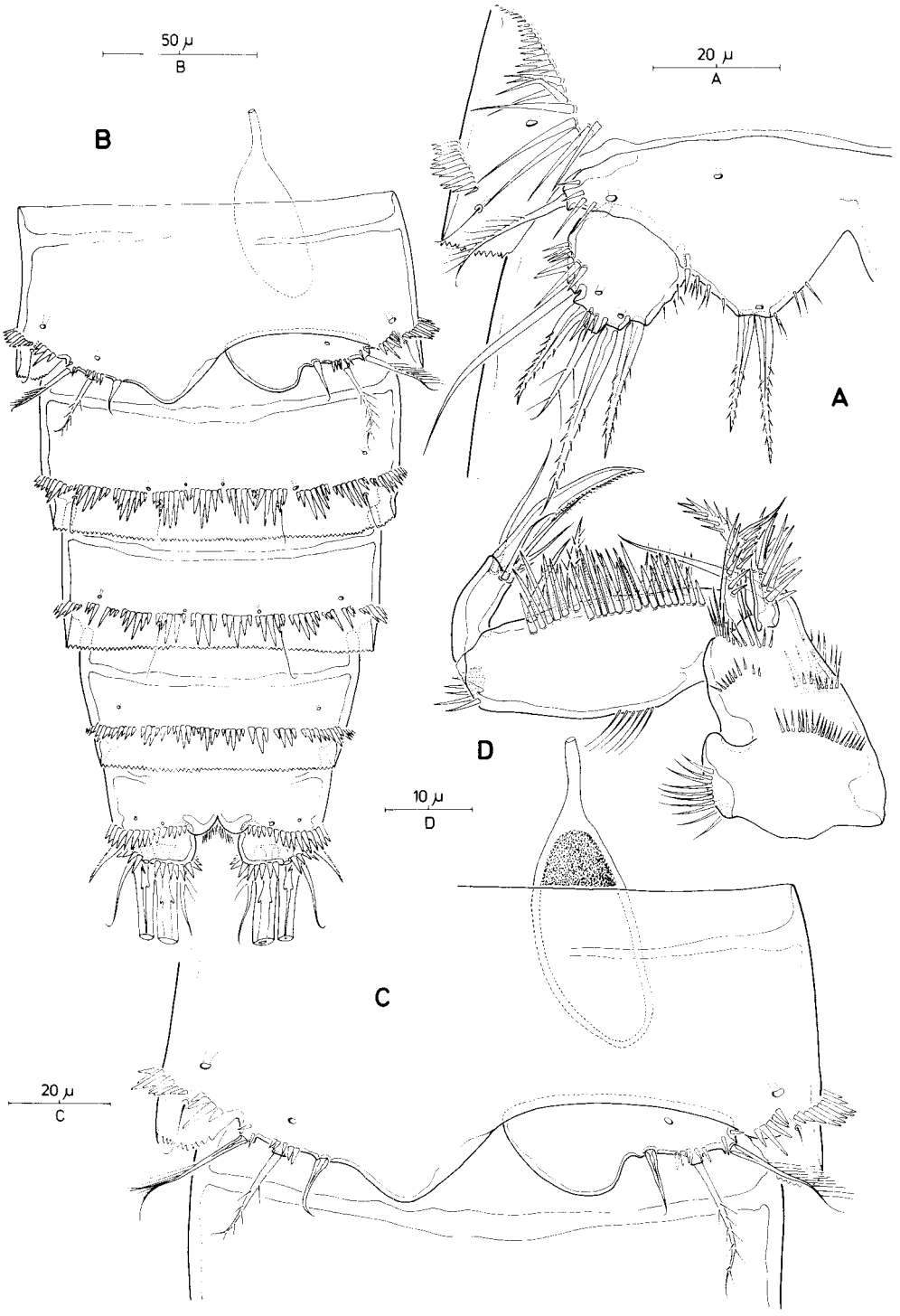
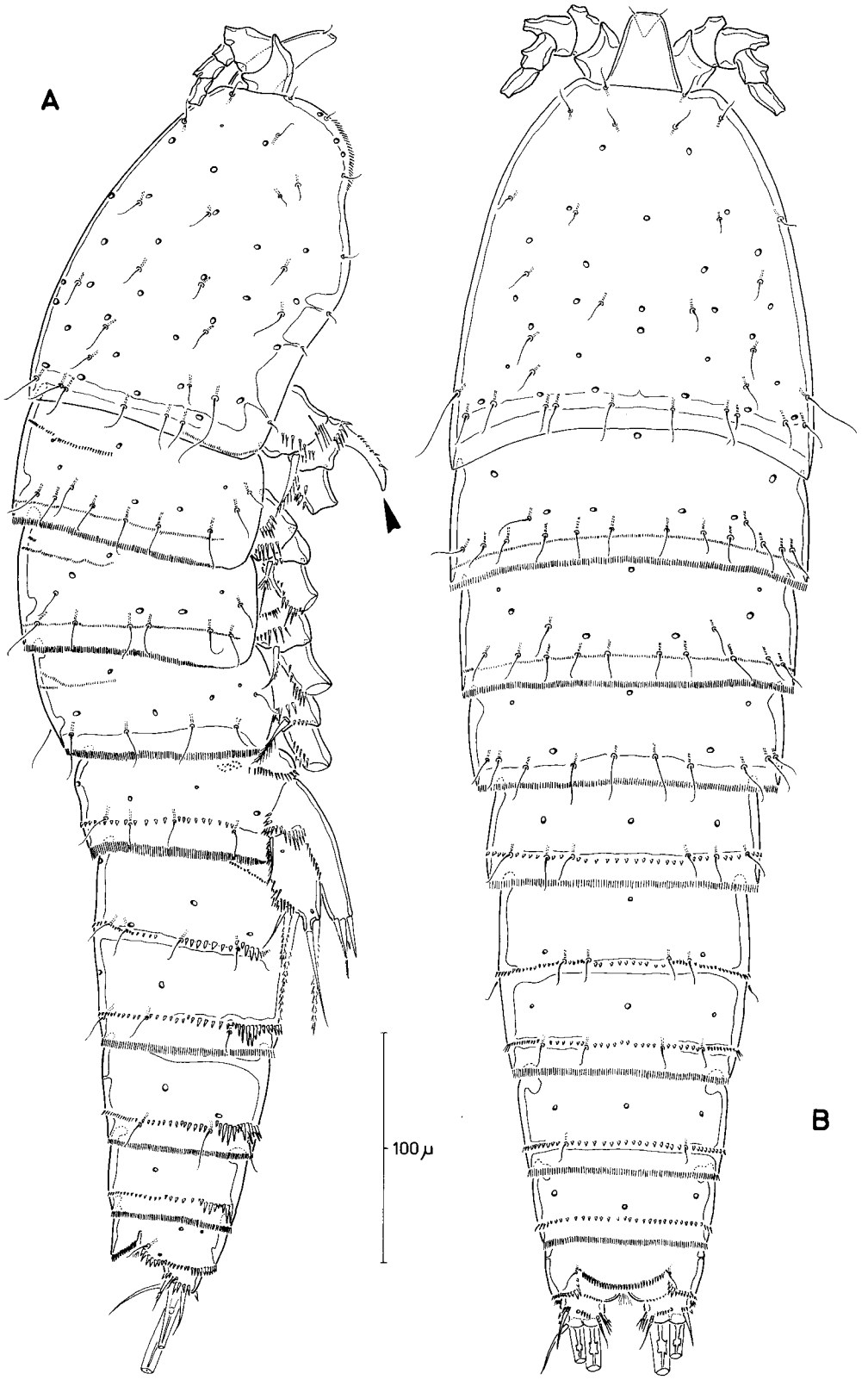


Figure 18. *Thompsonula curticauda*. A, Male P5. B, Urosome (excluding P5-bearing somite), ventral view. C, Male P6. D, Maxilliped.


A
B
100 μ

Caribbula elongata (Gee, 1988) **comb. nov.**

(Figs 19–26)

Synonyms. Thompsonula hyaenae elongata Gee, 1988b.

Material examined

1. Zoologisk Museum, Oslo. ZMO F20936. One female spirit preserved holotype. Muddy sand site (29°50′N;90°30′W) at 20 m depth in Gulf of Mexico, off Louisiana Coast (leg. Mr M. Murrell); ZMO F20936. Two male spirit preserved paratypes, and two female and two male dissected paratypes. Same site as holotype (leg. Mr M. Murrell); ZMO F20937. Three female, spirit preserved. Mud at 6 m depth in Terrabonne Bay, Louisiana (leg. Dr J. Fleeger).

2. From Mr M. Murrel. 12 female and eight male from same site as holotype. Of these, two female and two male were deposited in British Museum (Natural History) under Reg. No. 1988.375–378 and in National Museum of Natural History (Smithsonian Institute) Washington D.C. under Reg. No. 383084.

Description of female

Body (Fig. 19). Not heavily sclerotized, sub-pyriform in shape with no clear distinction between prosome and urosome. Length 505–540 μm (mean 523 μm, n=6); maximum width at posterior border of cephalothorax, tapering posteriorly; slightly dorso-ventrally flattened. Cephalothorax equal in length to free prosomites, posterior border of cephalic shield smooth but dorsal and lateral surface with many sensillae and mucous pores, also found on free-prosomites. Posterior margins of prosomites smooth, except for a small row of spinules on the postero-lateral border of the last prosomite (Fig. 19A). All urosomites (except anal) with a dorso-lateral row of small spinules near posterior border, a few sensory setules on dorsal and ventral surfaces and with deeply incised (but not secondarily denticulate) hyaline frill (Figs 21B, 24A, B). Genital double-somite with continuous dorsal-ventral chitinous ridge; with dorso-lateral row of spinules medially and a ventral row on posterior borders (Figs 19, 24A). Genital field (Fig. 24A) with copulatory pore distinctly posterior to large, paired, kidney-shaped seminal receptacles and separate gonopores; vestigial P6 with a row of short (about 4–5 μm) spinules and one plumose seta and, in addition, a minute spine just inside gonopore opening. Ventral row of spinules on posterior border of penultimate urosomite discontinuous (Fig. 24A). Anal somite only slightly divided posteriorly with row of large spinules dorsally and ventrally and small spinules laterally around base of caudal rami. Dorsal anal operculum semi-circular with small teeth (about 40) on posterior border. Caudal rami (Figs 21B, 24) twice as broad as long with rows of spinules on inner and outer lateral posterior borders; seta I very small with filamentous tip and seta II coarsely spinulose; seta III smooth and seta VI minutely bipinnate, moderately long, reaching to the spinulose region of seta IV (Fig. 24B); setae IV and V well developed, with many minute spinules (Fig. 24B) in distal portion; seta IV

Figure 19. *Caribbula elongata*. A, Habitus of female, lateral view (arrow indicating orientaton of inner basal spine of P1). B, Habitus of female, dorsal view.

about half as long as seta V which is 53% of body length; seta VII triarticulate.

Rostrum (Figs 25A, 26A). Very large, slightly recurved, defined at base and rounded anteriorly; with pair of sensillae near lateral apical margins.

Antennule (Fig. 26A). Short and stout, borne on a strongly developed pedestal; five-segmented. Segment I not as long as wide, bearing a bipinnate spinulose seta at outer distal corner and a well-developed tube pore at the proximal inner corner. Structure and setation of remaining segments as in *Thompsonula hyaenae*.

Antenna (Fig. 20A). Coxa well developed with row of setules on inner margin. Allobasis with a proximal row of spinules on anterior and posterior face and another row at base of well developed abexopodal seta. Exopod three-segmented, slender, with exopod-3 about 4.3 times longer than broad; exopod-1 with one small and one larger, strongly spinulose spines; exopod-2 with one strongly spinulose spine; exopod-3 with a row of spinules and three large, strongly spinulose, bipinnate spines terminally and a sub-terminal, naked, seta only as long as longest terminal spine. Endopod one-segmented with a row of very stout spinules on outer margin and a small row of fine setules distally on inner margin; bears, sub-distally, two stout, spinulose spines and two small naked setae, fused at base, and, on distal margin, a spine, four geniculate setae and two normal setae (not a tube seta).

Mandible (Fig. 20B). Gnathobase with two well-developed pinnate setae (fused at base) at dorsal corner of cutting edge. Basis with four bipinnate setae on distal margin; a row of setules proximally, two lateral spinules rows and one row distally at base of rami. Endopod one-segmented; as long as exopod; with two lateral and seven, simple, terminal setae fused at base. Exopod one-segmented; with two lateral and four terminal setae.

Maxillule (Figs 21C, D). Precoxa with a row of spinules at outer corner. Arthrite of precoxa wth a row of spinules near base; two setae on anterior face, one pinnate seta on posterior face and ten elements on distal margin. Coxal epipodite represented by one plumose seta and coxal endite with a row of spinules and six setae on distal margin. Basal endite with eight setae on distal margin two of which are geniculate. Endopod one-segmented, with four terminal setae and a lateral row of setules. Exopod one-segmented with four plumose setae and a row of setules on lateral margin.

Maxilla (Fig. 20C). Syncoxa with two rows of spinules on outer margin; three endites, inner one bilobed with two pinnate setae, other two with a row of setules subterminally and three marginal spines. Basis extended into a strong spine with an articulating seta and spine at base. Endopod one-segmented with three geniculate and five simple setae.

Maxilliped. Prehensile. Coxa ornamented as in Fig. 20D; with one long and two short spinulose spines and one seta at distal inner corner. Basis with two setae and two rows of spinules on inner margin and a row of fine setules on outer margin. Endopod segment with a terminal claw not markedly recurved at tip and five accessory setae, innermost minute.

P1 (Fig. 22A). Intercoxal plate well developed, narrow, unadorned. Coxa with a row of coarse spinules near outer margin and a row of setules on inner margin; anterior face with four spinule rows, the proximal median row being composed of minute spinules (arrowed in Fig. 22A); posterior face with a small row of fine spinules near outer margin. Basis with a row of spinules on median distal margin; a pore at base of exopod; an outer, pinnate seta and a very stout, ventrally directed, spinulose inner spine, both with a row of spinules around

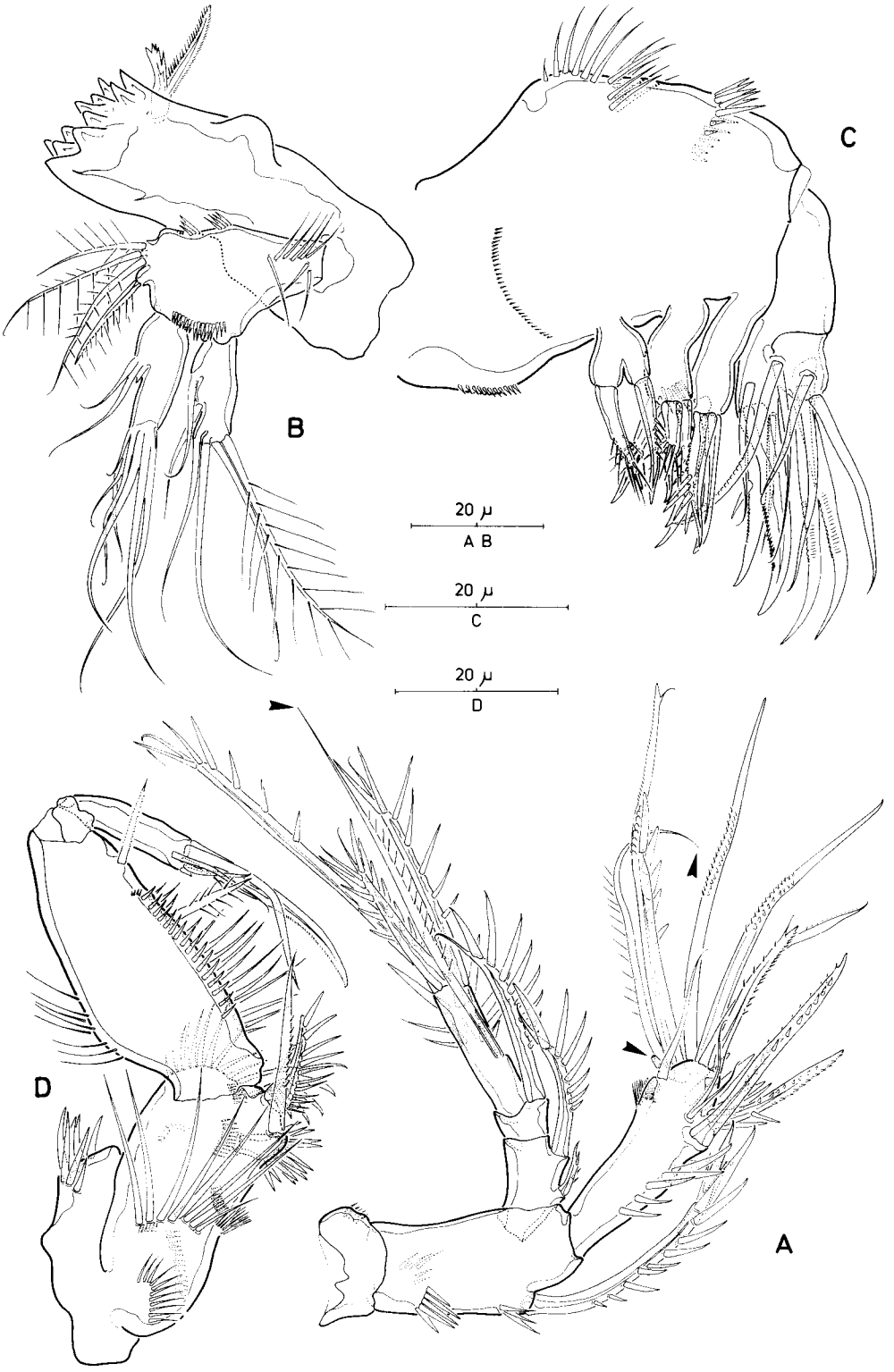


Figure 20. *Caribbula elongata*. A, Antenna (arrows indicating tube pore and condition of apex of setae). B, Mandible. C, Maxilla. D, Maxilliped.

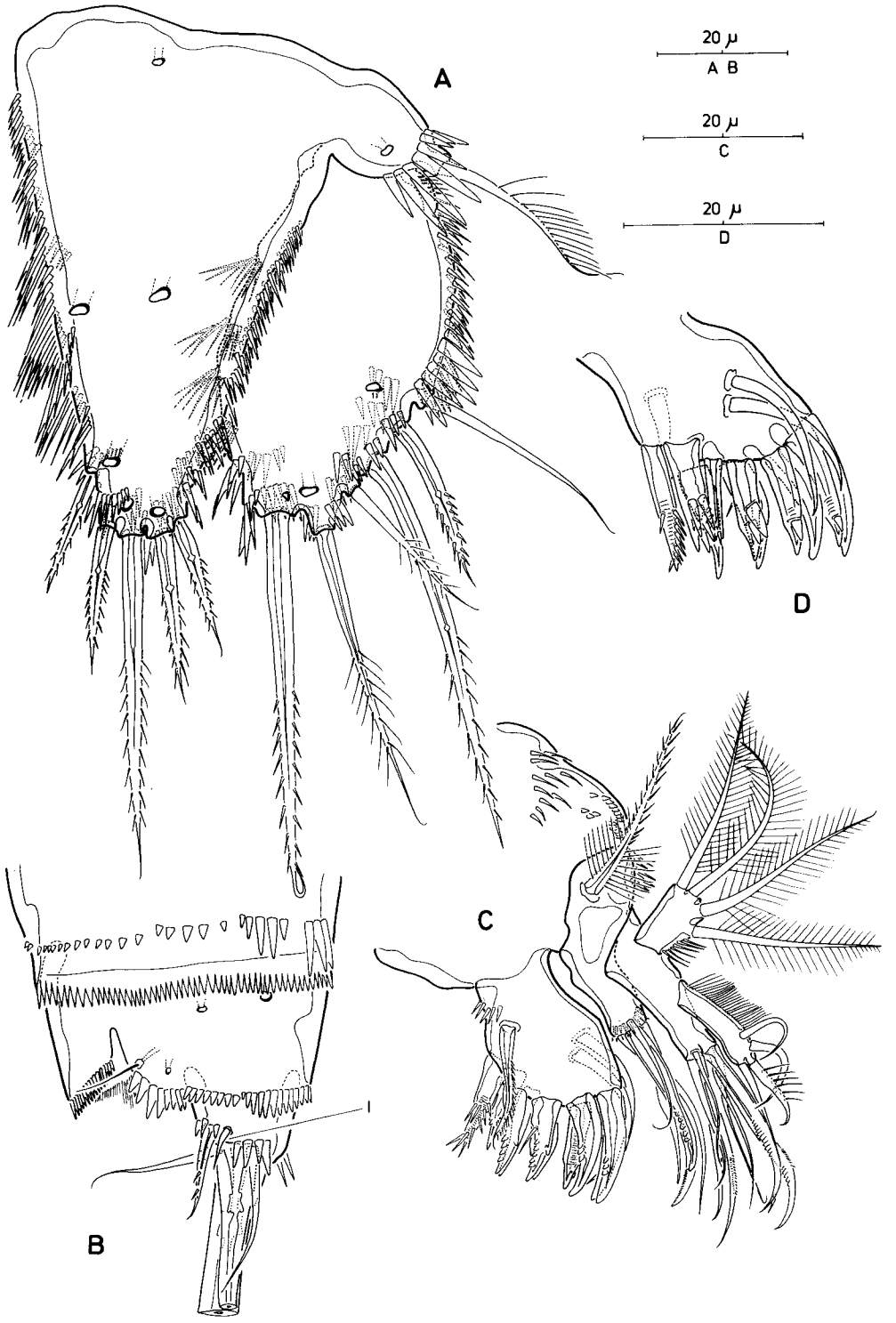


Figure 21. *Caribbula elongata*. A, Female P5. B, Anal somite and caudal ramus, lateral view. C, Maxillula, posterior view. D, Precoxal arthrite of maxilla, anterior view.

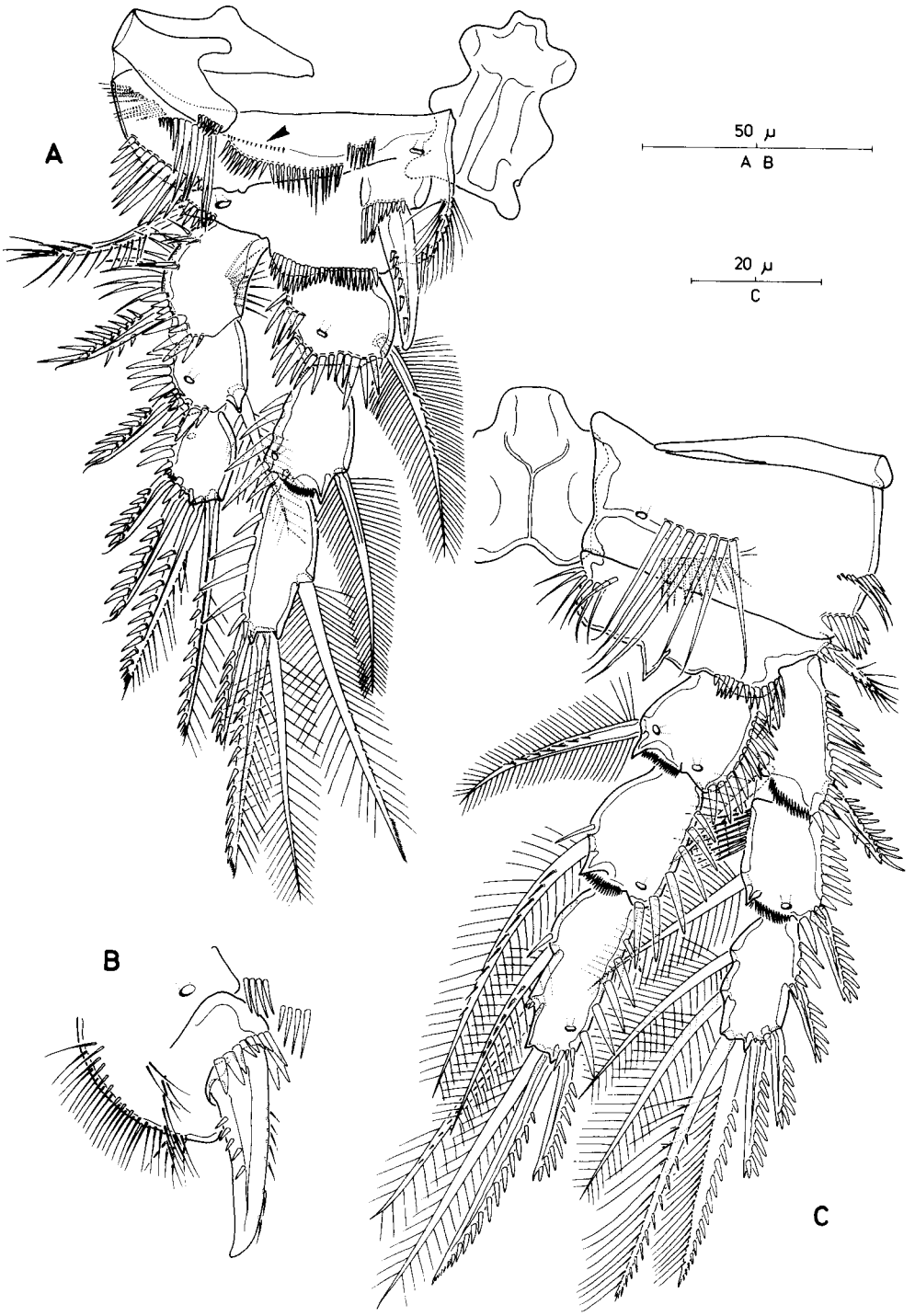


Figure 22. *Caribbula elongata*. A, P1 (arrow indicating minute spinular row). B, Inner basal spine of P1. C, P2.

base. Both rami unmodified and three-segmented with one or more rows of coarse spinules around outer and distal margins of all segments; exopod-3 same length as exopod-2; inner distal spine on exopod-3 shorter than ramus; endopod-2 and endopod-3 robust, 1.6 and 2.3 times longer than broad respectively.

P2–P4 (Figs 22B, 23). Intercoxal plate unadorned. Anterior face of coxa with a median row of elongate setules with an associated pore near inner margin; outer margin with two (P2), three (P3) or four (P4) spinule rows; posterior face with a median spinule row. Basis with rows of spinules round base of outer spine/seta, on distal margin at base of rami and on inner margin. All rami three-segmented with endopod longer than exopod; middle and distal segments of both rami with a pore near distal outer margin, exopod-1 without a pore and endopod-1 with two pores; distal inner seta of P4 exopod-3 very small and implanted on posterior face rather than on margin (Fig. 23C).

P5 (Fig. 21A). Endopodal lobe markedly triangular in shape, with straight inner margin; distal margin narrow, bearing five spinulose spines with filamentous tips, middle spine not as long as baseoendopod; ventral surface with a number of pores. Exopod oval, 1.6 times longer than broad, reaching distal margin of endopodal lobe; with six elements of which I, IV & V are spinulose spines with filamentous tips, II & III are plumose setae and VI is a slender, naked seta.

Description of male

Body (Fig. 25D). Length 472–493 μm (mean 485 μm, n=4). Genital somite not fused to third urosomite. Otherwise as in female except that hyaline frill of urosomites not as deeply incised and ventral spinule rows more strongly developed and arranged in groups of varying spinule length.

Antennule (Fig. 26B). Mounted on a very small pedestal, seven-segmented and sub-chirocer, with segment V very swollen. Setal arrangement as in *T. hyaenae*. *Mouth parts* and *P1–P3* as in female.

P4 (Fig. 25B). Sexual dimorphism in that exopod-3 with only two setae on inner margin (proximal seta of female lost in male).

P5. (Fig. 25C). Baseoendopods of each side fused in centre but endopodal lobes distinct, with two pores on ventral surface, a row of stout spinules on inner and outer margin and two pinnate setae of more or less equal length on distal margin; outer peduncle with a surface pore and a row of spinules around base of seta on distal margin. Exopod almost circular with row of stout spinules around free margins and two surface pores; five elements on distal margin of which I, II and IV are spinulose spines, III and V are naked setae.

P6 (Fig. 25D). One element fused to somite wall, other element articulating, both almost rectangular with acutely rounded inner distal corner; each with three plumose setae.

***Caribbula fleegeri* sp. nov.**

(Figs 27–31)

Material examined

Museum of Natural History (Smithsonian Institute) Washington D.C. Three females and four males from a vial containing *Thompsonula curticauda*, labelled *T. hyaenae* (leg. B. C. Coull). NMNH 30384.

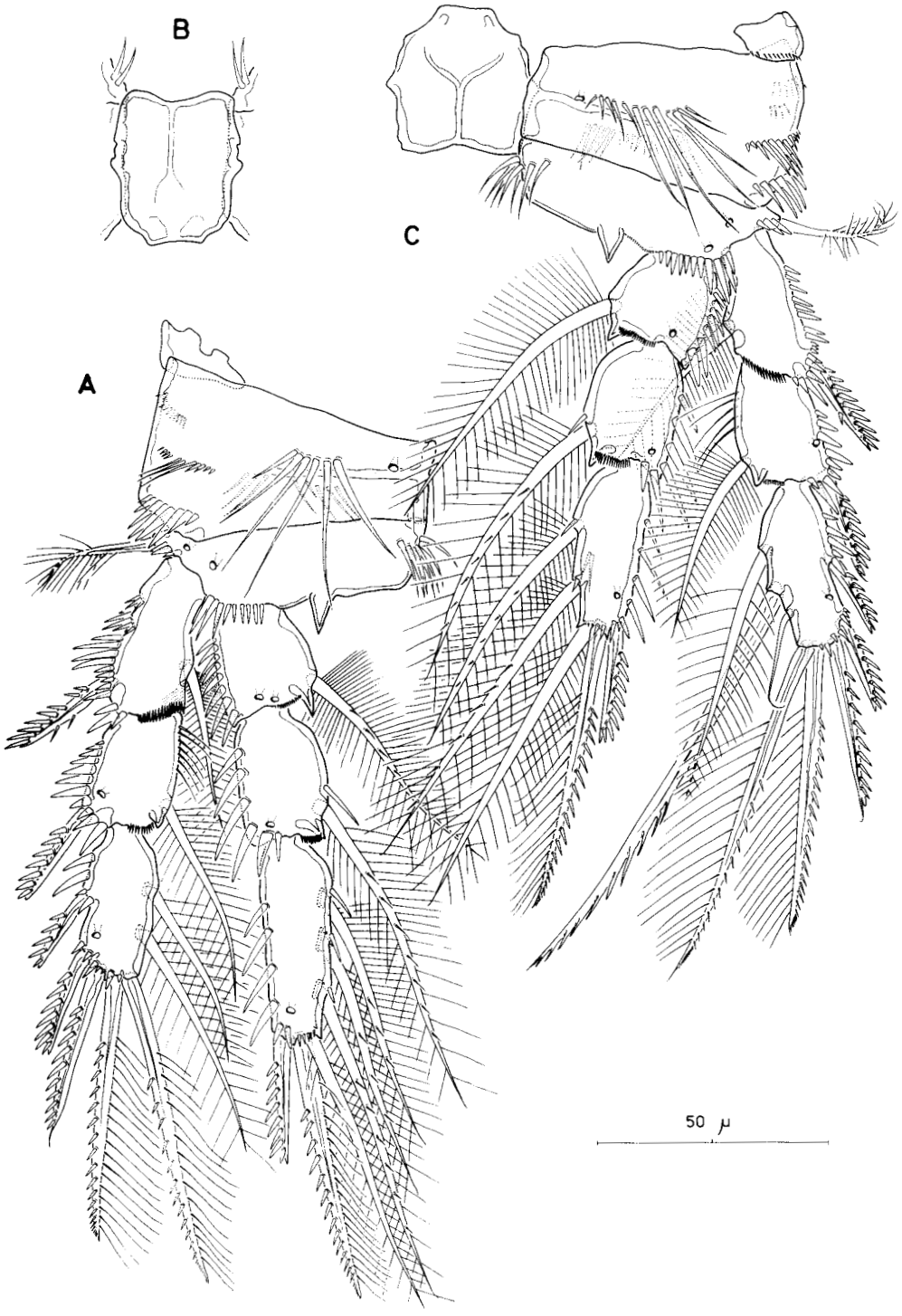


Figure 23. *Caribbula elongata*. A, P3. B, Intercoxal sclerite of P3. C, Female P4.

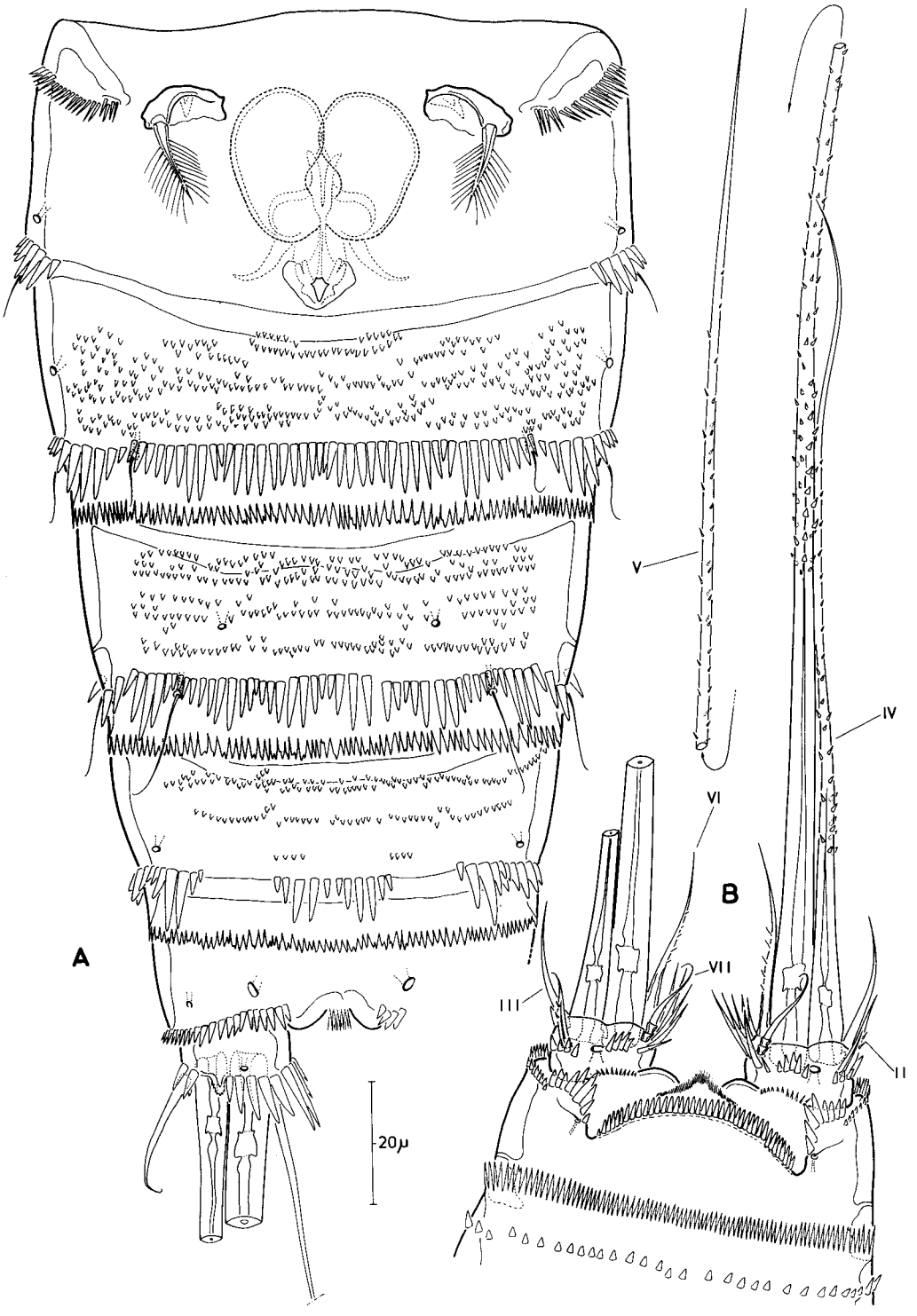


Figure 24. *Caribbula elongata*. A, Urosome (excluding P5-bearing somite) of female, ventral view. B, Anal somite and caudal ramus, dorsal view.

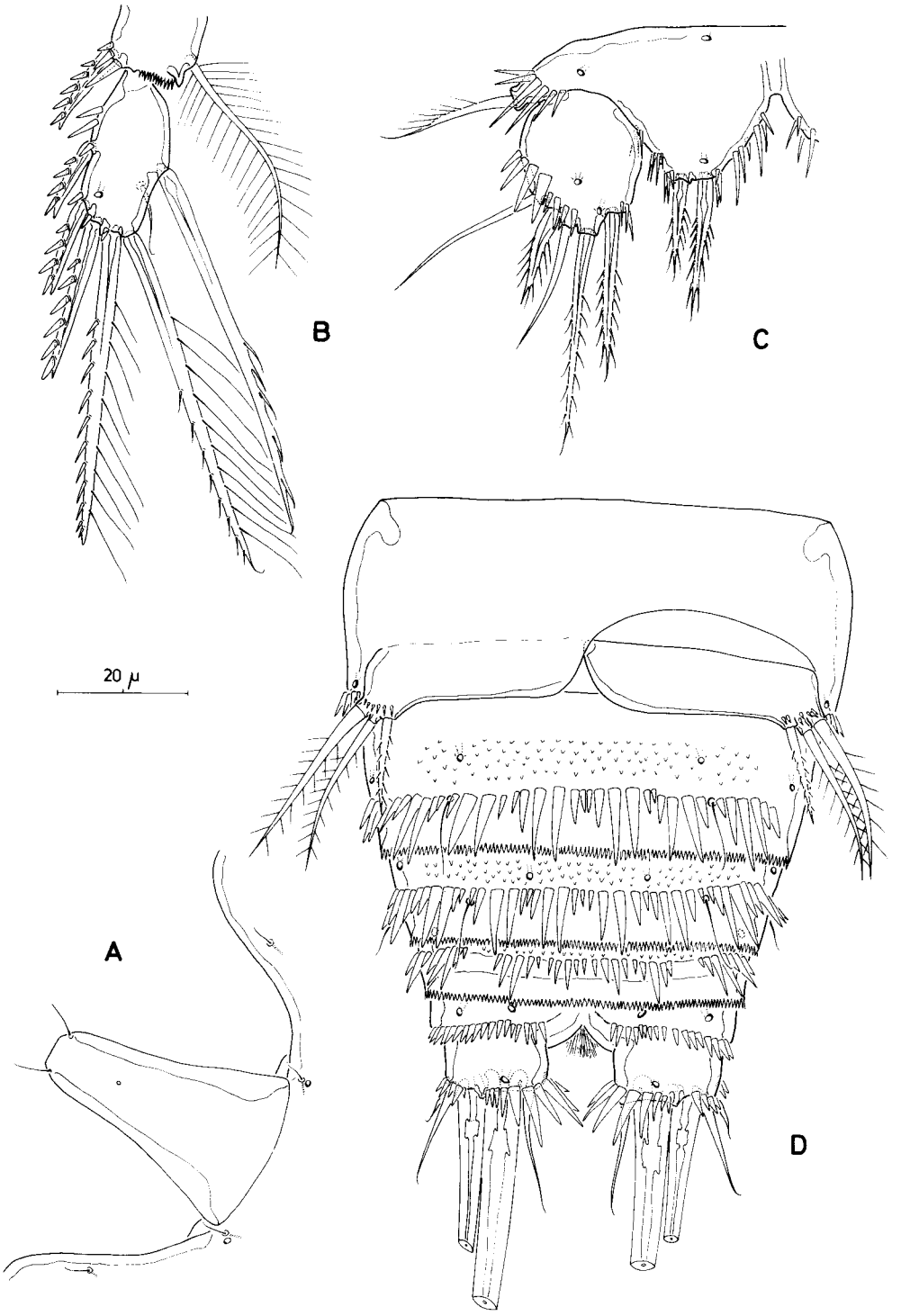


Figure 25. *Caribbula elongata*. A, Rostrum. B, P4 exopod-3 in male. C, Male P5. D, Urosome (excluding P5-bearing somite) of male, ventral view.

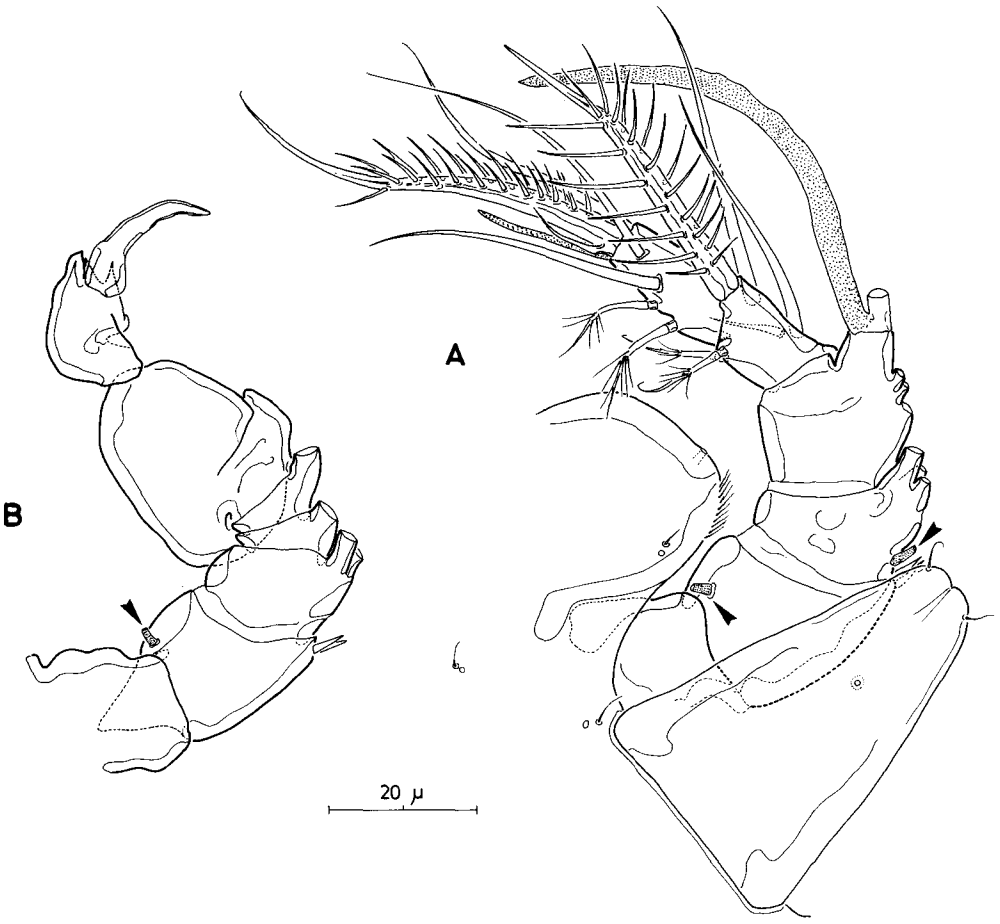


Figure 26. *Caribbula elongata.* A, Female antennula, setation of proximal segments omitted (arrows indicating tube pores). B, Antennula of male, setation omitted (arrow indicating tube pore).

Type locality. North Carolina continental shelf; specimens present in vial were collected from stations three, five and seven at depths ranging from 14 m to 50 m on different dates (February or April 1969), see Coull (1971).

Description of female

Only those features which differ from the type species are described.

Body (Figs 29A, B). Length 635 µm. Genital field with seminal receptacles almost rectangular in shape and spinules associated with gonopores 11–14 µm long (much longer than in type species). Hyaline frill of urosomites deeply incised but also secondarily denticulate. Anal operculum coarsely toothed on posterior margin (about 15 teeth). Setae IV and V of caudal rami stoutly spinulose.

Antenna (Fig. 28A). Exopod robust, exopod-3 2.7 times longer than broad with sub-terminal tube seta much longer than terminal spine.

Mandible (Figs 28B, C). Basis without proximal spinule row and with endopod much longer than exopod.

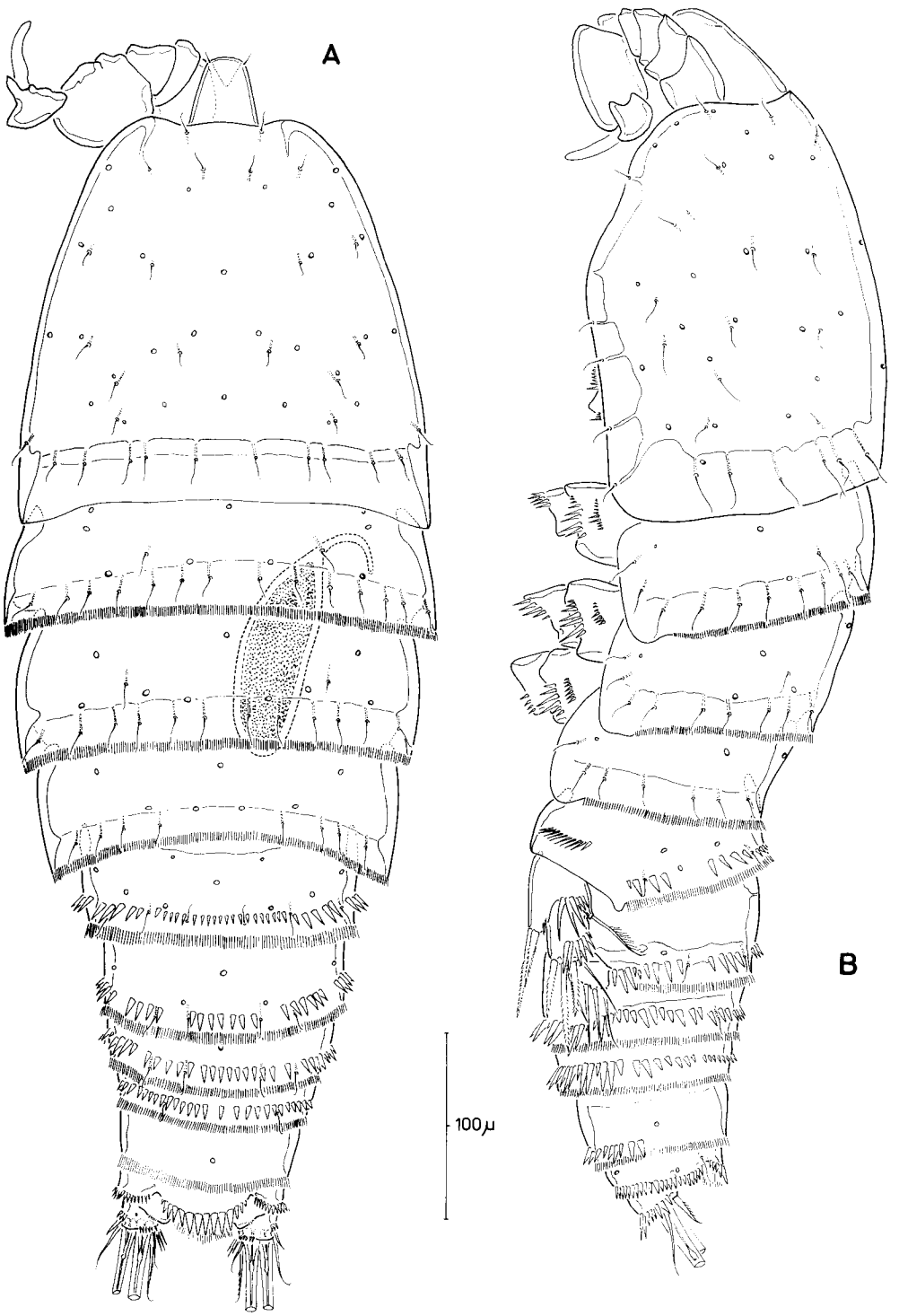


Figure 27. *Caribbula fleegeri*. A, Habitus of male, dorsal view. B, Habitus of male, ventral view.

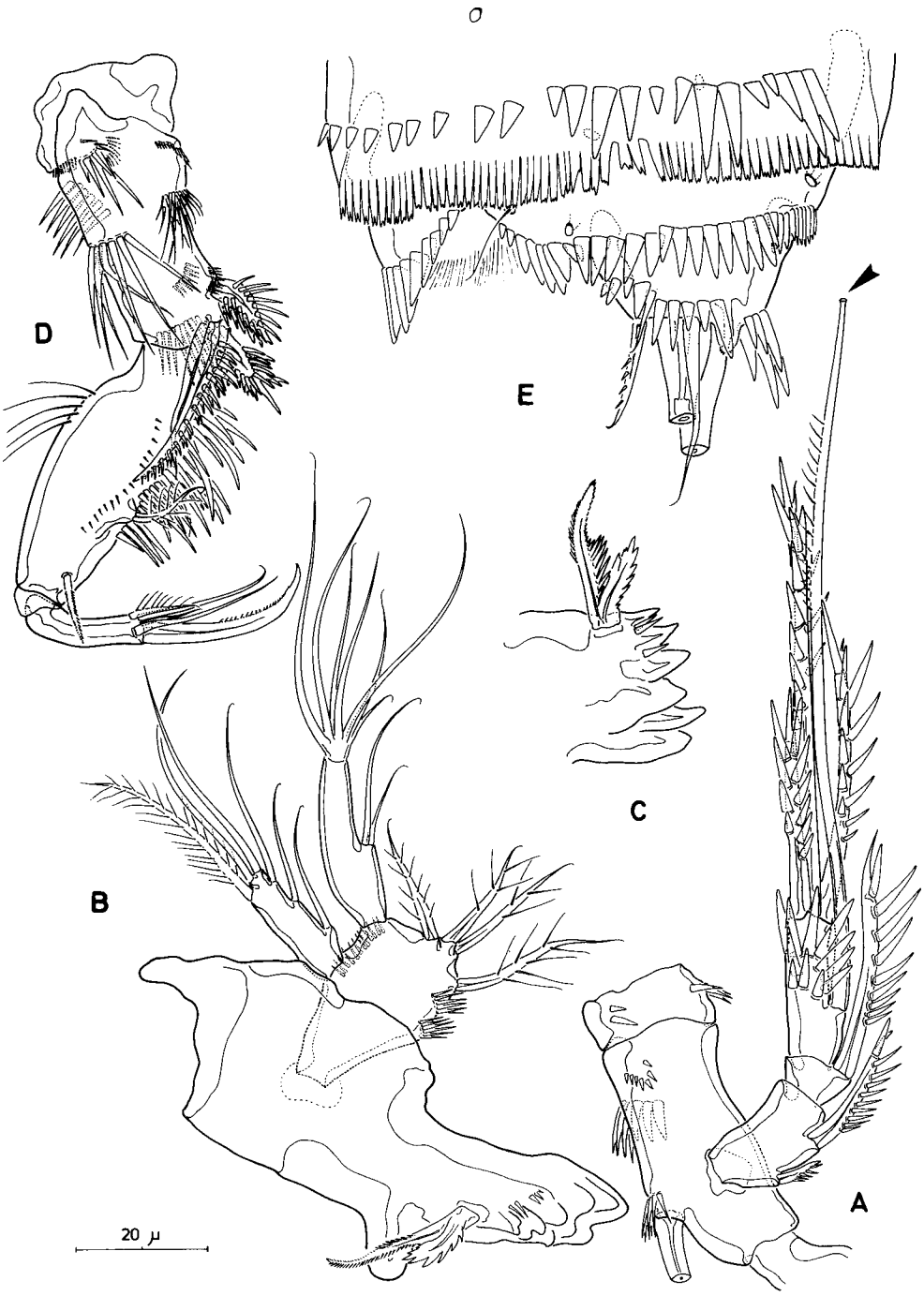


Figure 28. *Caribbula fleegeri*. A, Antennal allobasis and exopod (arrow indicating tube pore). B, Mandible. C, Mandibular gnathobase. D, Maxilliped. E, Anal somite and caudal ramus, lateral view.

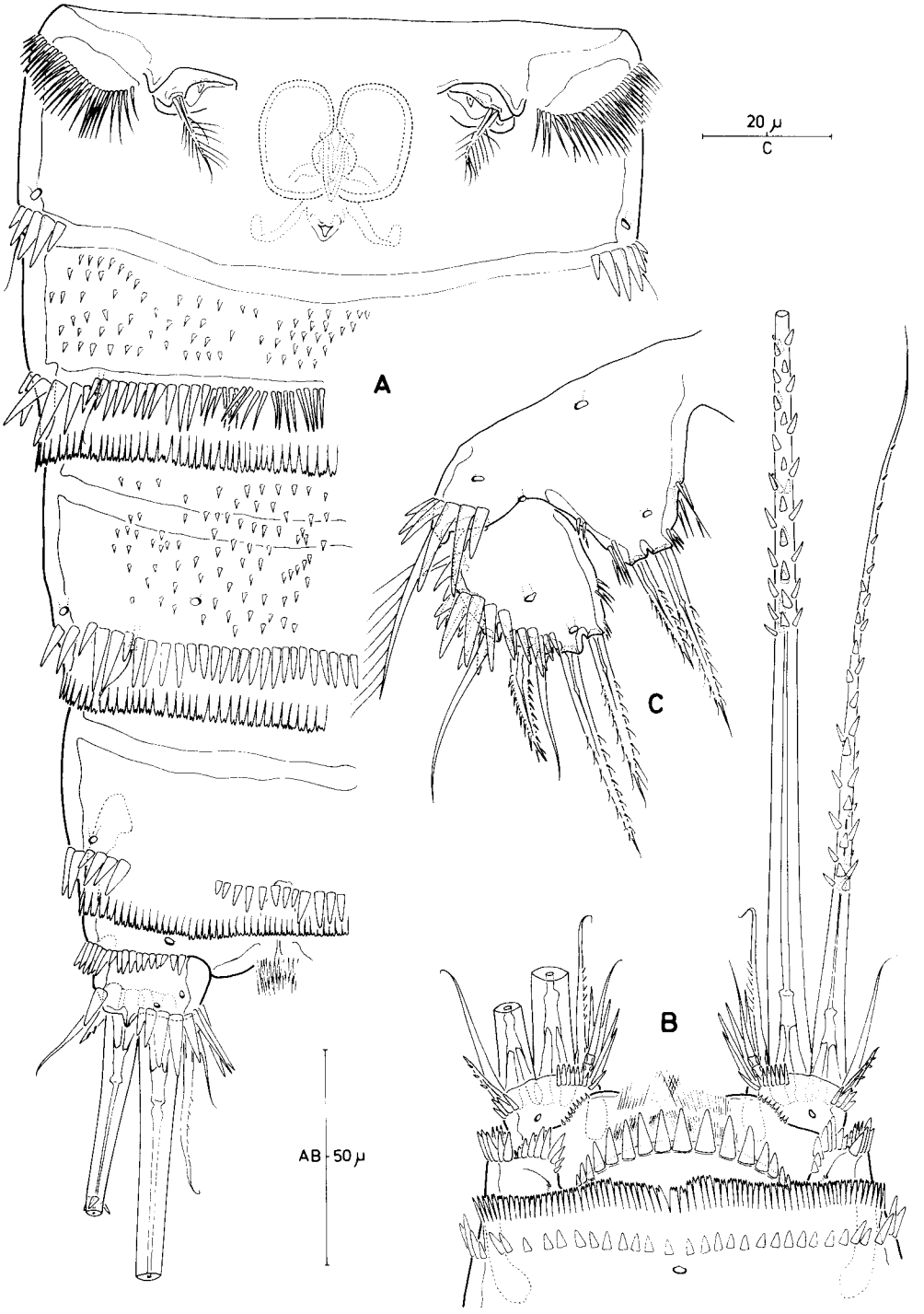


Figure 29. *Caribbula fleegeri*. A, Urosome of female (excluding P5-bearing somite), ventral view. B, Anal somite and caudal ramus, dorsal view. C, Male P5.

Maxilliped (Fig. 28D). Endopod with terminal claw markedly recurved at tip and with four accessory setae (loss of minute inner seta present on type species).

P1 (Fig. 30A). Coxa with proximal median spinule row on anterior face (arrowed in Fig. 27A) composed of stout spinules. Exopod-3 longer than exopod-2; distal inner spine of exopod-3 longer than ramus; endopod-2 and endopod-3 slender, 2.4 and 3.5 times longer than broad respectively.

P3 (Fig. 31A). Coxa with spinule row associated with pore on anterior face composed of three setules and a number of spinules (in type species they are all long setules in this row).

P5 (Fig. 30C). Inner margin of endopodal lobe convex.

Description of male

As in female of this species or male of type species except for following characters.

Body (Figs 27, 31B). Length 580 μm. Hyaline frill of urosomites not secondarily incised (as in female) but much more deeply incised than in type species.

P5 (Fig. 29C). Inner margin of endopodal lobe with fewer spinules than in type species and exopod more rectangular in shape.

P6 (Fig. 31B). Fused element with oblique posterior free margin.

Etymology. The species is named after Professor John Fleeger of the Zoology Department, Louisiana State University.

DISCUSSION

Wilson (1932) described three species, *Echinocornus pectinatus*, *Rathbunula agilis* and *R. curticauda*, from material collected in July 1927 on a beach in Buzzards Bay, Woods Hole, U.S.A. It is obvious, even from Wilson's drawings, that *Echinocornus* was described from copepodites, and Lang (1948) recognized it as a synonym of *Thompsonula hyaenae*. Of the *Rathbunula* species, Lang re-examined material of *R. agilis* only. This he compared with Klie's specimens of *T. hyaenae* and concluded that both were identical (Lang, 1948: 283–284). The reason why Lang retained *R. curticauda* as a species of *Thompsonula* was not because he recognized the differences that we outline in this paper but because he accepted Wilson's description and figures which showed *R. curticauda* as having only five setae on the exopod of P5. On this point Wilson was mistaken, as he was in his description and figuring of the P2 (Wilson, 1932, plate 20) which is, in fact, the P1. Lang also listed some other differences between the two species which we also consider significant (e.g. the segmentation of the antennule and relative lengths of the setae on the endopodal lobe of the male P5).

Because both Wilson and Lang distinguished between the two species of *Thompsonula* on the basis of the setation of the P5 exopod, all material of *Thompsonula* from the eastern seaboard of America (except for Coull, 1971) has been identified as *T. hyaenae* when it is, in fact, *T. curticauda* as defined in this paper. On the other hand, we have examined material of *Thompsonula* from Banyuls-sur-Mer, France, and can confirm that this is identical with *T. hyaenae* from north-west Europe. Therefore, it is likely that all previous records of this species from the Mediterranean are correct. Thus, from a biogeographical point of view, it would appear that *T. hyaenae* is confined to western Europe, where it

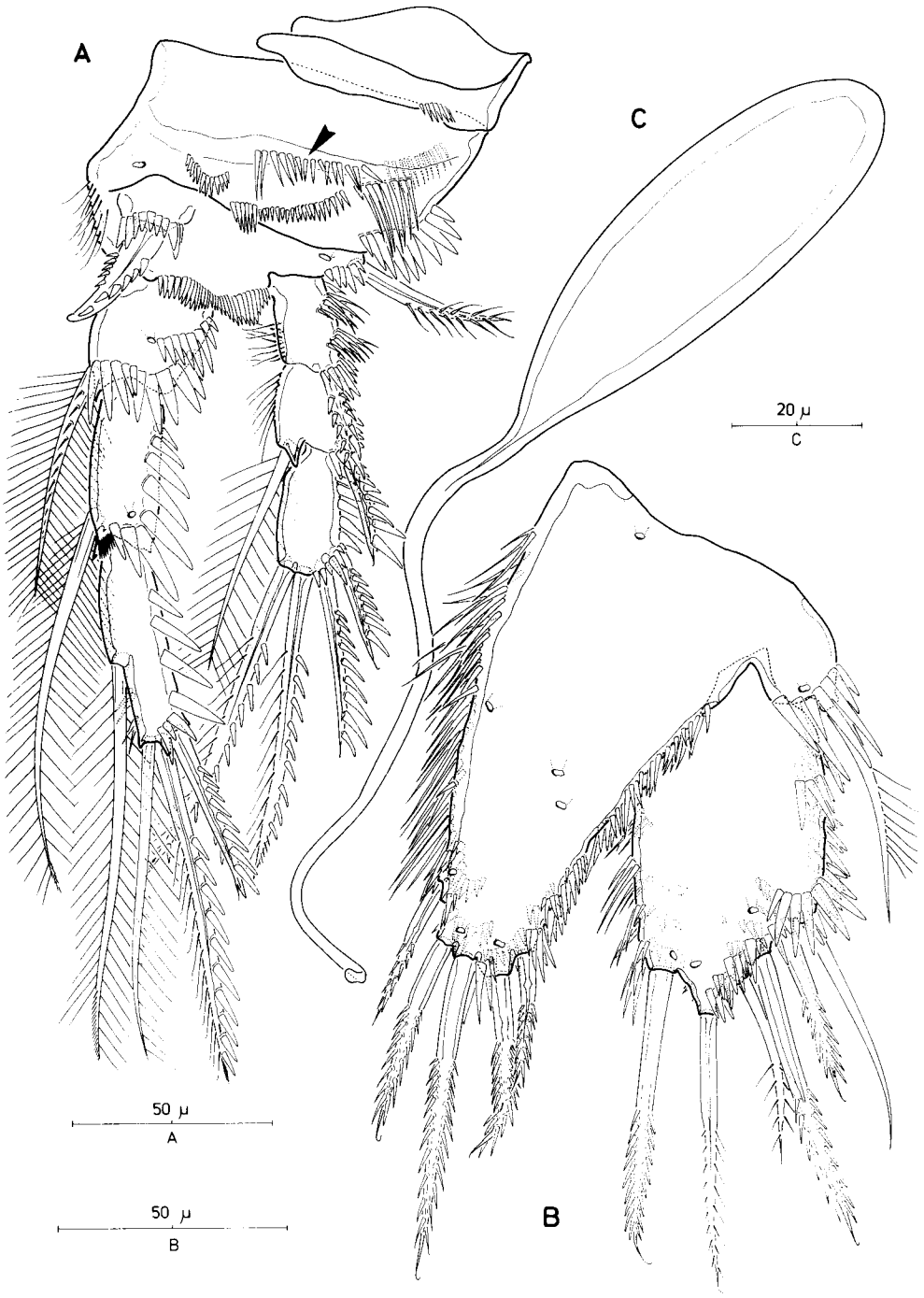


Figure 30. *Caribbula fleegeri*. A, P1 (arrow indicating large median spinular row). B, Female P5. C, Spermatophore.

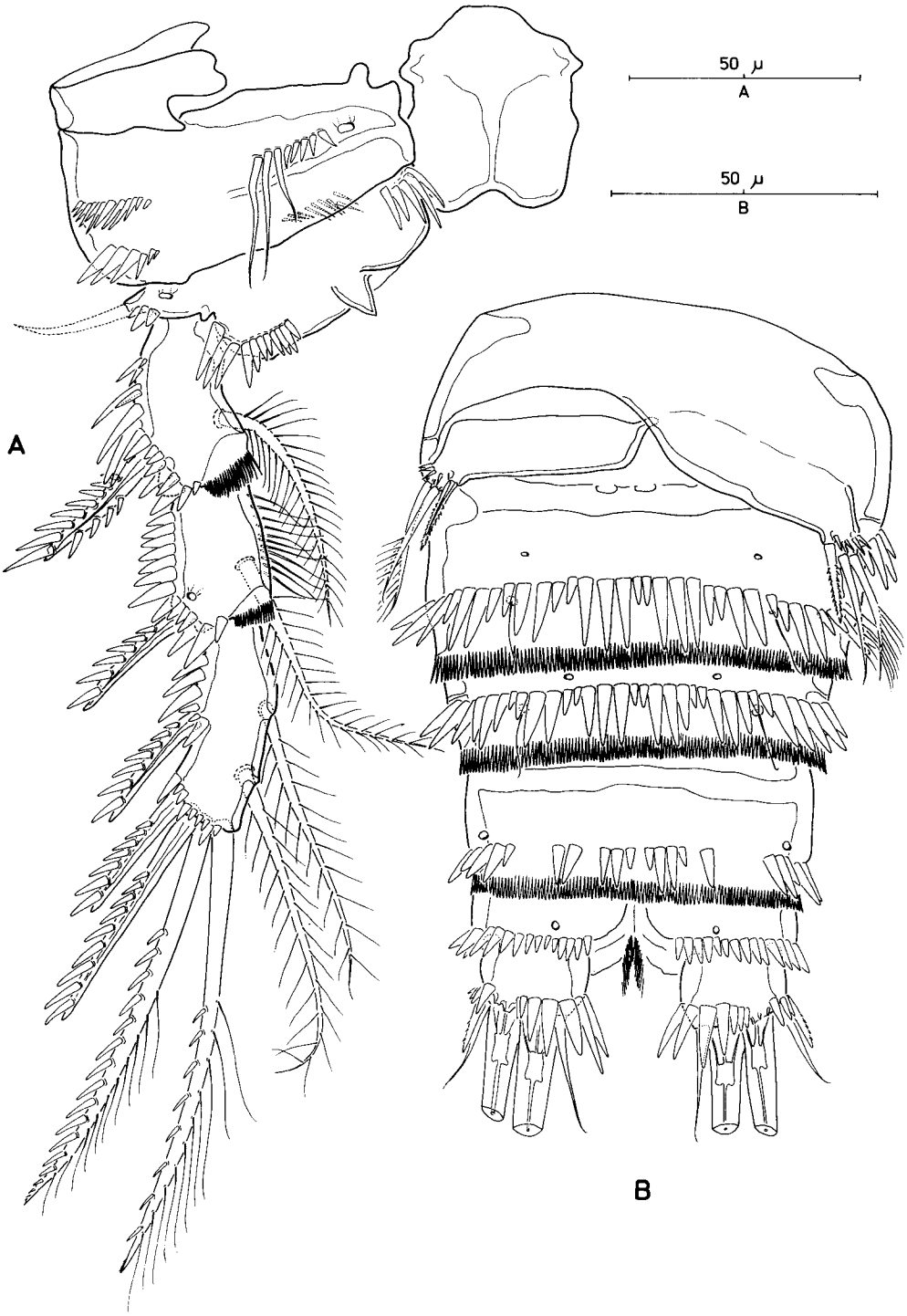


Figure 31. *Caribbula fleegeri*. A, P3 (excluding endopod). B, Urosome of male (excluding P5-bearing somite), ventral view.

has a typical boreo-mediterranean distribution, and that *T. curticauda* has a similar distribution along the eastern seaboard of North America.

So far, the genus *Caribbula* has been recorded only from the southern United States (North Carolina continental shelf and Gulf of Mexico). Gee (1988b) noted the sexual dimorphism on the P4 exopod of *T. hyaenae elongata* (one of the principal differences between the two genera) but was unable to compare it with male specimens of *Thompsonula*. In the same paper he pointed out that the setation of this ramus in female *Thompsonula* from Europe and North America had been misinterpreted in previous descriptions and assumed the same thing had happened with respect to the male. Thus he failed to recognize the significance of his observations on the male and did not place his material in a separate genus.

Lang (1948) used the following characters to unite the genera he placed in the subfamily Thompsonulinae and to distinguish it from the Tachidiinae.

1. Body only slightly flattened, urosome only slightly narrower than prosome and without nuchal and accessory nuchal organs.
2. Rostrum large, broad and hyaline.
3. Female antennule four to six-segmented, male antennule sub-chirocer.
4. Antenna with allobasis and three-segmented exopod.
5. Mandible with one to two-segmented exopod.
6. Maxillule with well-defined rami.
7. P1 with two to three segmented endopod.
8. P2 endopod without sexual dimorphism or middle segment of P2 endopod with process; sometimes P2 endopod-1 and P3 endopod-2 somewhat modified.
9. P5 rami usually separate in female, always separate in male.

Huys (in press) has already advanced arguments as to why the Langian subfamilies Euterpininae and Tachidiinae should be raised to the status of families, and in that paper he suggested that the Thompsonulinae were not a natural grouping, hinted at by Lang (p. 306) whose phylogenetic scheme implied that *Danielssenia* and *Psammis* were more closely related to each other than to *Thompsonula*. The following comparisons of the above, and other, characters will indicate that the Thompsonulinae *sensu* Lang (1948) fall into two well-defined groups, almost certainly having completely different phylogenetic origins and relationships. For this purpose, the genera *Danielssenia*, *Psammis*, *Paradanielssenia*, *Micropsammis* and *Leptotachidia* will be referred to as the 'danielsseniid genera' and *Thompsonula* and *Caribbula* as the 'thompsonulid genera'.

1. A slightly flattened body with little distinction between prosome and urosome is common to many harpacticoids, is a very variable character and there is not sufficient difference in degree of body flattening between the two groups for this character to be of significance. The absence of nuchal organs was included by Lang to distinguish between the Thompsonulinae and Tachidiinae but since Huys (in press) has already amended the diagnosis of the Tachidiidae to exclude the Thompsonulinae, a negative character such as this has no phylogenetic significance. What may be of significance however, is the fact that the thompsonulid genera have only a slightly divided anal somite with a well-defined operculum whereas the danielsseniid genera have a deeply divided anal somite and no operculum, its function being taken over by a pseudoperculum (posterior extension of the hyaline frill of the penultimate urosomite).

2. In the thompsonulid genera the rostrum does not have a noticeable hyaline area and has only one pair of lateral sensillae whereas in the danielsseniid genera the rostrum always has a hyaline area but, more importantly, there are two pairs of sensillae (one on the anterior margin and one on the dorsal surface), an unusual character which is also present in the Pseudotachidiinae Lang and extremely developed in the Donsiellinae Lang (see Hicks, 1988).

3. In thompsonulid genera, the second segment of the male antennule bears 16 setae (Fig. 9) whereas in the danielsseniid genera there is only one seta. Huys & Boxshall (in press) showed homologies in segmentation between the multi-segmented male antennule of calanoids and the shortened antennule of male harpacticoids and suggested that the retention of segments bearing one seta is a key character in assessing phylogenetic relationships. The presence therefore of a uni-setose second segment in danielsseniid genera suggests that the male antennular condition is more primitive than the one in thompsonulid genera.

4. The structure of the antenna is a good character for distinguishing the Tachidiidae *sensu* Huys from the Thompsonulinae *sensu* Lang (see Huys, in press). However, in the thompsonulid genera the abexopodal element of the allobasis is a spine; there are three distal spines and a sub-distal seta on exopod-3; and the sub-distal elements on the endopod consist of two large spines and two small, basally fused, setae. In the danielsseniid genera, on the other hand, the abexopodal element of the allobasis is a seta; there are only two distal spines and a sub-distal seta on exopod-3; and the sub-distal elements on the endopod consist of two spines, a large geniculate seta-spine and a seta.

5. The segmentation of the mandibular rami is variable within both groups of the Thompsonulinae *sensu* Lang and is therefore not a useful character. The usual condition is a one-segmented exopod but in both groups a two-segmented condition is occassionally found, e.g *T. curticauda* (Fig. 11D) and *Danielssenia quadriseta* Gee, 1988a: fig. 5).

6. Both groups have well-defined rami on the maxillule. However, of considerable significance is the presence of a coxal epipod seta in the thompsonulid genera (Fig. 4C) which is absent from all other genera in the Tachidiidae *sensu* Lang. In addition, in the thompsonulid genera there are four seta on each ramus of the maxillule whereas in the danielsseniid genera there are only three setae on each ramus.

There are also other, previously unnoticed or unmentioned, differences in the mouth parts between these two groups (suggesting very different phyletic origins), the most significant of which are in the maxilliped. In the thompsonulid genera, the syncoxa of the maxilliped (Fig. 3B) has three short spines and a seta; there are two setae on the inner margin of the basis; and the endopod has a claw and five accessory setae. In the danielsseniid genera, on the other hand, an important feature of the syncoxa is the presence of one very large seta and, normally, one small seta; the basis has only one seta on the inner margin, probably homologous with the distal-most of the two setae in *Thompsonula*; and the endopod has only two accessory setae in addition to a claw.

7. The endopod of P1 is always three-segmented in the thompsonulid genera and always two-segmented in the danielsseniid genera. Although the armature of the distal segment in both groups is the same, they are not homologous as the distribution of spinule rows and surface pores in the danielsseniid genera, indicates that the distal segment has been derived from the fusion of two segments and subsequent loss of a seta rather than the loss of a middle segment.

The distal segment of the exopod of P1 in the thompsonulid genera always has only four spines whereas in danielsseniid genera there are always four spines and a seta. We have re-examined *Danielssenia spinipes* Wells and found that the setal arrangement of the P1 described by Wells (1967) was incorrect.

8. Pronounced sexual dimorphism in the endopod of P2 is found in all danielsseniid genera, except *Leptotachidia iberica* and *Psammis borealis* (according to the descriptions given in Becker, 1974 and Klie, 1941) and it is not yet clear whether one, or both, these species are members of the danielsseniid group. However, in the thompsonulid genera, the absence of sexual dimorphism in the swimming legs is the primitive condition and the sexually dimorphic condition found in the P4 exopod in *Caribbula* has arisen secondarily within the family. Sexual dimorphism in the exopod is unusual in the Harpacticoida and, when found, usually involves swelling of segments or enlargements of setae-spines (e.g. Tachidiidae *sensu* Huys, some Laophontidae and Harpacticidae). The only other family that displays sexual dimorphism exclusively on the P4 exopod is the Latiremidae. Here, the sexual dimorphism often involves enlargement and/or fusion of exopodal segments and extreme modification of setae (Bozic, 1969; Cottarelli, 1971), and is regarded as being an apomorphy for the family (Huys & Kunz, 1988). Modification of the setae on P4 exopod is found also in the Canthocamptid genus *Fibulacamptus* (Hamond, 1987) but the sexual dimorphism shown by *Caribbula* (loss of a seta on P4 exopod) is rare within the Harpacticoida. A reduction in the number of setae on this limb is found in some species of the tetragonicipitid genus *Phyllopodopsyllus* (Kunz, 1984) and an increase in the number of setae has been reported in the family Huntemanniidae Por (Geddes, 1968).

9. In both the thompsonulid and danielsseniid groups the only genera in which the rami of the P5 are not separate are *Psammis* (females) and *Micropsammis*. However, secondary modifications to the P5 have arisen many times within different families of harpacticoids and is not usually a useful character at the familial level. The structure of the genital field, on the other hand, has considerable phylogenetic significance. In the thompsonulid genera the female gonopores are separate, the copulatory pore is always located considerably posterior to the gonopores; in the male the P6 members are separate, with one member fused to the somite wall and one articulating with it. In danielsseniid genera the female gonopores are connected by a median slit, the copulatory pore is immediately adjacent to the median slit (see Gee, 1988a, b) and in the male both elements of the P6 are symmetrical, fused medially and to the somite wall to form a single valve with the spermatophore probably being released in the centre at the junction of both plates.

Based on the foregoing arguments, we feel justified in removing the danielsseniid genera from the Thompsonulinae *sensu* Lang and raising the latter to family status. Although the Thompsonulidae display some primitive characters (such as the epipod of the maxillule, the rich armature of the maxillipedal endopod and syncoxa, the absence of sexual dimorphism in the swimming legs, the relatively unmodified P1, separate gonopores), at the moment it is difficult to assess their exact relationships within the order. However, we feel that there are at least some remarkable similarities, especially in the mouthparts, with the Diosaccidae and more particularly the Tetragonicipitidae.

With our present state of knowledge, the systematic position and relationships

of the danielsseniid genera is very uncertain and will be discussed more fully after further research. However, the structure of the genital field, the antenna, mouthparts and P1, as well as the sexual dimorphism of the male P2 and P3 endopods, all suggest that the danielsseniid genera are closely related to the two genera at present constituting the family Paranannopidae, as defined by Por (1986). In a very preliminary investigation of this family, we have failed to find any apomorphies by which the danielsseniid genera can be separated from the family Paranannopidae, or more particularly the genus *Paranannopus* as it is presently constituted, and so we tentatively assign them to this family.

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