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Canuellidae (Copepoda, Harpacticoida) from the Bohai Sea, China

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Both sexes of *Scottolana geei* n. sp. (Copepoda: Harpacticoida: Canuellidae) are described from the Bohai Sea, China. The species belongs to the *longipes*-group of *Scottolana* which includes *S. longipes*, *S. longipes sensu* Por (1964), *S. longipes sensu* Wells (1967), *S. longipes sensu* Wells and Rao (1987), *S. uxoris* and *S. dissimilis*. This lineage can be differentiated from other congeners by the presence of only two postgenital somites in the female and three in the male, the modified P4, the sexual dimorphism of the P3 endopod and caudal rami, the presence of a spinous process on the bases of P2–P4, and the characteristic caudal ramus with hook-like extension along the inner margin and spinular patch near the distal outer corner. *S. geei* is unique among the Harpacticoida in displaying a nine-segmented antennary exopod. It is most closely related to *S. longipes sensu* Wells and Rao (1987) from the Andaman Islands. *Scottolana bulbifera* (Chislenko, 1971) is redescribed in detail on the basis of Bohai Sea material and discrepancies with Chislenko's original description, based on specimens from the Sea of Japan, are re-evaluated.

KEYWORDS: Copepoda, Harpacticoida, Canuellidae, *Scottolana*, Bohai Sea, China.

Introduction

The harpacticoid family Canuellidae currently accommodates 17 genera (Huys, 1995). The most speciose genus, *Scottolana* Por, 1967, is marked by an intricate nomenclatural history. Por (1967) proposed the genus to accommodate three species which were originally placed in *Sunaristes* Hesse, 1867: *Sunaristes inopinata* Thompson and A. Scott, 1903; *S. longipes* Thompson and A. Scott, 1903; and *S. bulbosus* Por, 1964. He also considered *Canuella scotti* Sewell, 1940 [=*nomen novum* for *Canuella curticaudata* (Thompson and A. Scott) *sensu* A. Scott (1909); but see Hamond (1973) for alternative opinion] as a probable member of *Scottolana*, as well as *Sunaristes curticaudata* Thompson and A. Scott, 1903 which he tentatively assigned to the genus. Although *Canuella canadensis* Willey, 1923 was not included in Por's (1967) review of the Canuellidae, it was subsequently transferred to

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Scottolana on the basis of a redescription of both sexes (Coull, 1972). Similarly, Wells (1976) assigned *Canuella bulbifera* Chislenko, 1971 to *Scottolana* but did not make a specific recommendation for this placement. This course of action was adopted by Fiers (1984).

In his second outline revision of the Canuellidae, Por (1984) restricted the genus to just two species, *Scottolana longipes* (Thompson and A. Scott, 1903) and *S. uxoris* Por, 1983, and for some inexplicable reason cited it as a 'new combination'. He continued to consider *Canuella scotti* as a candidate for inclusion in this genus, provisionally removed *S. bulbosa* back to *Sunaristes*, proposed a new genus *Coullana* for *S. canadensis*, and regarded the status of both *S. curticaudata* and *S. inopinata* as too problematic for further discussion. *Scottolana bulbifera* was not included in Por's (1984) review and neither were *S. glabra* Fiers, 1982 and *S. dissimilis* Fiers, 1982, possibly as a result of coinciding submission of the respective manuscripts. The genus has seen the addition of four new species since: *S. antillensis* Fiers, 1984; *S. oleosa* Wells and Rao, 1987; *S. rostrata* Wells and Rao, 1987 and *S. tumidiseta* Wells and Rao, 1987. Finally, *Canuella brevifurca* Wells, 1967 was cited as a member of *Scottolana* by Wells and Rao (1987: 11) but to our knowledge no formal recommendation has been made for this new combination. Huys (1995) removed *S. curticaudatus* to the new genus *Intersunaristes* and assigned *S. inopinata* to the *Scottolana* 'complex'. Likewise, there is no factual justification for maintaining *S. bulbosus* in the genus *Sunaristes* and it is here transferred to *Scottolana*. As a result of these discussions the genus *Scottolana* currently comprises 13 species: *S. longipes*, *S. inopinata*, *S. scotti*, *S. bulbosa*, *S. brevifurca*, *S. bulbifera*, *S. dissimilis*, *S. uxoris*, *S. glabra*, *S. antillensis*, *S. oleosa*, *S. rostrata* and *S. tumidiseta*.

In neither of Por's (1967, 1984) reviews, nor subsequently by any other authors, was a type species designated. Since definite type fixation by original designation or indication is mandatory as a requirement for availability for generic names published after 1930 [ICZN Art. 13.3], it follows that *Scottolona* Por, 1967 is unavailable. In order to maintain nomenclatural stability one of us (R.H.) submitted an application (Case 3218) to the International Commission on Zoological Nomenclature for the conservation of the generic name *Scottolana* Por, 1967 and the designation of *Sunaristes bulbosus* Por, 1964 as type species. *Sunaristes bulbosus* was selected since insufficient information is available on the males of the other two species originally included in the genus, *S. inopinata* and *S. longipes*. The former has never been recorded again since its original description from washings of Sri Lankan invertebrates (Thompson and A. Scott, 1903). Conversely, *S. longipes* has been the subject of redescription on three different occasions (Por, 1964; Wells, 1967; Wells and Rao, 1987), however, there is strong evidence that neither the Levantine material (Por, 1964) nor the specimens from Mozambique (Wells, 1967) are conspecific with Thompson and A. Scott's (1903) single female from Sri Lanka. Unfortunately, the original description by Thompson and A. Scott (1903) provides a limited base for comparison, presenting only illustrations of the habitus in lateral view, P4 and the caudal rami in dorsal aspect. Since the latter are usually sexually dimorphic, it is not clear whether Wells and Rao's (1987) male from the Andaman Islands belongs to *S. longipes*.

Apart from exclusively nomenclatural reasons we regard type fixation in *Scottolana* as particularly essential, given the artificial composition of the genus. It is obvious that there are several lineages within *Scottolana* characterized by distinct differences in body segmentation, genital morphology and sexual dimorphism in

antennules, swimming legs and caudal rami. As part of this generic revision we report on two *Scottolana* species from the Bohai Sea (China): *S. geei* n. sp., closely related to *S. longipes*, and *S. bulbifera*, originally described from Possjet Bay, Sea of Japan.

Materials and methods

Specimens were collected during an ongoing sampling survey in 1997–1999 from the central region of the Bohai Sea (38°30′N, 120°E), China. Sediments range from muddy sand to mud. Sediment samples were collected at an average depth of 20 m (range 11–70 m) with a 0.1 m^2 box corer. Harpacticoid copepods were extracted using a 48 μm sieve and Ludox centrifugation flotation, from a standard subsample taken from the box core by three 26-mm diameter plastic tubes inserted to a depth of 5 cm.

Samples were fixed in 10% formalin, and specimens were preserved in 4% formalin. Before dissection the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the parts individually mounted in lactophenol under coverslips, which were subsequently sealed with transparent nail varnish. All drawings were prepared using a camera lucida on a Zeiss Axioskop differential interference contrast microscope.

Females of *S. bulbifera* were examined with a Philips XL30 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with palladium. The terminology of the body and appendage morphology follows that of Huys and Boxshall (1991). Abbreviations used in the text and figures are P1–P6 for thoracopods 1–6; exp(enp)-1(-2-3) to denote the proximal (middle, distal) segment of a ramus; and ae for aesthetasc. Body length was measured from the anterior margin of the cephalic shield to the posterior margin of the caudal rami. Type and other material was deposited in the Natural History Museum, London.

Taxonomy

Family CANUELLIDAE Lang, 1944

Scottolana Por, 1967
Scottolana geei n. sp.
(figures 1–12)

Material examined

HOLOTYPE: adult ♀ dissected on 18 slides (NHM reg. no. 2002.230). PARATYPES: one ♂ dissected on 18 slides and three ♂♂ preserved in alcohol (NHM reg. nos 2002.231–234).

Description

Female (holotype) (figures 1–6, 7A, 8, 9). Body length: 880 μm. Body (figure 1A, B) robust, comprising cephalosome, five pedigerous somites and three-segmented urosome. Urosome consisting of genital double-somite and two postgenital somites. Cephalic shield increasing in width posteriorly; thoracic and abdominal somites both gradually tapering posteriorly. Body covered with pattern of minute pimples and spinules varying in size and shape (not illustrated in figure 1 but comparable to

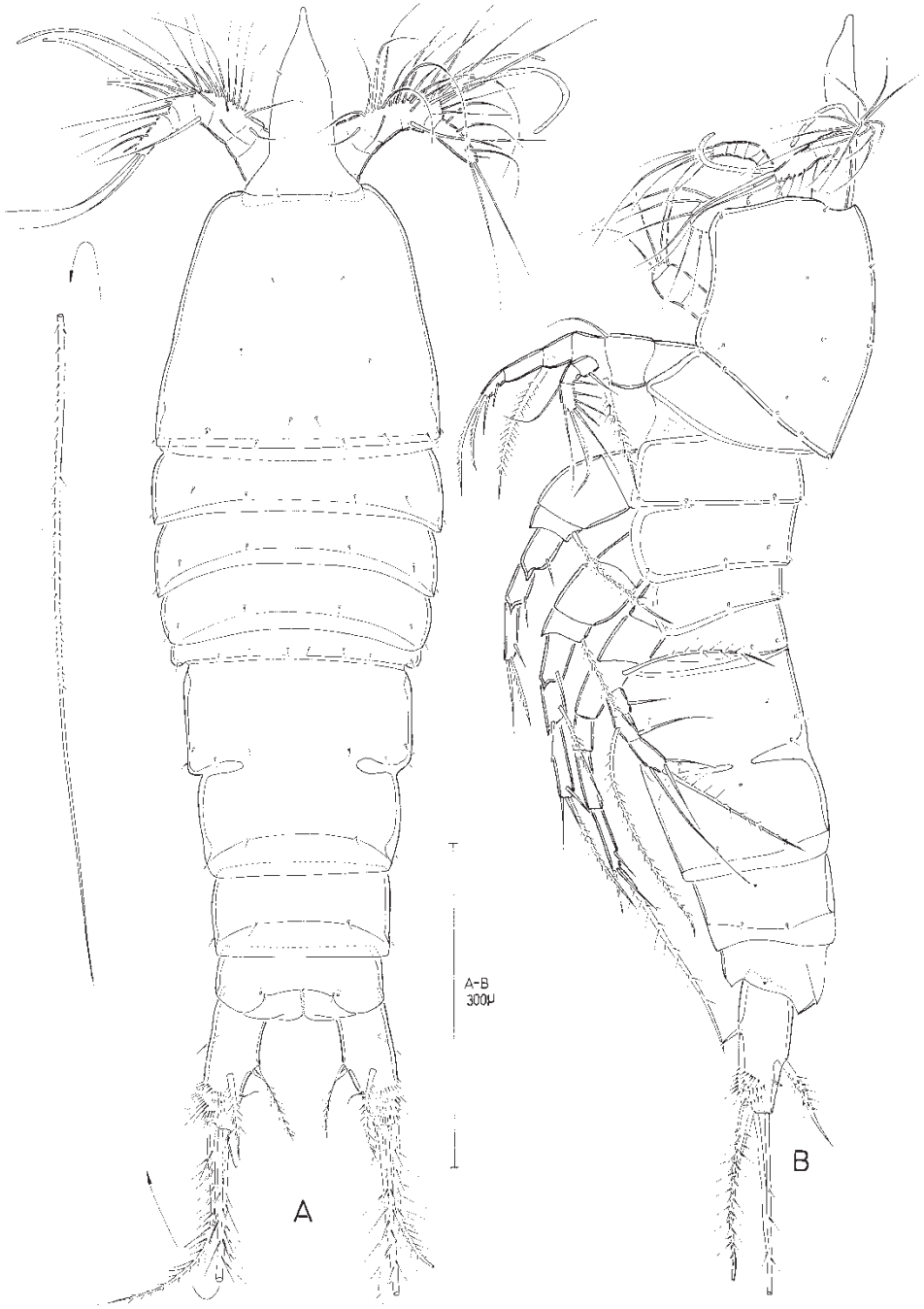

FIG. 1. *Scottolana geei* n. sp. (♀): (A) habitus, dorsal; (B) habitus, lateral.

those in *S. bulbifera*: figure 23A). P1-bearing somite separated from the cephalosome but concealed by cephalic shield in dorsal aspect (figure 1B). Original segmentation of genital double-somite marked by discontinuous internal chitinous rib laterally (figures 1A, B, 2A). Intersomitic membranes well developed; hyaline frills smooth

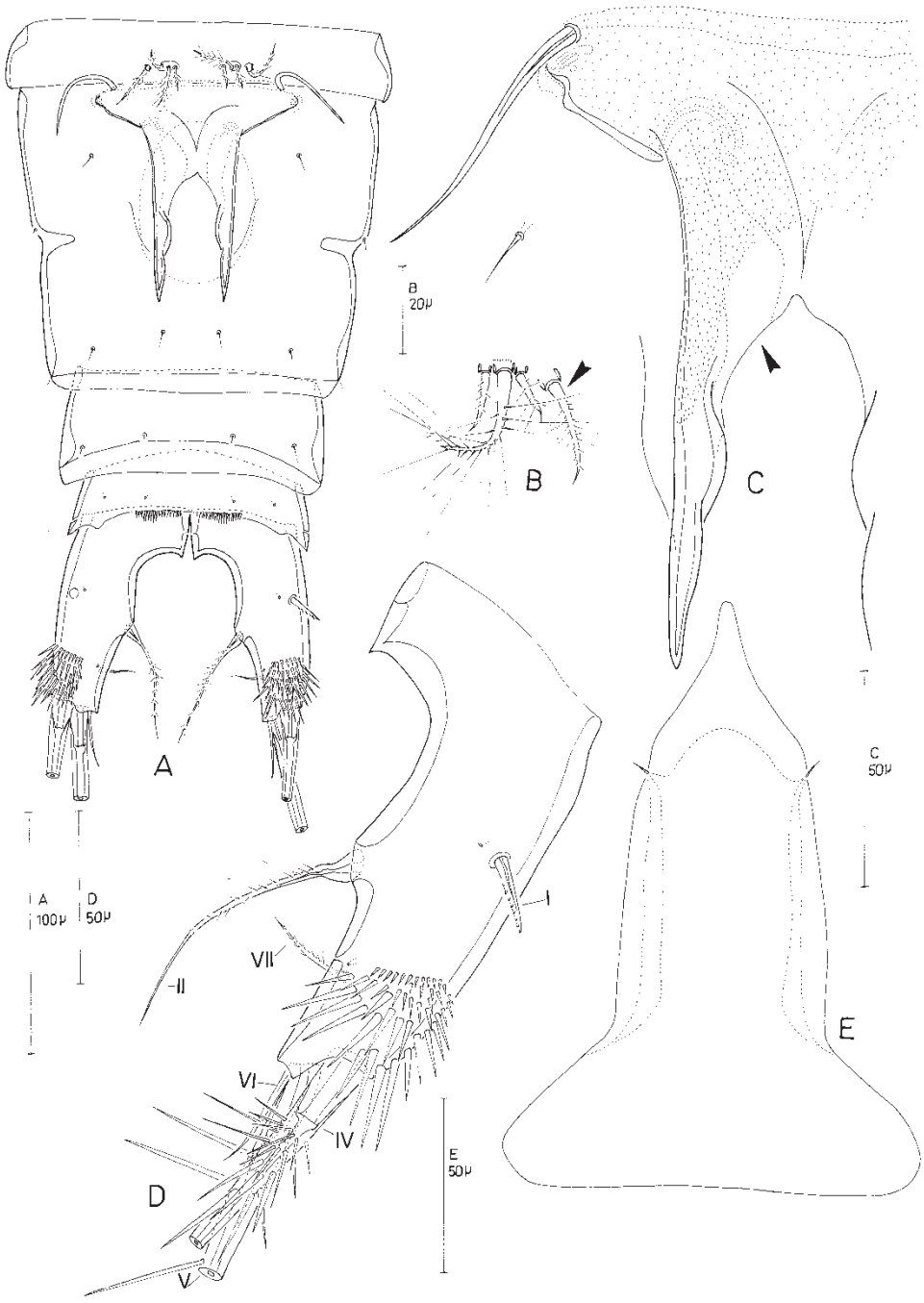

FIG. 2. *Scottolana geei* n. sp. (♀): (A) urosome, ventral; (B) P5 (outer basal seta arrowed); (C) genital field (left half omitted; copulatory pore arrowed); (D) left caudal ramus, ventral; (E) rostrum, dorsal.

FIG. 3. *Scottolana geei* n. sp. (♀): antennule (disarticulated).

(figures 1A, B, 2A). Anal operculum weakly developed (figures 1A, 7B). Anus terminal.

Rostrum (figures 1A, 2E) very large, about three-quarters length of cephalic shield; bell-shaped, with distal third tapering abruptly; with two tiny lateral sensillae.

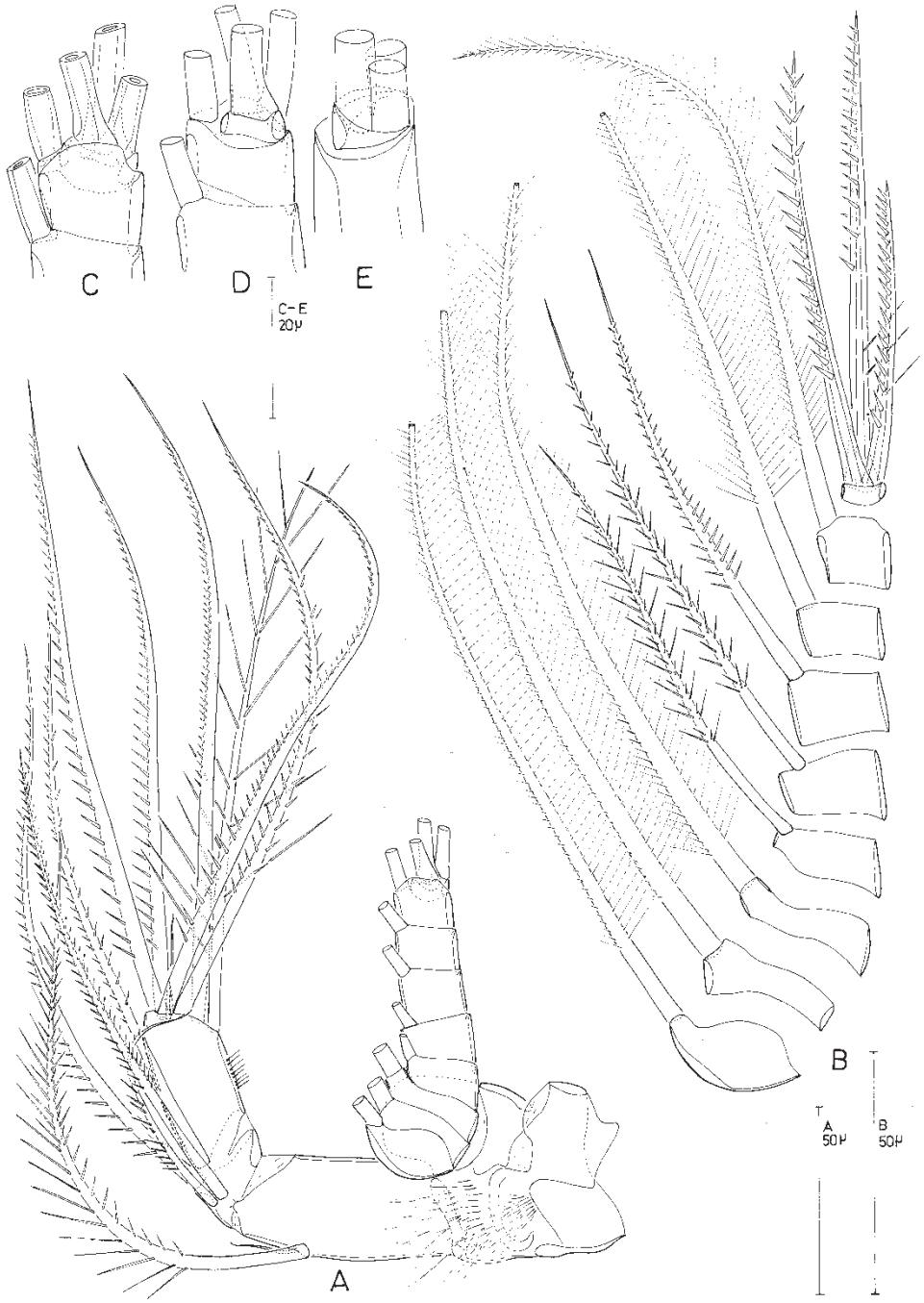

FIG. 4. *Scottolana geei* n. sp. (♀): (A) antenna; (B) antennary exopod (disarticulated); (C–E) apical segments of antennary exopod, viewed from different angles.

Antennule (figure 3) three-segmented. First segment largest, showing three incomplete sutures around posterior margin but no functional articulations; proximal part with setular tuft and spinule row ventrally; with 29 pinnate or spinulose setae/spines

FIG. 5. *Scottolana geei* n. sp. (♀): (A) mandible; (B) maxilla (armature of coxal endites shown in inserts); (C) detail of maxillary endopod showing armature patterns on individual segments.

FIG. 6. *Scottolana geei* n. sp. (♀): (A) maxillule, posterior (armature of coxal endite shown in insert, anterior); (B) maxilliped.

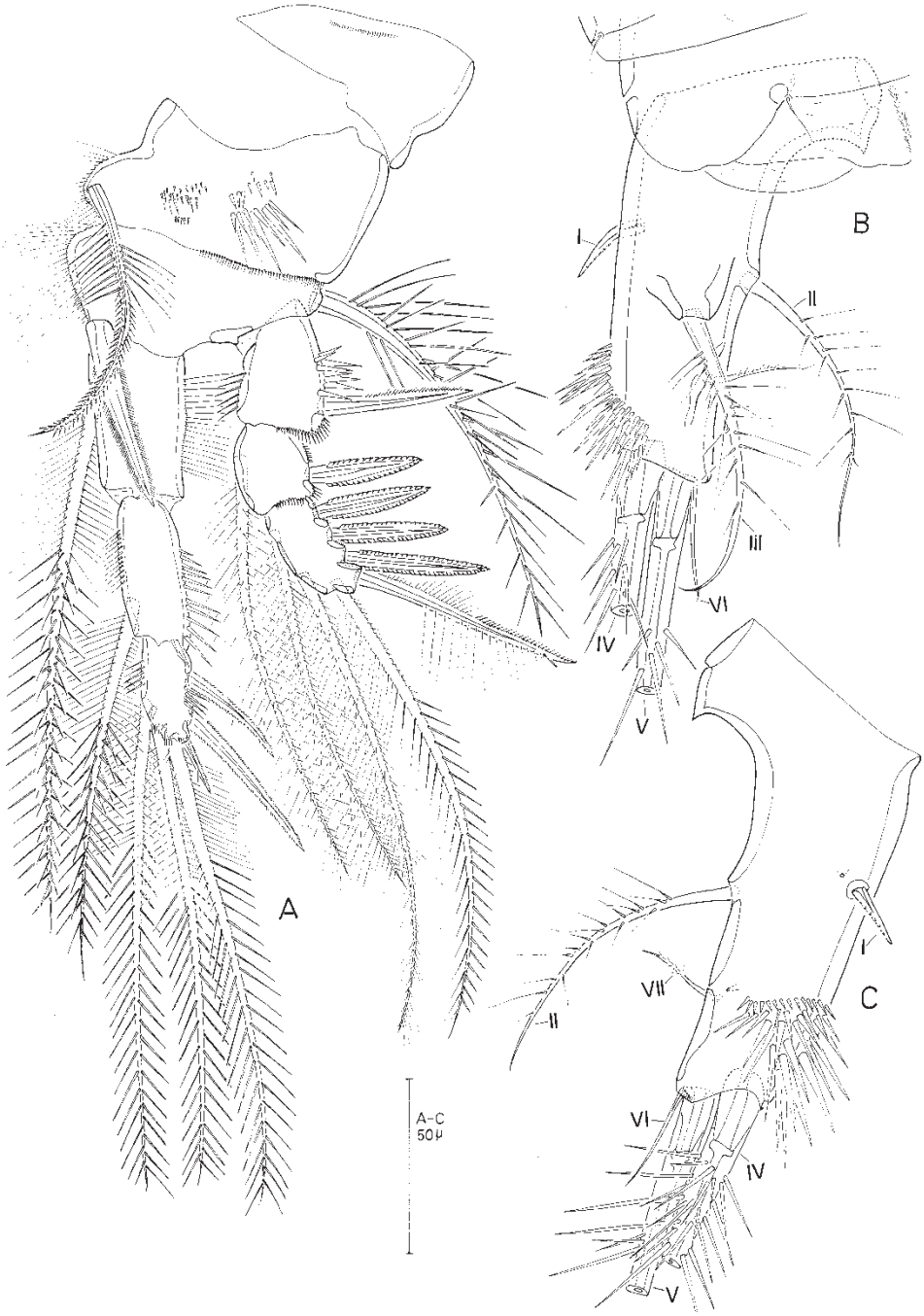

FIG. 7. *Scottolana geei* n. sp.: (A) P1 ♀, anterior; (B) left half of anal somite and left caudal ramus (♂), dorsal; (C) left caudal ramus (♂), ventral.

(four bi-articulate at base) and two aesthetascs. Middle segment short, with three pinnate and one plumose setae. Distal segment with three long plumose setae apically, a plumose seta posteriorly and five naked plus five pinnate setae around anterior margin.

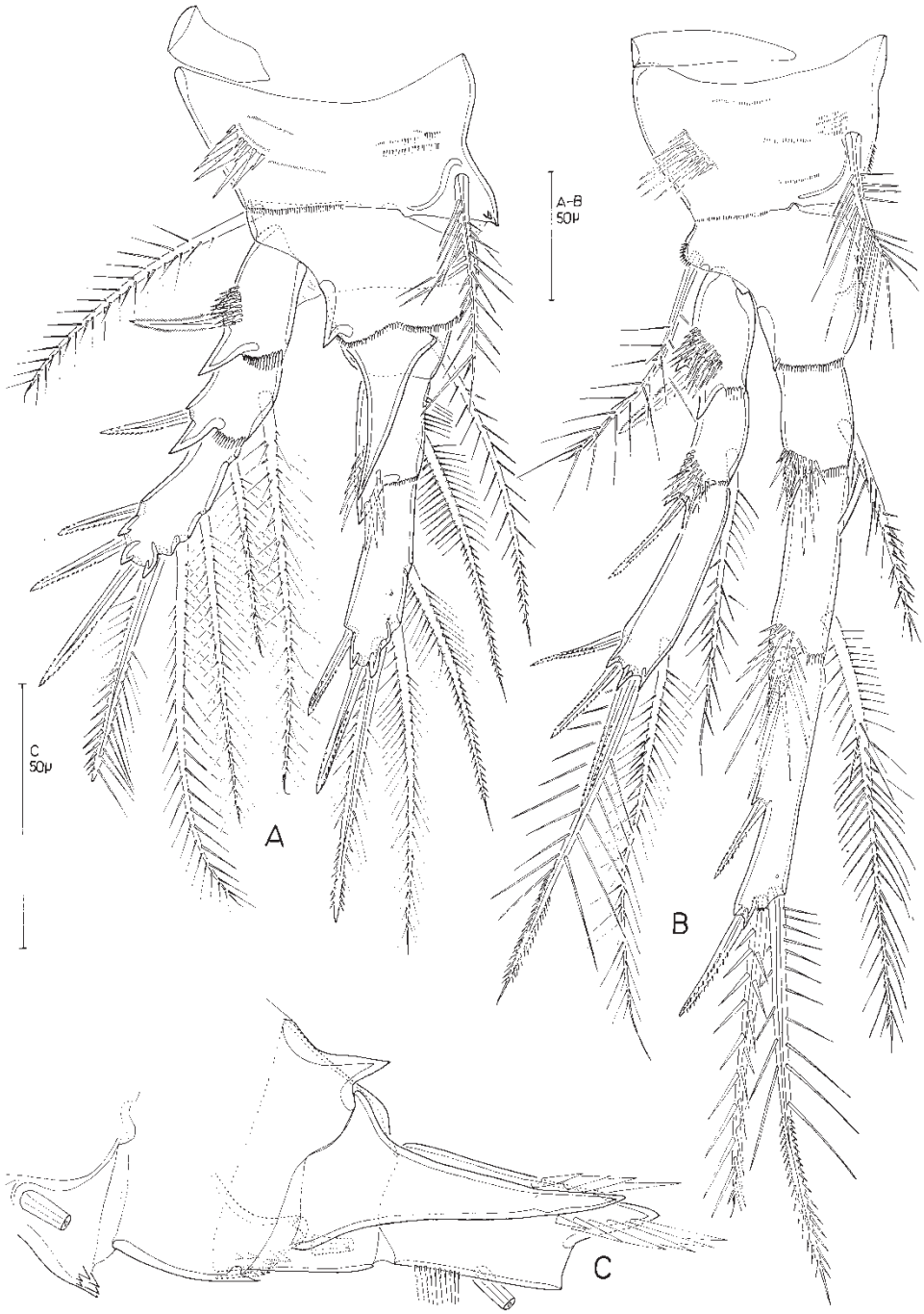

FIG. 8. *Scottolana geei* n. sp. (♀): (A) P2, anterior; (B) P3, anterior; (C) basis, enp-1 and enp-2 of P2, anterior.

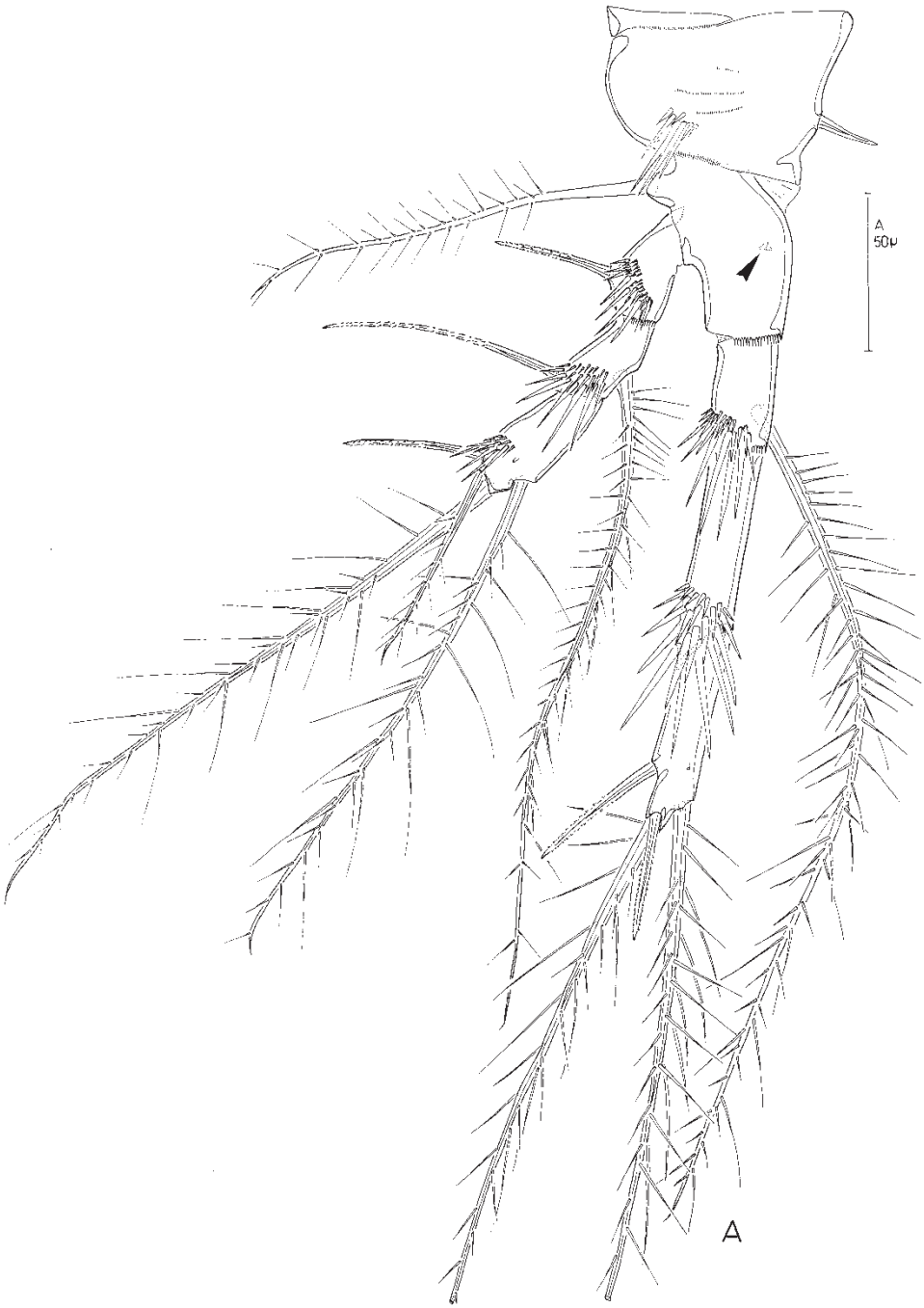

FIG. 9. *Scottolana geei* n. sp. (♀): (A) P4, anterior (minute spinous process on posterior surface of basis arrowed).

Antenna (figure 4A–C) comprising coxo-basis, two-segmented endopod and nine-segmented exopod. Coxo-basis relatively short, produced into cylindrical pedestal supporting exopod; with setular patches on anterior surface. Endopod with two

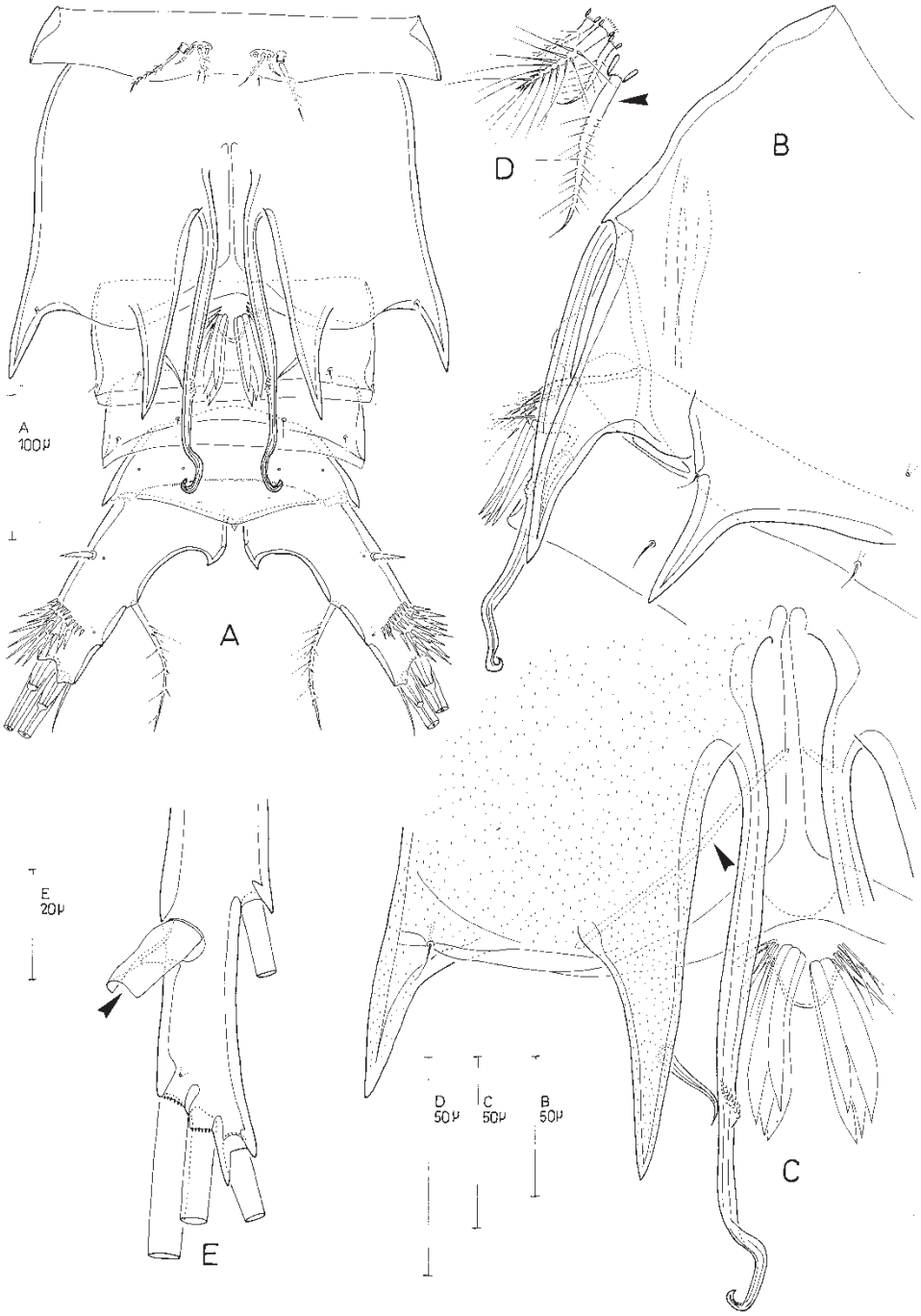

FIG. 10. *Scottolana geei* n. sp. (♂): (A) urosome, ventral; (B) genital field, lateral; (C) genital field, ventral (genital aperture arrowed); (D) P5 (outer basal seta arrowed); (E) P3 exp-3 showing modified tube pore along inner margin (arrowed).

FIG. 11. *Scottolana geei* n. sp. (♂): (A) antennule (armature largely omitted; illustrated completely on segment 2); (B) proximal segment of antennule.

setae on proximal segment, one of them minute and smooth; distal segment with incomplete transverse membranous insert indicating original segmentation; with four lateral and seven apical setae, six of them pinnate, the other one short and smooth.

FIG. 12. *Scottolana geei* n. sp. (♂): (A) distal two segments of antennule with setae on distal segment not drawn at full length (spinous recurved process on apical segment arrowed); (B) armature of distal segment of antennule (ribbed modified element on penultimate segment arrowed). *Scottolana bulbifera* (Chislenko, 1971) (♂): (C) segmentation of antennule, showing complete armature on swollen segment; (D) distal two segments of antennule (ribbed surface on penultimate segment arrowed).

Exopod with nine distinct segments; segments 1–3 and 7–8 each with plumose seta; segments 4–6 each with pinnate seta; terminal segment minute, U-shaped and partly concealed in segment 8, with three setae.

Mandible (figure 5A): gnathobase with row of six strong teeth superimposed on second row of smaller teeth; dorsal corner with one tripinnate spine; with additional spinules around gnathobasal teeth and dorsal margin. Basis with two pinnate setae and three rows of small spinules. Endopod two-segmented; enp-1 with three pinnate setae; enp-2 with six pinnate and two plumose setae. Exopod without complete segment boundaries but showing indications of ancestral four-segmented condition with probable setal formula [2, 1, 1, 2]; all setae plumose; setular row present on ancestral segment 2.

Maxillule (figure 6A): praecoxa and coxa partly fused. Praecoxal arthrite with nine spines and two setae around distal margin and two tube-setae on anterior surface; posterior surface with two rows of spinules. Coxa with epipodite represented by two plumose setae; endite cylindrical, with two smooth and three pinnate setae, anterior surface with one row of spinules. Basis with closely set endites, proximal endite with four pinnate setae, distal endite with one smooth and three pinnate setae; with row of spinules on posterior surface. Exopod large, foliaceous; with five smooth setae on inner margin, six plumose setae around distal margin and one small, pinnate seta on outer margin; inner edge with a row of fine setules. Endopod two-segmented; enp-1 with five pinnate setae laterally; enp-2 with six setae, outer four plumose, inner two pinnate.

Maxilla (figure 5B) comprising praecoxa, coxa, allobasis and three-segmented endopod. Praecoxa with spinules around base of endites and near distal outer corner; proximal endite with five (four pinnate, one smooth), distal with two pinnate setae. Coxa with two cylindrical endites, with three pinnate setae each. Allobasis produced into endite, bearing fused pinnate claw, two strong pinnate spines and four setae (three pinnate, one smooth). Endopod three-segmented (figure 5C); segments 1–2 each with three setae; segment 3 small, with two basally fused setae; all setae smooth.

Maxilliped (figure 6B) phyllopodial, two-segmented, comprising undivided protopod and one-segmented endopod; incomplete suture indicating boundary between syncoxa and basis. Inner margin of protopod with 12 setae/spines; with rows of small spinules on surface; outer margin with row of long setules. Endopod with 11 setae; inner and apical setae (seven) pinnate, outer ones (four) plumose.

All swimming legs with well-developed praecoxae and three-segmented rami; coxae with distinct spinular pattern on anterior surface as figured.

P1 (figure 7A) smaller than other swimming legs. Intercoxal sclerite wide and narrow. Coxa with long, inner pinnate seta. Basis with long, heavily ornamented outer seta and strong bipinnate inner spine. Inner margin of both coxa and basis with long setules. Exp-1 outer spine unipinnate, outer margin with strong spinules, inner margin with finer spinules; exp-2 outer spine serrate, inner seta long and plumose; exp-3 distinctly longer than exp-2, outwardly directed, with three serrate spines along outer margin, one bipinnate and two plumose setae along inner margin and one apical spine bearing combination of setules and spinules as figured. Endopod much longer than exopod; enp-1 with long, multipinnate inner seta inserting proximally and long setules along outer margin; enp-2 with long, multipinnate inner seta and spinules along both inner and outer margins; enp-3 with two bipinnate spines along outer margin, three strongly pinnate setae along inner margin and one short spine (with subterminal tubular extension) at the apex.

P2 (figure 8A, C). Intercoxal sclerite larger and broader than in P1. Coxa with inner pinnate seta; inner distal corner produced, with row of sharp teeth. Basis with bipinnate outer seta; posterior surface with large recurved process bearing several rows of marginal teeth (figure 8C). Exp-1 and -2 with pinnate outer spine and outer distal corner forming spinous process; exp-1 with spinular patch and exp-2 with plumose inner seta; exp-3 with four spines and three setae. Enp-1 with pinnate inner seta, proximal half of segment covered by basis; anterior surface produced into long mucroniform process, extending to distal margin of enp-2 where it fits into a spinule-flanked groove on the outer spinous process (figure 8C). Enp-2 with pinnate seta and spinular row along inner margin. Enp-3 with three spines and two setae; anterior surface with two pores.

P3 (figure 8B): intercoxal sclerite similar to P2. Coxa with pinnate inner spine; inner margin with row of small spinules. Basis attenuated into cylindrical pedestal for endopod; with pinnate outer seta; posterior surface with dorsally recurved spinous process. Exp-1 and -2 with pinnate outer spine accompanied at base by spinular patch; outer distal corner forming spinous process; exp-2 also with inner seta; exp-3 with four spines and one seta. Endopod much longer than exopod; enp-1 and -2 each with pinnate inner seta and outer distal corner produced into process bearing strong spinules; enp-3 with four spines; anterior surface with a pore.

P4 (figure 9): intercoxal sclerite similar to P2–P3. Coxa with short, smooth inner spine. Basis elongate, forming long cylindrical pedestal, displacing exopod to more marginal position; with long pinnate outer seta; posterior surface with small process. Exp-1 and -2 with pinnate outer spine (that of exp-2 much longer and more slender) accompanied at base by strong spinular patch; exp-2 also with very long, pinnate inner seta; exp-3 with one slender spine and three setae, spinular patch and pore on anterior surface, outer terminal seta typically crossing over inner terminal seta. Endopod much longer than exopod; enp-1 and -2 with coarse spinules around distal margin; enp-1 with very long pinnate inner seta; enp-2 unarmed; enp-3 with two spines and two setae, anterior surface with pore.

Spine and seta formulae as follows:

	Exopod	Endopod
P1	0.1.313	1.1.222
P2	0.1.322	1.1.221
P3	0.1.122	1.1.121
P4	0.1.121	1.0.121

P5 (figure 2B) vestigial, incorporated into somite; with four plumose setae; outermost seta (=homologue of outer basal seta; arrowed in figure 2B) separated from others; middle one of other three longest and with very long setules.

Genital field (figure 2A, C) large, extending over three-quarters of ventral surface of genital double-somite. Copulatory pores paired, posteriorly displaced to inner margin of wing-like processes; each pore wide (arrowed in figure 2C) and leading via copulatory duct to median seminal receptacle. Gonopores located far anteriorly, closed off by P6 bearing one long smooth seta and two internal projections (one large, one small; =vestigial armature elements) involved in subsurface interlocking mechanism. Ventral surface covered with small spinules.

Caudal rami (figure 2A, D) broad at base, produced into posteriorly directed hook-like extension at inner proximal margin; outer distal corner with dense patch of strong spinules, increasing in length posteriorly; with two pores on ventral surface

and one at inner margin; with seven setae. Seta I spiniform, unipinnate and short, positioned ventrally on outer margin near pore; seta II plumose, with bulbiform base, located halfway on inner margin; seta III long and multipinnate, implanted on dorsal pedestal as in ♂ (figure 7B). Distal margin of ramus with three setae; setae IV and V well developed and strongly pinnate; seta V about three times longer than seta IV (figure 1A); seta VI short and smooth, fused at base to seta V; seta VII plumose, short, bi-articulate at base, displaced to inner margin.

Male (figures 7B, C, 10A–E, 11A, B, 12A, B). Body length 830–1062 μm ($N=4$, mean = 922 μm). Sexual dimorphism in antennule, P3, P5, abdomen and caudal ramus.

Antennule (figures 11A, B, 12A, B) four-segmented, with geniculation between segments 3 and 4. First segment very large; with sutures around posterior margin, possibly indicating ancestral segmentation; with three rows of long setules in proximal part; with 23 setae/spines (four bi-articulate at base) and two aesthetascs. Segment 2 short, with two pinnate setae anteriorly and one short plumose seta (bi-articulate) posteriorly. Segment 3 large and swollen, with constricted proximal part (figure 11A); with very long plumose seta proximally (figure 12A), four additional setae in proximal half (three pinnate, one smooth) and three setae near geniculation (one pinnate, two smooth); distal anterior margin with modified ribbed element (arrowed in figure 12B). Segment 4 small; produced into backwardly directed recurved process (arrowed in figure 12A), interlocking with modified element on segment 3; armature consisting of two pinnate and five smooth setae.

P3 (figure 10E): enp-3 with large, transparent, modified tube-pore along inner margin at level of outer spine.

P5 (figure 10D): with armature as in ♀ but outer basal seta distinctly longer.

Urosome (figure 10A–C) consisting of P5-bearing somite, genital somite and three postgenital somites. Genital somite largest, with paired lateral, posteriorly directed spinous extensions. First abdominal somite with mid-ventral nodular process bearing setules laterally and transparent lanceolate spinules medially (figure 10B, C). Genital apertures (arrowed in figure 10C) closed off by modified sixth legs (figure 10A–C). P6 fused to genital somite, each produced into large spinous process bearing short naked seta on ventral surface; additional element arising from inner proximal part of P6, fused at base, very long (extending to distal margin of anal somite), dark brown, distal half with denticulate raised ridge and characteristically twisted apex.

Caudal rami (figure 7B, C): as in ♀ except seta II not modified, without bulbiform base.

Etymology

The species is dedicated to our friend and colleague Dr Michael Gee, in recognition of his excellent contributions to the systematics and phylogeny of harpacticoid copepods.

Scottolana bulbifera (Chislenko, 1971)

Canuella bulbifera Chislenko, 1971: 151–157, figures 1–4.

Material examined

Three ♀♀ dissected on 13, 17 and 18 slides, respectively; one ♂ dissected on 17 slides; 20 ♀♀ and 15 ♂♂ preserved in alcohol (NHM reg. nos 2002.235–248) from central part of the Bohai Sea.

Redescription

Female (figures 13A–20B, 22–23). Body length 700–940 μm ($N = 14$; mean = 833 μm). Body (figure 13A, B) cylindrical, comprising cephalosome, five pedigerous somites and four-segmented urosome. Urosome consisting of genital double-somite and three postgenital somites. Maximum width of cephalic shield measured at one-quarter distance from posterior margin; thoracic and abdominal somites both slightly tapering posteriorly. Body somites and posterior zone of cephalosome covered with pattern of minute pimples and spinules varying in size and shape (figure 23A). P1-bearing somite separated from the cephalosome but concealed by cephalic shield in dorsal aspect (figure 13B). Original segmentation of genital double-somite marked by continuous internal chitinous rib laterally (figure 13B) and discontinuous rib dorsally (figure 13A). Intersomitic membranes well developed; hyaline frills smooth (figures 13A, B, 14A). Anal operculum weakly developed (figures 13A, 17A). Anus terminal.

Rostrum (figures 13A, 16D, 22A, B, D) large, bell-shaped; with two sensilla subapically and median integumental pore apically.

Antennule (figure 15A–D) three-segmented. First segment largest, showing three incomplete sutures around posterior margin (figure 22A, C) but no functional articulations; proximal part with setular tuft ventrally (figure 22B) and three rows of long and two rows of short spinules; with 29 pinnate or spinulose setae/spines (four bi-articulate at base) and two aesthetascs. Middle segment short, with three pinnate and one naked setae. Distal segment with one naked and two long plumose setae apically, a short plumose seta posteriorly and four naked plus six pinnate setae around anterior margin.

Antenna (figure 16A, B) comprising coxo-basis, two-segmented endopod and eight-segmented exopod. Coxo-basis relatively short, produced into cylindrical pedestal supporting exopod; with setular patches on anterior surface and at abexopodal margin. Endopod with two setae on proximal segment, one of them minute and smooth; distal segment with incomplete transverse membranous insert indicating original three-segmented condition of endopod; with four lateral and seven apical setae (six pinnate, one smooth). Exopod with eight distinct segments; segments 1–3 and 7 each with plumose seta; segments 4–6 each with pinnate seta; terminal segment with one apical and three subapical pinnate setae.

Mandible (figure 18A): gnathobase with row of five strong teeth superimposed on second row of smaller teeth; dorsal corner with one pinnate spine; with additional spinules around gnathobasal teeth and dorsal margin. Basis with two pinnate setae and three rows of small spinules. Endopod two-segmented; enp-1 with three pinnate setae; enp-2 with one smooth, five pinnate and two plumose setae. Exopod with faint segment boundaries, showing indications of ancestral five-segmented condition with probable setal formula [1, 1, 1, 1, 2]; all setae plumose; apical segment minute and partly embedded in penultimate one.

Maxillule (figure 17B): praecoxa and coxa partly fused. Praecoxal arthrite with eight spines and two setae around distal margin and two tube-setae on anterior surface; posterior surface with one row of spinules. Coxa with epipodite represented by two plumose setae; endite cylindrical, with four smooth and three pinnate setae, anterior surface with one row of spinules. Basis with closely set endites, each with four pinnate setae; with row of strong spinules on posterior surface. Exopod large, foliaceous; with two smooth setae on inner margin, six plumose setae around distal margin and one small, smooth spine on outer margin; inner edge with a row of fine

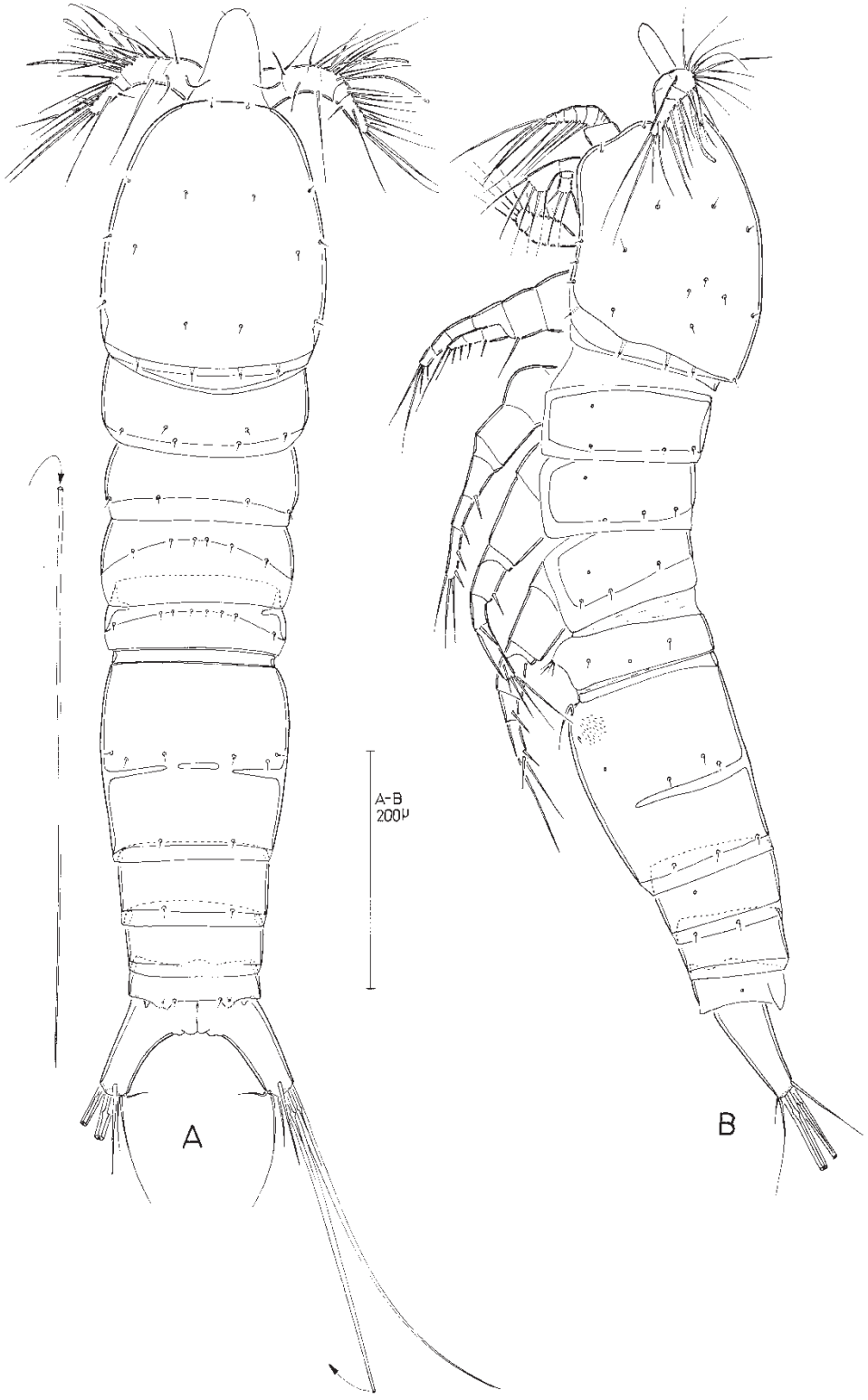

FIG. 13. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) habitus, dorsal; (B) habitus, lateral.

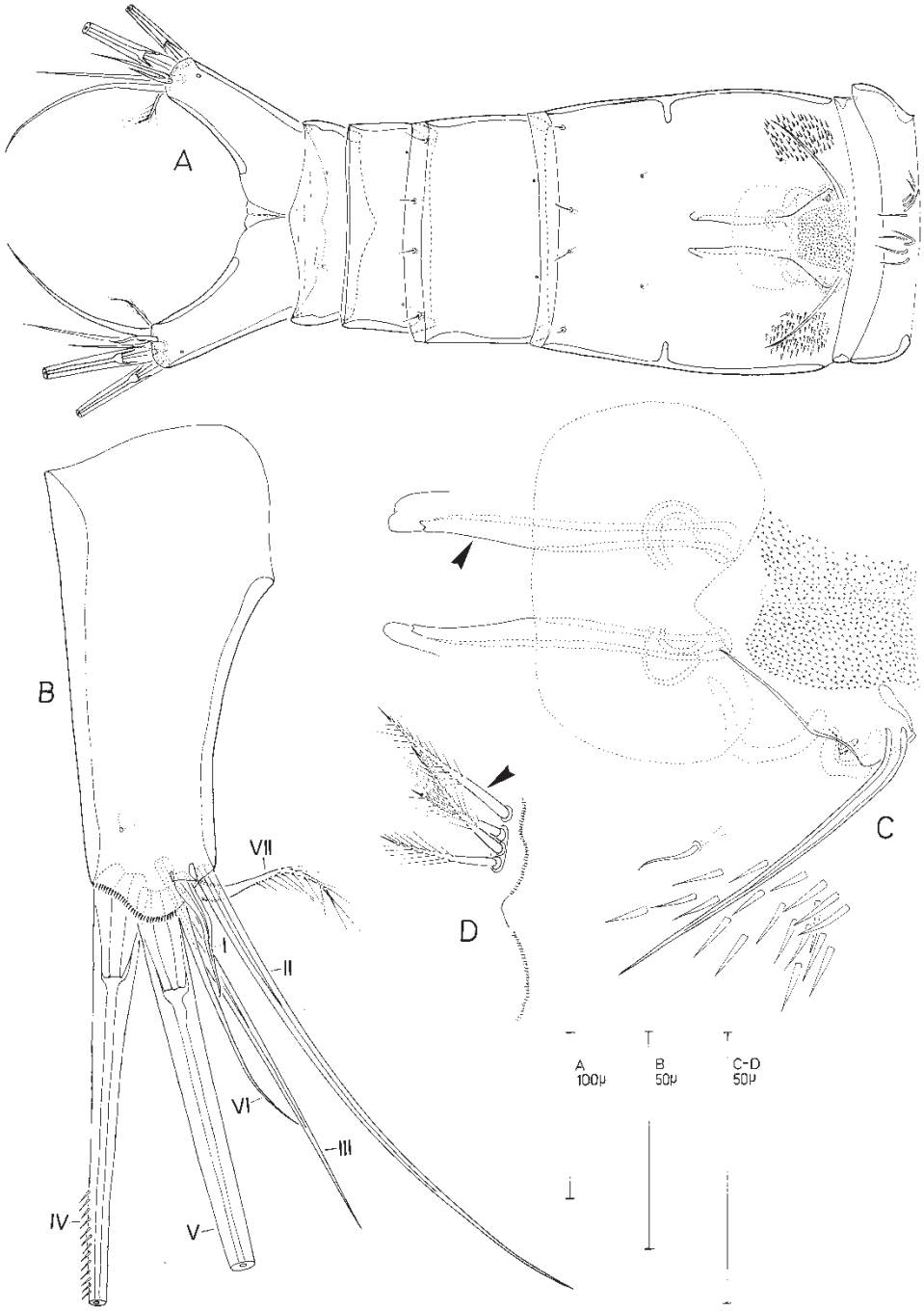

FIG. 14. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) urosome, ventral; (B) right caudal ramus, ventral; (C) genital field (copulatory pore arrowed); (D) P5 (outer basal seta arrowed).

setules. Endopod two-segmented; enp-1 with five pinnate setae laterally; enp-2 with six setae, outer five plumose, inner one pinnate.

Maxilla (figure 16C) comprising praecoxa, coxa, allobasis and unsegmented

FIG. 15. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) segmentation of antennule; (B) antennulary segment 1, drawn in three sections according to principal dorsolateral furrows (not representing fully functional articulations); (C) antennulary segment 2; antennulary segment 3.

FIG. 16. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) antenna (armature of exopod not illustrated); (B) antennary exopod, disarticulated; (C) maxilla; (D) rostrum, dorsal.

FIG. 17. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) anal somite and left caudal ramus, dorsal; (B) maxillule, posterior [armature of coxal endite shown in insert, anterior]; (C–F) distal part of caudal ramus showing variability of seta II.

endopod. Praecoxa with spinules on anterior surface and around outer margin; proximal endite with four (three pinnate, one smooth), distal with two pinnate setae. Coxa with two cylindrical endites, with three pinnate setae each. Allobasis produced into endite, bearing fused pinnate claw, two strong pinnate spines and four setae (two pinnate, two smooth). Endopod with one pinnate and seven smooth setae.

Maxilliped (figure 18B) phyllopodial, three-segmented, comprising syncoxa, basis and one-segmented endopod. Inner margin of syncoxa with 10 setae/spines; with rows of small spinules on surface. Basis with two smooth setae; outer margin with row of setules. Endopod with 11 setae; inner and apical setae (seven) pinnate, outer ones (four) plumose.

All swimming legs with well-developed praecoxae and three-segmented rami; coxae with distinct spinular pattern on anterior surface as figured.

P1 (figures 19A, 23B) smaller than other swimming legs. Intercoxal sclerite wide and narrow. Coxa with long, inner pinnate seta. Basis with very long, heavily ornamented outer seta and strong bipinnate inner spine. Inner margin of both coxa and basis with long setules. Exp-1 outer spine bipinnate, outer margin with strong spinules, inner margin with setules; exp-2 outer spine serrate, inner seta long and plumose; exp-3 not distinctly longer than exp-2, with three serrate spines along outer margin, one bipinnate and two plumose setae along inner margin and one bipinnate spine apically. Endopod slightly longer than exopod; enp-1 with long, multipinnate inner seta inserting proximally and long setules along outer margin; enp-2 with long, multipinnate inner seta, strong spinules along outer margins and setules along inner margin; enp-3 with two bipinnate spines along outer margin, three strongly pinnate setae along inner margin and one short spine (with subterminal tubular extension) at the apex. Enp-3 produced into terminal spinous process displacing apical spine to a more medial position.

P2 (figures 19B, 23C, D): intercoxal sclerite larger and broader than in P1. Coxa with inner pinnate spine. Basis attenuated into cylindrical pedestal for endopod; with bipinnate outer spine; posterior surface with recurved process. Exp-1 and -2 with strong spinular patch at base of pinnate outer spine, and outer distal corner forming spinous process; exp-2 with plumose inner seta; exp-3 with four spines and three setae. Enp-1 with plumose inner seta; anterior surface produced into long mucroniform process with subapical slit (figure 23C, D), extending to distal margin of enp-2 where it fits into a spinule-flanked groove on the outer spinous process. Enp-2 with plumose inner seta and spinular row along inner margin. Enp-3 with three spines and two setae; anterior surface with one pore.

P3 (figure 20A): intercoxal sclerite similar to P2. Coxa with pinnate inner spine. Basis with short pinnate outer seta; posterior surface with recurved spinous process. Exp-1 and -2 with pinnate outer spine accompanied at base by spinular patch; outer distal corner forming spinous process; exp-2 also with inner seta; exp-3 with four spines and one seta. Endopod much longer than exopod; enp-1 and -2 each outer distal corner produced into long process bearing strong spinules; enp-1 with inner bipinnate spine, enp-2 with inner plumose seta; enp-3 with four spines; anterior surface with a pore.

P4 (figure 20B): intercoxal sclerite similar to P2–P3. Coxa unarmed. Basis with short pinnate outer seta; posterior surface with small process. Exp-1 and -2 with pinnate outer spine (that of exp-2 shortest) accompanied at base by strong spinular patch; exp-2 also with bipinnate inner spine. Exp-3 with one outer, one inner and two apical pinnate spines; long spinous process between inner distal and inner spines;

FIG. 18. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) mandible; (B) maxilliped.

FIG. 19. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) P1, anterior; (B) P2, anterior.

spinular patch and pore on anterior surface. Endopod not distinctly longer than exopod; enp-1 and -2 with coarse spinules around outer distal process; enp-1 with inner bipinnate spine; enp-2 unarmed; enp-3 with four spines, anterior surface with pore.

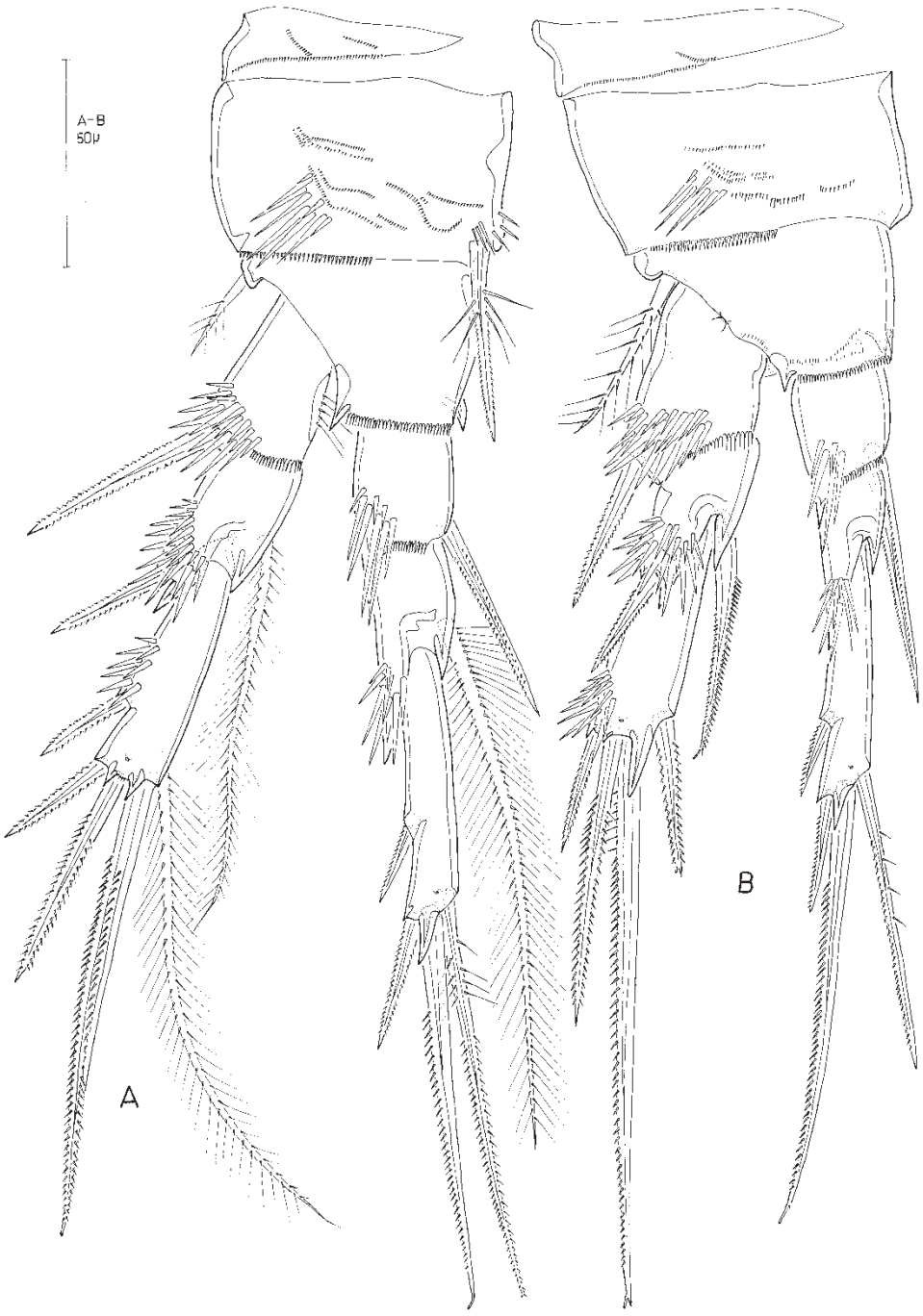

FIG. 20. *Scottolana bulbifera* (Chislenko, 1971) (♀): (A) P3, anterior; (B) P4, anterior.

Spine and seta formulae as follows:

	Exopod	Endopod
P1	0.1.313	1.1.222
P2	0.1.322	1.1.221
P3	0.1.122	1.1.121
P4	0.1.121	1.0.121

P5 (figure 14D) vestigial, incorporated into somite; with four plumose setae; outermost seta (=homologue of outer basal seta; arrowed in figure 14D) slightly separated from others; middle one of other three longest.

Genital field (figure 14A, C) large, extending over anterior half of ventral surface of genital double-somite. Copulatory pores paired, posteriorly displaced to inner margin of wing-like processes; each pore wide (arrowed in figure 14C) and leading via long copulatory duct to median seminal receptacle. Gonopores located far anteriorly, closed off by P6 bearing one long smooth seta and two internal projections involved in subsurface interlocking mechanism. Mid-ventral surface covered with small spinules. Genital field flanked by spinular patches.

Caudal rami (figures 13A, B, 14B, 17A, C–F) tapering posteriorly, without basal hook-like extension; with one pore on ventral surface at inner margin; with seven setae. Seta I spiniform, dilated and short, positioned ventrally near inner distal corner; seta II typically bulbiform at base (figure 17F), smooth and relatively short, located at inner distal corner; seta III long and smooth, displaced to dorsal surface. Distal margin of ramus with three setae; setae IV and V well developed; unipinnate seta V about three times longer than smooth seta IV (figure 13A); seta VI short and smooth, fused at base to seta V; seta VII plumose, short, bi-articulate at base, displaced to distal inner margin.

Variability: considerable variability was noticed in the shape of seta II on the caudal rami, ranging from distinctly bulbiform (figure 17F; the typical condition observed in the majority of specimens), over slightly swollen (figure 17D, E) to long and slender (figures 14B, 17C).

Male (figures 12C, D, 21A–D). Length 750–980 μm ($N=10$, mean = 794 μm). Sexual dimorphism in antennule, P4, abdomen and caudal ramus.

Antennule (figure 12C, D): precise segmentation hard to discern but presumably four-segmented, with geniculation between segments 3 and 4. First segment very large; with two sutures around posterior margin, possibly indicating ancestral segmentation; armature as in *S. geei*. Segment 2 short, with at least three sutures around the posterior margin; armature as in *S. geei*. Segment 3 large and swollen, distal posterior corner produced into spinous process; with very long plumose seta around mid-point of anterior margin, and seven additional setae (five pinnate, two smooth); distal anterior margin forming concavity for geniculating terminal segment, with striated zone (arrowed in figure 12D). Segment 4 small; produced into lobate process, with seven smooth setae.

P4 (figure 21D): innermost spinous process on distal margin of exp-3 much smaller than in ♀.

Urosome (figure 21A) consisting of P5-bearing somite, genital somite and four postgenital somites. Genital somite largest, without lateral spinous extensions. First abdominal somite with mid-ventral patch of fine spinules (figure 21B). Genital apertures closed off by modified sixth legs (figure 21B). P6 fused to genital somite but original demarcation marked by membranous zone; each produced into large

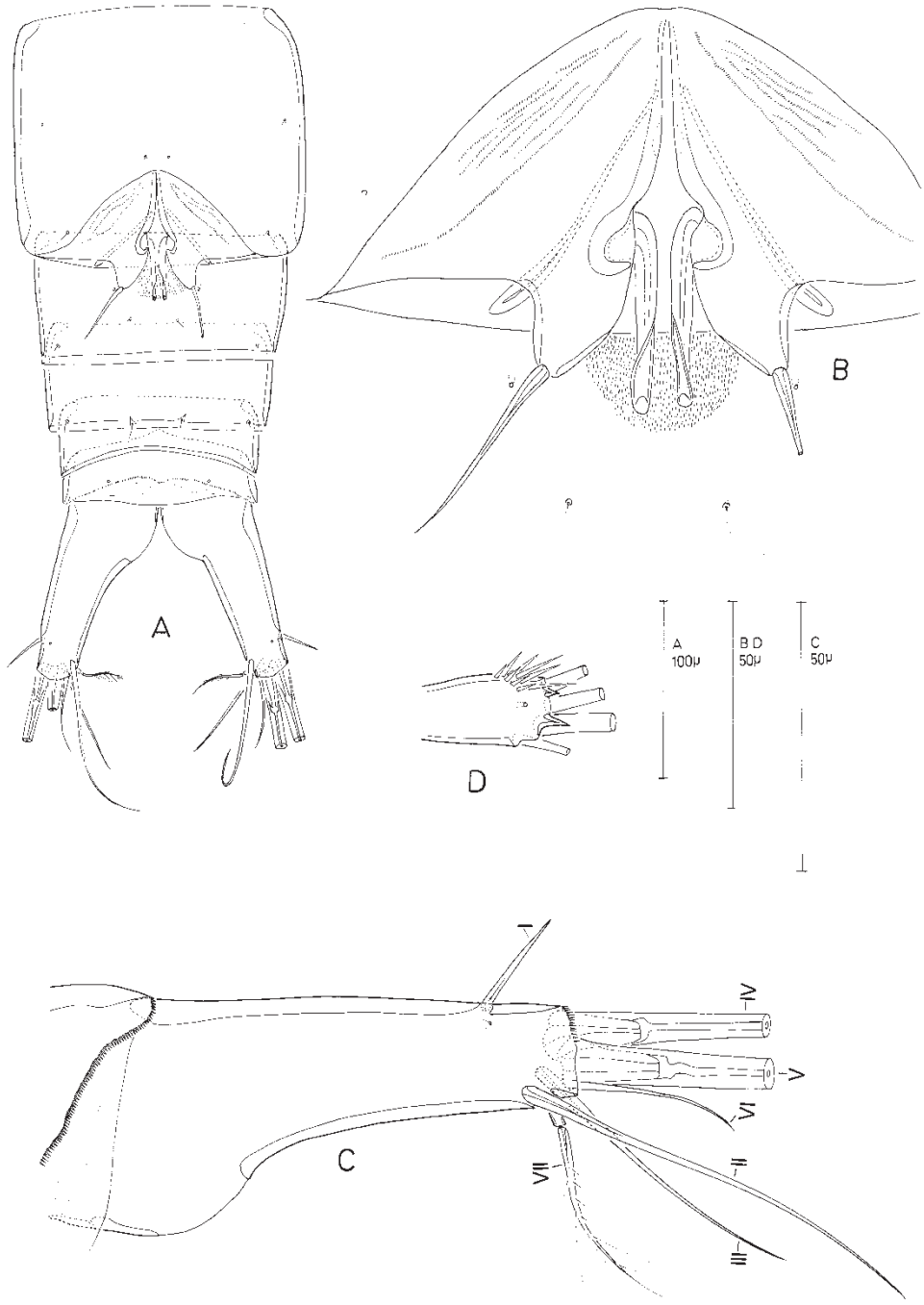

FIG. 21. *Scottolana bulbifera* (Chislenko, 1971) (♂): (A) urosome (excluding P5-bearing somite), ventral; (B) genital field, ventral; (C) left caudal ramus, ventral; (D) apical part of P4 exp-3, showing reduced inner spinous process.

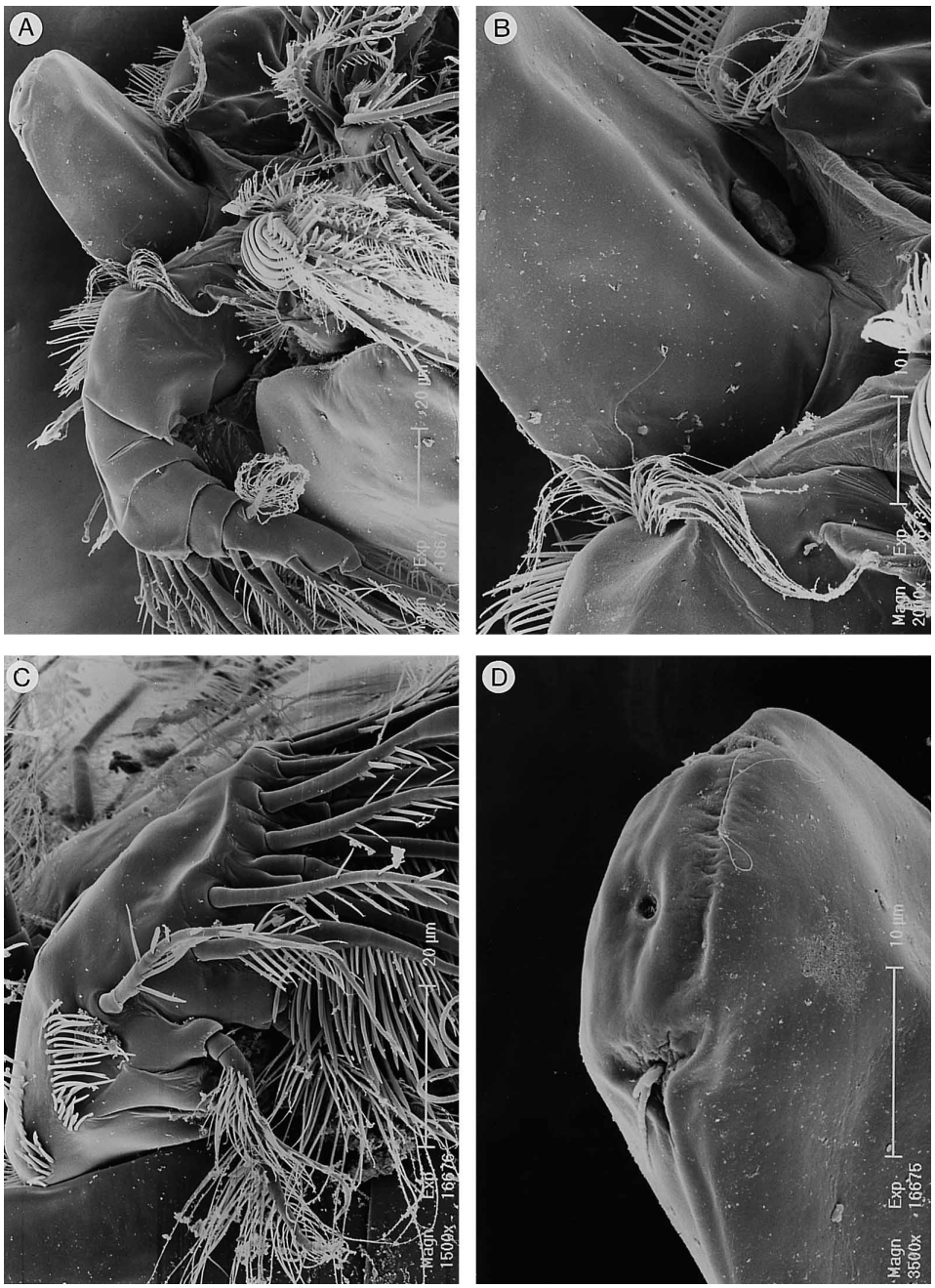

FIG. 22. *Scottolana bulbifera* (Chislenko, 1971) (♀) [SEM photographs]: (A) ventral view of cephalosome, showing rostrum, antennules and antennae; (B) base of rostrum and right antennule, ventral; (C) antennulary segment 1, dorsal; (D) rostrum, apical. Scale bars in μm.

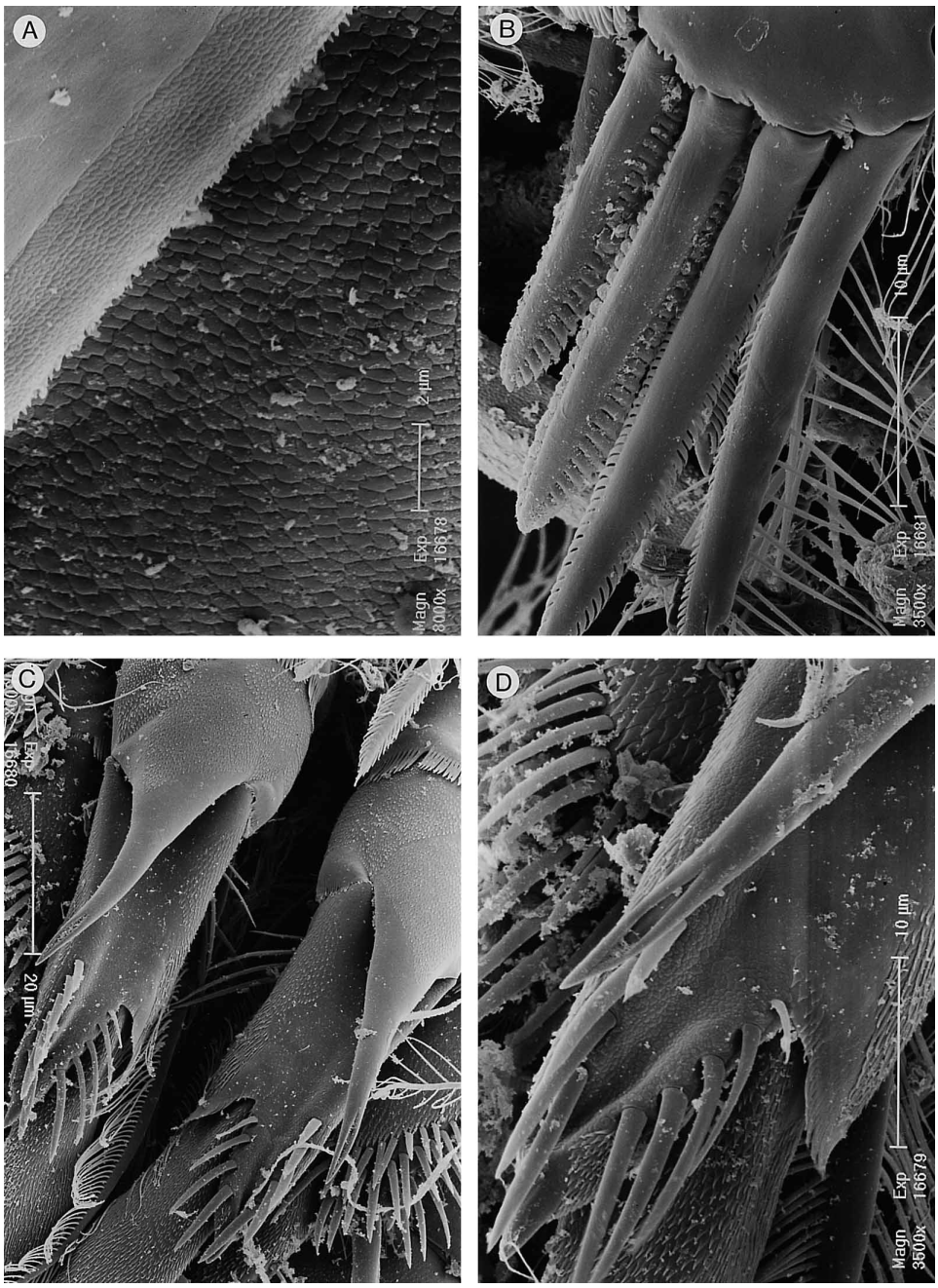

FIG. 23. *Scottolana bulbifera* (Chislenko, 1971) (♀) [SEM photographs]: (A) surface ornamentation of hind margin of cephalosome and of P2-bearing somite, dorsolateral; (B) pectinate spines of P1 exp-3; (C) P2 endopod, anterior; (D) P2, detail of spinous process arising from enp-1 and spinule-flanked furrow on enp-2. Scale bars in μm.

triangular process bearing naked seta at apex; additional element arising from around mid-point of inner margin of P6, articulated at base (just extending beyond distal margin of P6), distal half twisted with ventrally recurved blunt apex.

Caudal rami (figure 21C) as in ♀ except for (1) seta I being more slender, straight and spiniform, and positioned at outer margin, and (2) seta II not modified, being long and slender.

Discussion

Both *S. geei* and *S. bulbifera* are assigned to the genus *Scottolana* which was redefined by Por (1984) on the basis of the following combination of characters: (1) first pedigerous somite not fused to cephalosome; (2) large eight-segmented antennary exopod; (3) P1–P4 exp-3 with 7, 7, 5, 4 spines/setae, respectively; (4) P1–P4 enp-3 with 6, 5, 4, 4 spines/setae, respectively; (5) the shape and orientation of the P4 exopod; and (6) the morphology of the male genital field which Por (1984) considered to be 'primitive'. However, both species differ radically in body segmentation, rostrum shape, morphology of P1 and P4, swimming leg and caudal ramus sexual dimorphism and the structure of the genital field in both sexes. This suite of significant differences in conjunction with the vague diagnosis proposed by Por (1984) (only the outwardly directed P4 exopod and the presence of four elements on its distal segment can be regarded as apomorphic) strongly suggests that the genus *Scottolana* currently accommodates different evolutionary lineages. Pending a forthcoming revision and phylogenetic analysis of *Scottolana* we have retained both species in the genus and restricted the discussion to a comparison with their respective congeners.

S. geei belongs to a lineage which includes *S. longipes* (Thompson and A. Scott, 1903) described from the Gulf of Manaar (Sri Lanka), *S. longipes* (Thompson and A. Scott, 1903) *sensu* Por (1964) from the mediterranean coast of Israel, *S. longipes* (Thompson and A. Scott, 1903) *sensu* Wells (1967) from Inhaca Island (Mozambique), *S. dissimilis* Fiers, 1982 from Papua New Guinea, *S. uxoris* Por, 1983 from the Gulf of Elat and *S. longipes* (Thompson and A. Scott, 1903) *sensu* Wells and Rao (1987) from the Andaman Islands. These species, called hereafter the *longipes*-group, form a monophyletic lineage characterized by the following apomorphies: (1) urosome with only two postgenital somites in ♀ and three in ♂, resulting from failure of separation of the anal somite at the final moult (figures 1A, B, 10A); (2) modified P4 in both sexes, involving outward displacement of exopod, secondary elongation of endopod and elongation of various armature elements such as the outer spine on exp-2 and the inner seta on enp-1 (figure 9); (3) P3 enp-3 with modified tube-pore along inner margin in ♂ (figure 10E); (4) bases of P2–P4 with recurved spinous process on posterior surface; (5) caudal ramus with hook-like extension along anterior inner margin and spinular patch near distal outer corner (figure 2D); (6) caudal ramus sexual dimorphism involving modification of seta II in ♀ (but not of seta I).

The reduction in number of urosomites is the result of progenetic development defined by the early offset of somite addition at the copepodid V stage. The progenetic urosome has remained unnoticed thus far although Por (1964, 1983) has figured it. Wells and Rao (1987) stated that the last abdominal somite was extremely reduced in their specimens of *S. longipes* and no trace of articulation with the penultimate somite could be discerned. In fact, the position of the anal operculum in their figure 11c shows that the minute last 'somite' represents the membranous areas

located around the bases of the caudal rami. It is conceivable that a similar observational error was made in Thompson and A. Scott's (1903) lateral habitus view of *S. longipes*. Fiers (1982) illustrates three postgenital somites in his habitus drawings (pl. VI, figures 2a, b) of *S. dissimilis*, however, his detailed drawings of the caudal rami (pl. VII, figures 4, 5) indicate that in reality there are only two somites posterior to the genital double-somite in the ♀ and three somites posterior to the genital somite in the ♂. Evidence for this interpretation is found in the presence of sensillae around the posterior margin of the penultimate somite in Fiers' drawings. Since this somite normally lacks sensillae in harpacticoid copepods it is assumed here that it represents the second abdominal somite and that the anal somite failed to separate at the final moult. Finally, Por (1983) illustrates three postgenital somites in the ♂ of *S. uxoris* (his figure 3) but clearly four such somites in his additional figures of the urosome (his figures 2, 4). Considering the significant differences in the shape of the genital somite and caudal rami it is highly likely that Por (1983) illustrated an amalgamate of two species.

The modified tube-pore along the inner margin of the male P3 enp-3 was described as a 'slit' with possible glandular function by Wells and Rao (1987) in their Andaman material of *S. longipes*, and its presence was confirmed by these authors in male *S. longipes* from Inhaca Island.

Two species, *S. longipes sensu* Por (1964) and *S. uxoris*, occupy an isolated position within the *longipes*-group. The former possesses a large modified spine on the proximal endopod segment of the male P4 (see also Por, 1984: figure 18) which is homologous to the inner seta on this segment in the female. This sexual dimorphism is unique within the Canuellidae and casts doubt on the assumption that the specimens from the Andaman Islands, Sri Lanka, Mozambique and the Mediterranean represent distinct geographical races of the same species (Wells, 1967; Wells and Rao, 1987). *Scottolana uxoris* differs from the other species by the structure of the male genital field, which lacks distinct spinous processes but exhibits very long plumose setae near the inner distal corners. The caudal rami in the male are also highly diagnostic by their shape and shortness, and the presence of densely ornamented setae IV–V. The presence of such modified caudal rami in the male is unusual since in Canuellidae it is the female that exhibits sexual dimorphism in these appendages. Unfortunately Por (1983) did not illustrate the female caudal ramus.

Within the *longipes*-group *S. geei* appears to be most closely related to *S. longipes sensu* Wells and Rao (1987). It differs from the latter species by (1) shape of the rostrum; (2) segmentation of antennary exopod nine-segmented (instead of eight-segmented); (3) segments of exopod and endopod in P1–P4 generally longer and more slender; (4) P2 basis with strong recurved process on posterior surface and only minute process on P4 basis (in *S. longipes* apparently absent in P2 but well developed in P4); (5) lateral projections on ♂ genital somite strongly developed (minute in *S. longipes*; not mentioned by Wells and Rao (1987) but see their figure 11b); (6) P6 ♂ with very long proximal armature elements, twisted in apical part (much shorter and straight in *S. longipes*); (7) first abdominal somite with mid-ventral nodular process bearing setules laterally and transparent lanceolate spinules medially (only spinules in *S. longipes*); (8) caudal ramus longer (at least in the ♂♂).

The discovery of a distinctly nine-segmented exopod in the antenna of *S. geei* is remarkable since the maximum number of segments recorded thus far in the Harpacticoida is eight. The apical segment is represented by a U-shaped sclerite bearing three elements and is clearly delimited at the base (figure 4C–E). Comparison

with the hypothetical ancestral pattern reconstructed by Huys and Boxshall (1991) suggests that ancestral segments IX and X are free and that ancestral segment I is either fused to segment II (and has lost its seta) or is not expressed.

Scottolana bulbifera was originally described from the Possjet Bay in the Sea of Japan (Chislenko, 1971). Our material from the Bohai Sea, a semi-closed extension of the Yellow Sea, agrees with Chislenko's description in most aspects. The type material of *S. bulbifera*, consisting exclusively of slide preparations deposited in the Zoological Institute of St Peterburg, is in a bad condition (T. Agapova, personal communication) and unavailable for study at present. Despite discrepancies in the armature of the mouthparts, P1 and P4 between Chislenko's (1971) description and our observations, we have assigned the Bohai Sea material to *S. bulbifera*. According to Chislenko there is no inner seta on the proximal endopod segment of P1. However, in view of the remarkable conservatism in the setation of this leg in the *Canuella–Scottolana* lineage we assume that in the holotype this seta was lost prior to or during dissection. Similarly, Chislenko illustrates not four but five elements on the distal exopod segment of P4, the supernumerary element being a small spine positioned between the inner spine and the long inner distal spine. It is conceivable that Chislenko misinterpreted the spinous projection found in this position in the Bohai Sea specimens (figure 20B). Other differences in the armature of the antennule, antenna and mouthparts are likewise the result of imperfect observation.

The specific epithet *bulbifera* alludes to the bulbiform caudal ramus seta II in the female. Examination of a large number of specimens from the Bohai Sea revealed considerable variability in the shape and size of this seta, ranging from the typical female condition (figure 17F) to the typical male condition (figure 14B). The transformation of this seta during female development happens at the final moult, the copepodid V condition being identical to that in the adult male. We consider the retention of the long, unmodified seta II in some females to be the result of accidental postdisplacement whereby the modification to a bulbiform element is suppressed.

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