



On some new species of *Canuelloida* Khodami, Vaun MacArthur, Blanco-Bercial & Martínez Arbizu, 2017 (Crustacea: Copepoda) from a shallow coastal lagoon in north-western Mexico

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Abstract

Several benthic copepods were found in sediment samples taken during a short-term project on the diversity and distribution patterns of macro- and meiofauna in Ohuira Bay (northern Sinaloa state, north-western Mexico). The material turned out to belong to two new species, *Scottolana tama* sp. nov. and *Canuellina pacifica* sp. nov., and to *Longipedia corteziensis* Gómez, 2001 previously known from a shallow coastal lagoon not far from Ohuira Bay. New groupings of the species of *Scottolana* Huys, 2009 and *Canuellina* Gurney, 1927 are proposed and the description of the new species is provided. Additionally, the distribution patterns of *S. tama* sp. nov., *C. pacifica* sp. nov., and *L. corteziensis* in Ohuira Bay are discussed.

Key words: *Canuellina*, diversity, *Longipedia*, new records, Polyarthra, *Scottolana*

Introduction

Ohuira Bay, located in the northern part of Sinaloa state in north-western Mexico, is part of the Santa María-Topolobampo-Ohuira lagoon system. This area has been designated as an UNESCO Biosphere Reserve, RAMSAR, and World Heritage site (RAMSAR 2024). Its ecological significance can be attributed to the presence of mangrove wetlands, which serve as habitat for most migratory waterfowl in Mexico and is considered a priority hydrological basin (Arriaga *et al.* 2002). The main economic activities in the area are associated with the Topolobampo harbour, including shrimp and fishing. Significant amounts of wastewater, especially from agricultural runoffs and aquaculture, and from a thermal power station, are discharged into the coastal zone, potentially threatening water quality (RAMSAR 2024).

Recently, an ammonia production plant project promoted by the government has evidenced that current knowledge regarding benthic invertebrates in the Ohuira Bay is scarce (Páez-Osuna *et al.* 2018). Benthic assemblages are known to be sensitive to human impacts and are important components of international monitoring programs (Warwick 1993; European Commission 2003). Thus, understanding the consequences of effluents associated with the ammonia production plant requires a better knowledge of the benthic assemblages. During a short-term project in Ohuira Bay to characterise the diversity and distribution patterns of macro- and meiofauna, sediment samples were collected, and previously unreported benthic copepods were discovered.

The macrofauna fraction contained 203 large copepods that turned out to belong to three genera of *Canuelloida* Khodami, Vaun MacArthur, Blanco-Bercial & Martínez Arbizu, 2017: *Scottolana* Huys, 2009, *Canuellina* Gurney, 1927, and *Longipedia* Claus, 1862. The specimens of *Longipedia* were identified as *L. corteziensis* Gómez, 2001

reported earlier from a coastal lagoon in central Sinaloa state, not far from Ohuira Bay. The specimens attributed to *Scottolana* were identified as representatives of a new species, *S. tama* **sp. nov.**, closely related to *S. antillensis* (Fiers, 1984) from Jamaica. The material of *Canuellina* showed to be closely related to *C. secunda* (Coull, 1971) known from several sites in the Gulf of Mexico and Caribbean Sea, and was determined as a new species, *C. pacifica* **sp. nov.** The full descriptions of *S. tama* **sp. nov.** and *C. pacifica* **sp. nov.** are provided. Additionally, new groupings of *Scottolana* and *Canuellina* species are proposed. Finally, the distribution patterns of *S. tama* **sp. nov.**, *C. pacifica* **sp. nov.**, and *L. corteziensis* in Ohuira Bay are described and discussed.

Material and methods

Field and laboratory work

The study was carried out at 11 stations along Ohuira Bay (Fig. 1) during the drought season (February 2023) and at the beginning of the rainy season (June 2023). Sediment samples were taken with an Eckman grab (sampling area 625 cm²) and triplicate sediment cores were taken from each sample using 20-cm-long acrylic corers of 5.6 cm inner diameter (sampling area 24.63 cm²). The surface 3-cm layer of each sample was retrieved and fixed in 96% ethanol. Macro- and meiofauna were separated with 500 and 38 µm sieves. Macrofauna was sorted out using a Leica S6E stereomicroscope. Copepods reported here were found in the 500-µm sieve and were stored separately in 1 ml vials with 96% ethanol. Their dissected parts were mounted on separate slides using lactophenol as mounting medium. Illustrations and figures were made from whole individuals and their dissected parts using a Leica DMLB microscope equipped with L PLAN 10× eyepieces, N PLAN 100× oil immersion objective, drawing tube, and a Leica DMC2900 digital camera with which microphotographs were taken. Microphotographs were edited with Adobe Photoshop ver. 25.11.0. Huys and Boxshall (1991) was followed for general terminology. Abbreviations used in the text are: ENP = endopod; EXP = exopod; EXP (ENP)1 (2, 3...) = first (second, third...) exopodal (endopodal) segment; P1–P6= first to sixth legs.

The type material was deposited in the Copepoda collection of the Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán (ICML-EMUCOP).

Ecology and distribution

The following environmental variables were measured at each station: water temperature, dissolved oxygen (DO), salinity, and specific conductance. These measurements were taken directly 30 cm above the bottom using a YSI PRO2030 multiparameter probe. Additionally, a sediment core was taken at each station to determine grain size distribution using a Malvern Mastersizer 2000E particle size analyser, and organic carbon (C_{org}) content through the chromic acid titration method of Walkley & Black (1934) as modified by El-Rayis (1985).

The mean density of copepods by station was calculated as the average over the three cores and expressed as the number of individuals per 10 cm² of the bottom surface. Comparisons between the densities of *S. tama* **sp. nov.** and *L. corteziensis* in February and June were evaluated with a paired-sample Wilcoxon test in the RStudio environment 2022.12.0 (R Core Team 2024). *Canuellina pacifica* **sp. nov.** was excluded from the quantitative analysis due to its low abundance values. The Wilcoxon test was also used to evaluate seasonal environmental variations in bottom water and sediment. We used generalised linear mixed models with a Poisson distribution and log link function (Zuur *et al.* 2015) to determine the environmental variables that best explain the species distribution. Akaike's information criterion was used to determine the best model.

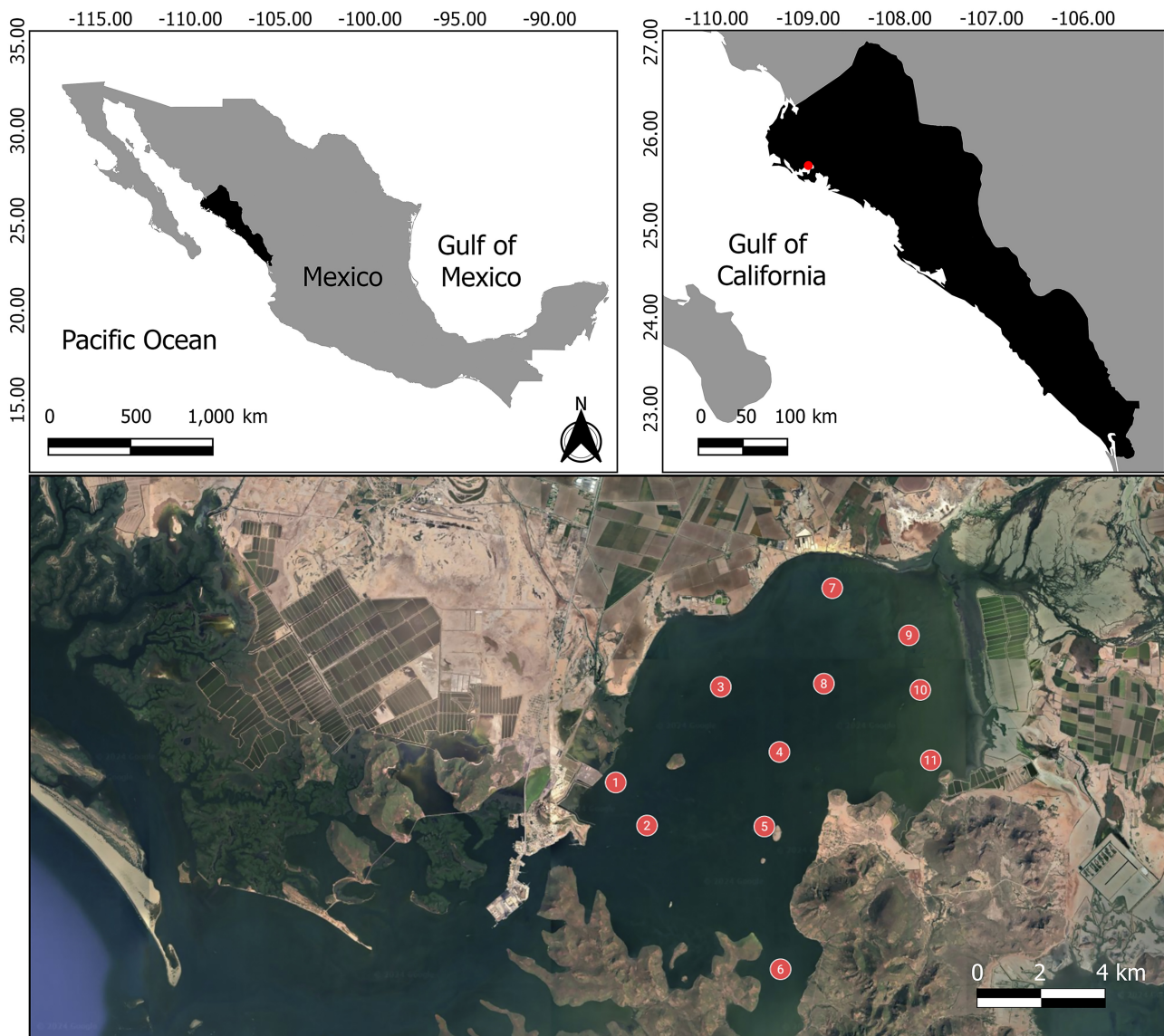


FIGURE 1. Station locations in Ohuirá Bay. Image download from Google Earth on 10/3/2023.

Results

Systematics

Order Canuelloida Khodami, Vaun MacArthur, Blanco-Bercial & Martínez Arbizu, 2017

Family Canuellidae Lang, 1944

Genus *Scottolana* Huys, 2009

Type species: *Scottolana geei* (Mu & Huys, 2004).

Other species: *Scottolana antillensis* (Fiers, 1984); *S. brevifurca* (Wells, 1967); *S. bulbifera* (Chislenko, 1971); *S. bulbosa* (Por, 1964); *S. daecheonensis* Bang, Moon & Back, 2022; *S. dissimilis* (Fiers, 1982); *S. glabra* (Fiers, 1982); *S. gomezi* Nazari, Mirshamsi, Sari, Aliabadian & Martínez Arbizu, 2018; *S. huysi* Song, Kangtia, Khim & Chullasorn, 2018; *S. inopinata* (Thompson I. C. & Scott A., 1903); *S. jasani* Song, Kangtia, Khim & Chullasorn,

2018; *S. longipes* (Thompson I. C. & Scott A., 1903); *S. oleosa* (Wells & Rao, 1987); *S. rostrata* (Wells & Rao, 1987); *S. scotti* (Sewell, 1940); *S. tama* sp. nov.; *S. tumidisetia* (Wells & Rao, 1987); *S. uxoris* (Por, 1983); *S. wonchoeli* Bang, Moon & Back, 2022.

***Scottolana tama* sp. nov.**

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(Figs. 2–11)

Material examined. Ovigerous ♀ holotype preserved in alcohol (ICML-EMUCOP-020223-01), ♂ allotype preserved in alcohol (ICML-EMUCOP-020223-02), three ♀ paratypes dissected and mounted on six, 14, and eight slides (ICML-EMUCOP-020223-03–05), one ♂ paratype dissected and mounted on seven slides (ICML-EMUCOP-020223-06), five ♀, one ♂ CV, and three ♀ paratypes (ICML-EMUCOP-020223-07), and two ♀ paratypes (ICML-EMUCOP-020223-08) preserved in alcohol; holotype, allotype and paratypes ICML-EMUCOP-020223-05–07 from the type locality (stn 8, see below), paratype ICML-EMUCOP-020223-08 from stn 7 (see below); February 2, 2023; Leonardo García-Vázquez leg.

Type locality. North-western Mexico, northern Sinaloa state, Ohuira Bay, stn 8 (25.64°N, 108.96°W), sand 57.26%, silt 25.67%, clay 17.08%, C_{org} 2.84%.

Other sites. North-western Mexico, northern Sinaloa state, Ohuira Bay, stn 7 (25.66°N, 108.96°W; sand 16.23%, silt 59.54%, clay 24.22%, C_{org} 2.24%); Ensenada del Pabellón lagoon, stn 4 (24.48°N, 107.65°W) [see Gómez Noguera & Hendrickx (1997)], clayish sediment, C_{org} 1.29 $\mu\text{mol g}^{-1}$.

Additional material preserved in alcohol. North-western Mexico, northern Sinaloa state, Ohuira Bay: one CIII (ICML-EMUCOP-020223-09; stn 1; 25.61°N, 109.03°W; sand 67.07%, silt 23.79%, clay 9.14%, C_{org} 1.07%), one ♀, one ♀ and one CV, and three ♀ and one ♂ (ICML-EMUCOP-020223-10–12; stn 2; 25.6°N, 109.02°W; sand 92.22%, silt 6.03%, clay 1.86%, C_{org} 0.37%), three ♀, and three ♀ (ICML-EMUCOP-020223-13–14; stn 4; 25.62°N, 108.98°W; sand 16.52%, silt 53.61%, clay 29.87%, C_{org} 3.36%), one ♀, and two ♀ (ICML-EMUCOP-020223-15–16; stn 5; 25.6°N, 108.98°W; sand 47.88%, silt 37.99%, clay 14.12%, C_{org} 2.19%), one ♀ and one ♂, and one ♀ (ICML-EMUCOP-020223-17–18; stn 6; 25.56°N, 108.98°W; sand 27.34%, silt 49.06%, clay 23.60%, C_{org} 2.37%), three ♀, and five ♀ and one ♂ (ICML-EMUCOP-020223-19–20; stn 7; 25.66°N, 108.96°W; sand 16.23%, silt 59.54%, clay 24.22%, C_{org} 2.24%), and three ♀, one ♂, and one CV (ICML-EMUCOP-020223-21; stn 8; 25.64°N, 108.96°W; sand 57.26%, silt 25.67%, clay 17.08%, C_{org} 2.84), collected in February, 2023; six ♀, two ♂, and two CV, and seven ♀ (ICML-EMUCOP-020623-05–06; stn 1; 25.61°N, 109.03°W; sand 71.68%, silt 21.48%, clay 6.84%, C_{org} 0.93%), two ♀, and three ♀ (ICML-EMUCOP-020623-07–08; stn 3; 25.64°N, 109.0°W; sand 41.93%, silt 40.88%, clay 17.19%, C_{org} 1.49%), three ♀ and one ♂ (ICML-EMUCOP-020623-09; stn 4; 25.62°N, 108.98°W; sand 20.77%, silt 53.54%, clay 25.68%, C_{org} 2.89%), one ♀ (ICML-EMUCOP-020623-10; stn 5; 25.6°N, 108.98°W; sand 30.62%, silt 52.75%, clay 16.62%, C_{org} 1.67%), one ♀, and two ♀ (ICML-EMUCOP-020623-11–12; stn 6; 25.56°N, 108.98°W; sand 15.37%, silt 58.58%, clay 26.06%, C_{org} 2.58%), three ♀ (ICML-EMUCOP-020623-13; stn 8; 25.64°N, 108.96°W; sand 41.42%, silt 38.45%, clay 20.12%, C_{org} 2.48%); June 2 2023; Leonardo García-Vázquez leg.

Additional material dissected. North-western Mexico, central Sinaloa state, Ensenada del Pabellón lagoon: one ♀ (ICML-EMUCOP-010591-64) mounted on four slides; May 5, 1991 (see above for some environmental variables).

Etymology. The species is dedicated to the fond memory of our friend and colleague Sergio “Tama” Rendón Rodríguez† (Instituto de Ciencias del Mar y Limnología).

Differential diagnosis. Canuellidae. Caudal rami with seven setae arising (sub)distally of which one inner element (seta II) transformed into a strong spine with a conspicuous setule-like structure (tube-pore?). Antennule seemingly six-segmented, with second to fifth segments imperfectly separated. Antenna with eight-segmented exopod, and three-segmented endopod; EXP1–7 with one, EXP8 with four setae; ENP1 with two, ENP2 with four, ENP3 with seven elements. Mandibular EXP three-segmented, EXP1 with two, EXP2 with one, EXP3 with three elements; ENP two-segmented, ENP1 with three, ENP2 with eight setae. Maxillary EXP one-segmented, with 11 setae. Maxillary ENP two-segmented. Maxilliped phyllopodial; syncoxa with one praecoxal seta, and three coxal endites bearing two, four and two setae, respectively; basis with two, ENP with 11 setae. Male P6 a triangular plate with one distal smooth seta, and genital area with two slender long elements with clawed distal part.

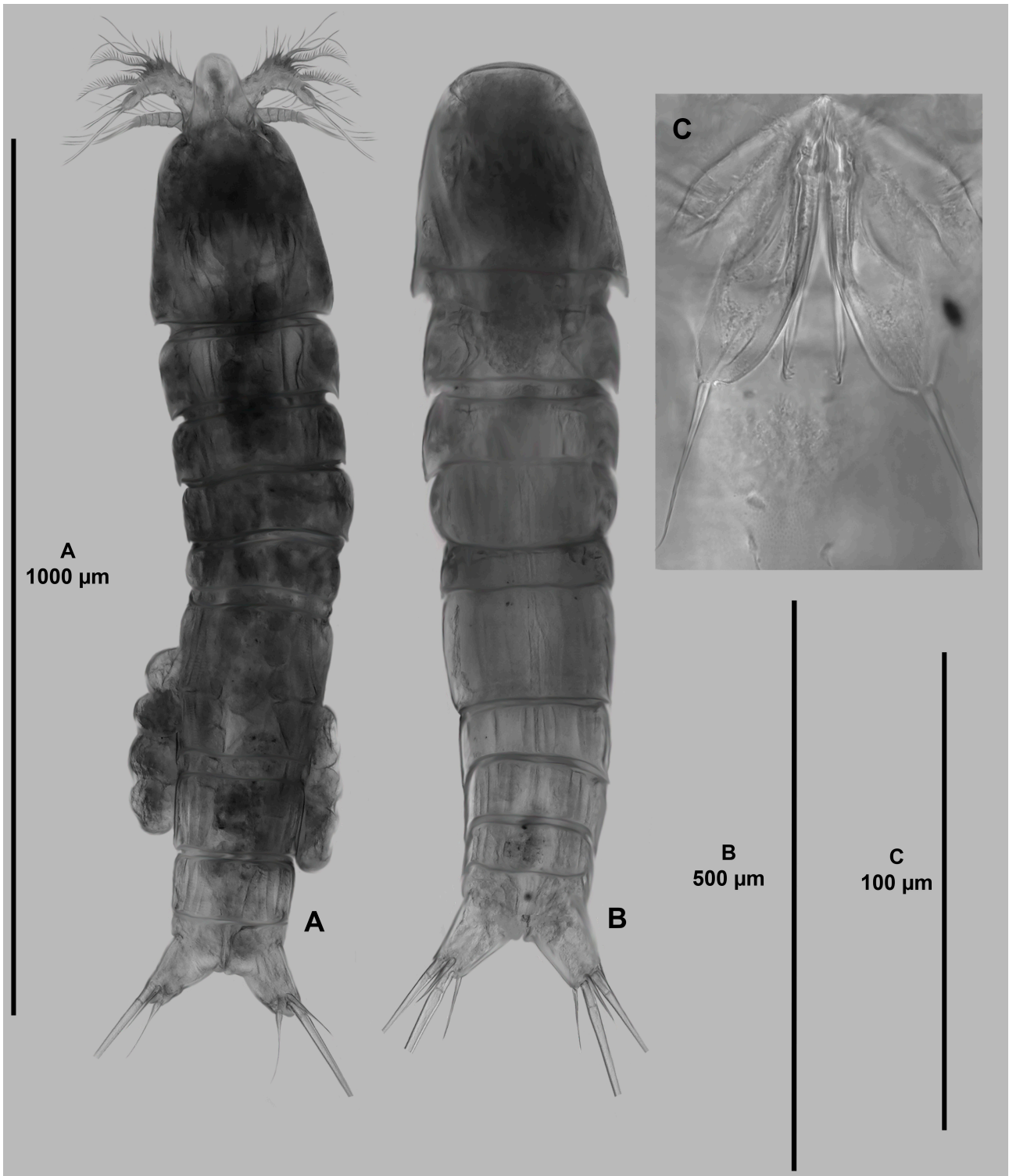


FIGURE 2. *Scottolana tama* sp. nov. A, female, habitus, dorsal, microphotograph; B, male, habitus, dorsal, microphotograph; C, male P5, microphotograph.

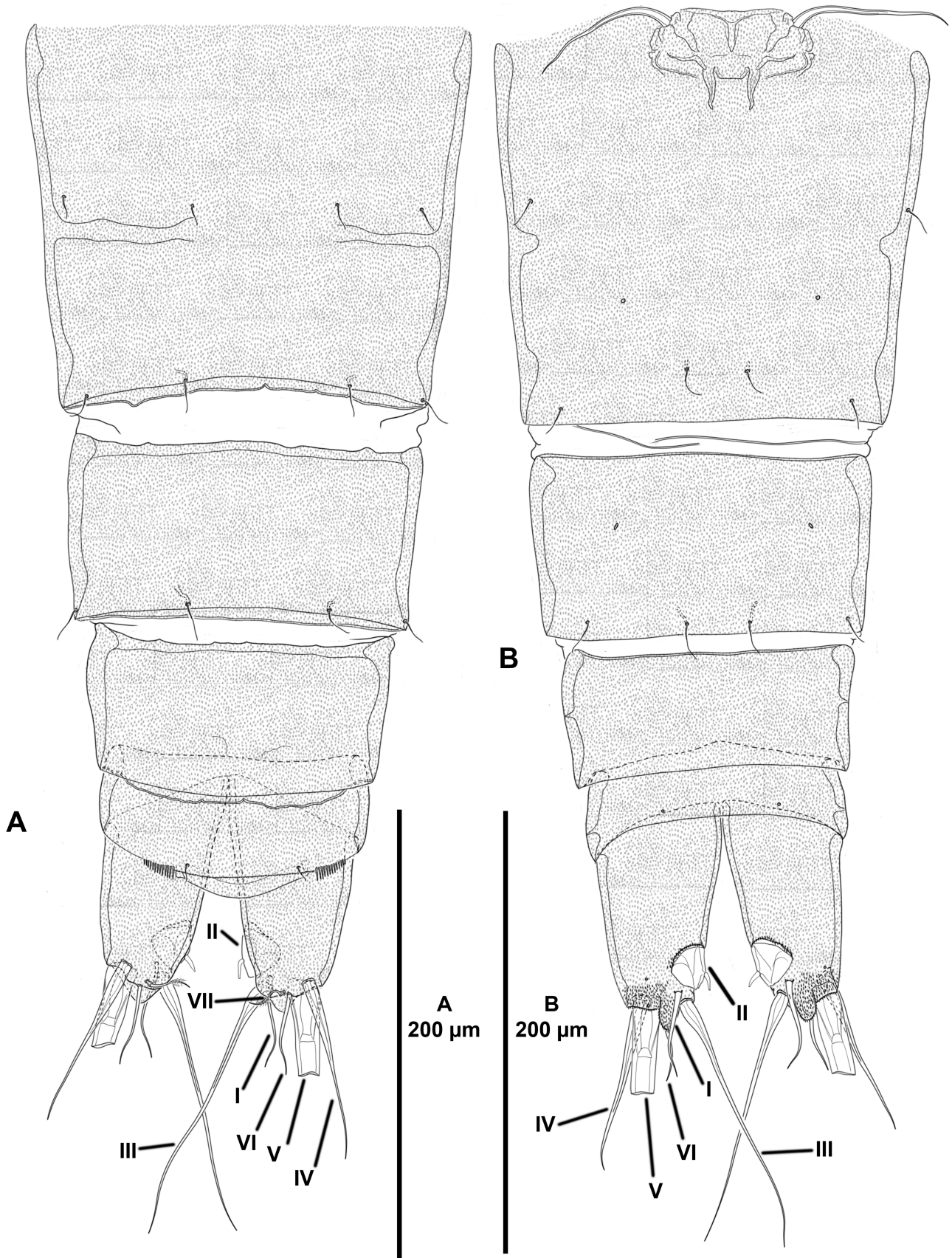


FIGURE 3. *Scottolana tama* sp. nov., female. A, urosome, dorsal (P5-bearing somite omitted), with caudal setae indicated with Roman numerals; B, urosome, ventral (P5-bearing somite omitted), with caudal setae indicated with Roman numerals.

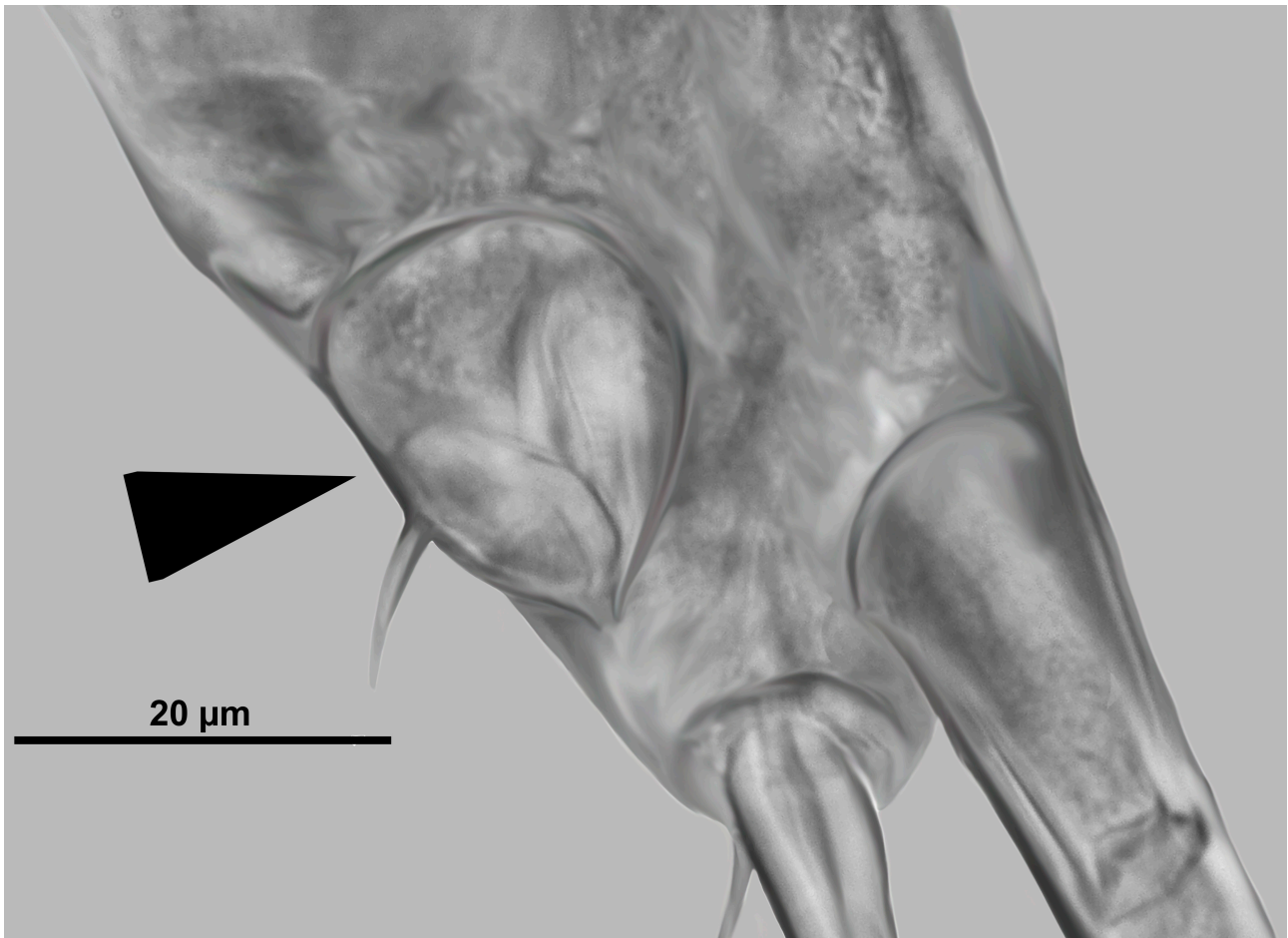


FIGURE 4. *Scottolana tama* sp. nov., female. Distal part of caudal rami, with arrowhead indicating modified caudal seta II, microphotograph.

Description of female. Habitus (Fig. 2A) semicylindrical; total body length measured from anterior tip of rostrum to posterior margin of caudal rami ranging from 860 μm to 1100 μm (mean= 1008.8 μm ; n= 8), with maximum width at the posterior margin of cephalosome. General body shape largely as in *S. antillensis*. Rostrum (Fig. 5E) not fused to cephalosome; large, triangular, with rounded tip; with one subapical sensilla on each side; no pore detected. First pedigerous somite free; first to fourth pedigerous somites of about the same width, with parallel lateral margins; surface of prosomites covered with minute denticles, with smooth posterior hyaline fringes. Urosome (Figs. 2A, 3A, B) tapering posteriad, consisting of fifth pedigerous somite, genital somite and third urosomite fused dorsally and ventrally forming genital double-somite (the latter slightly longer than wide, with lateral internal cuticular band indicating former division between somites and with genital area (Fig. 3B) situated proximally in the middle of ventral surface), two free urosomites, and anal somite with rounded anal operculum and caudal rami; surface of urosomites covered with tiny denticles, with sensilla and pores as shown; hyaline posterior fringe of fifth pedigerous somite, genital double-somite, fourth and fifth urosomites plain, hyaline fringe of anal somite minutely incised and flanked by two transverse rows of spinules. Caudal rami (Fig. 3A, B) as long as fifth and anal somites combined, slightly conical, slightly tapering posteriad; inner and outer margins nearly straight; with seven setae arising (sub)distally, homology of setae difficult to determine, most probably as follows: seta I and II displaced ventrally on inner margin, the former short and slender, the latter transformed into a strong blunt spine with a conspicuous setule-like structure (tube-pore?) (Figs. 3B, 4); seta III long, displaced ventrally close to inner distal corner; seta IV dorsal to seta V, the former without, the latter with fracture plane; seta VI short and slender, close to seta V; dorsal seta VII biarticulate at base, close to inner distal corner. Female holotype with two multiseriate egg sacs with 11 eggs each.

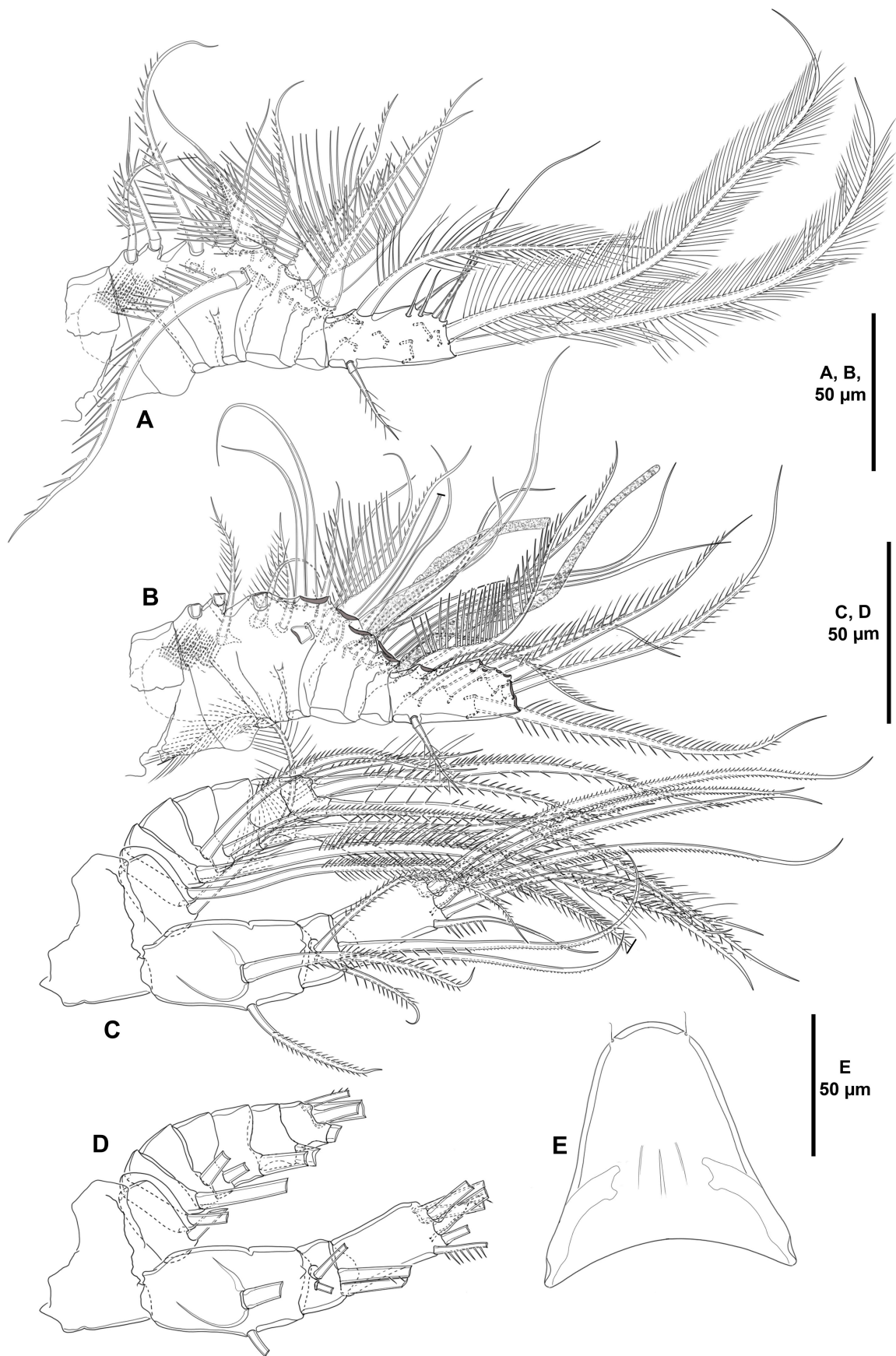


FIGURE 5. *Scottolana tama* sp. nov., female. A, antennule with anterior setae; B, antennule with posterior setae; C, antenna; D, antenna, setae omitted for clarity; E, rostrum.

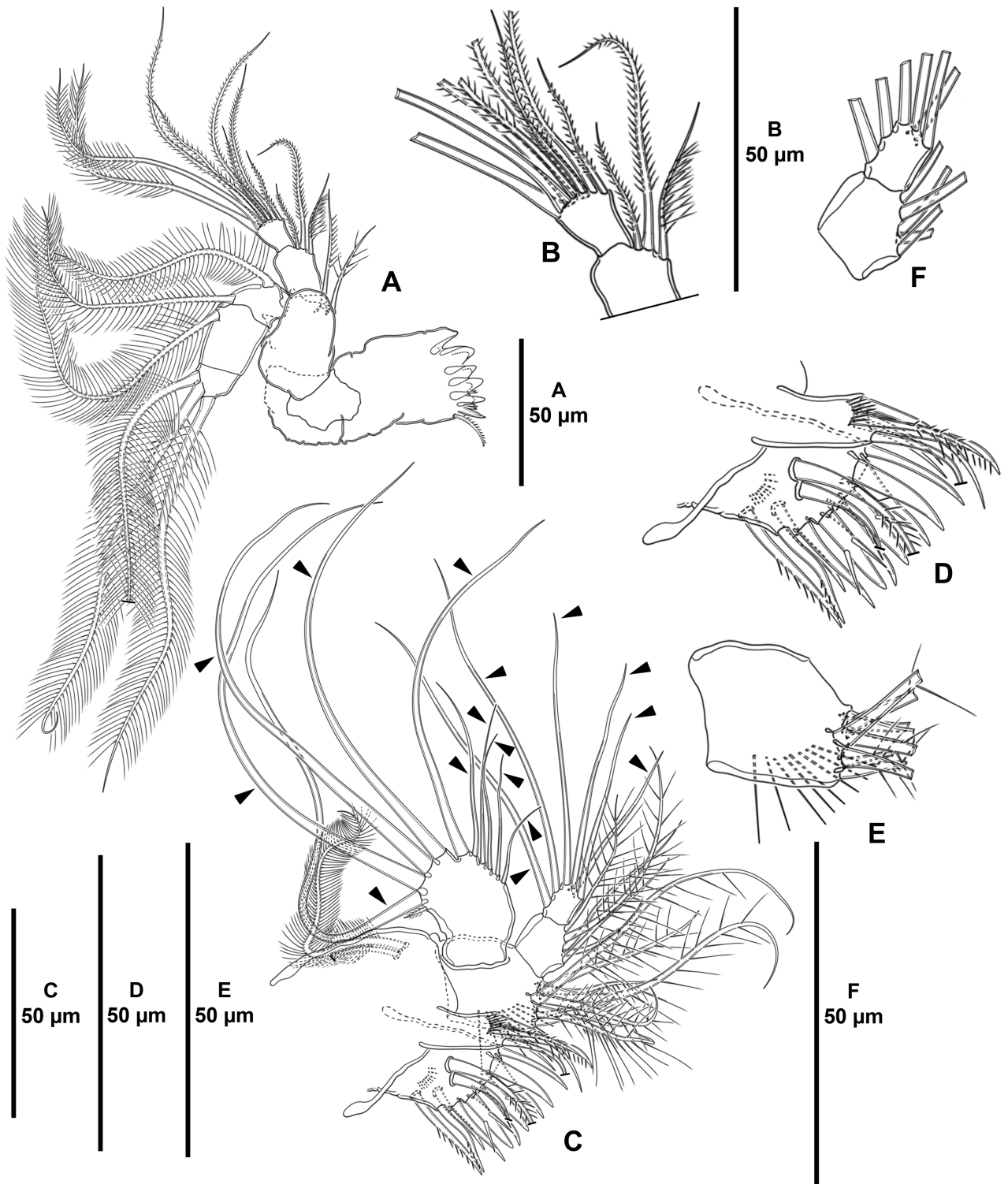


FIGURE 6. *Scottolana tama* sp. nov., female. A, mandible; B, endopod of mandible; C, maxillule, with arrowheads indicating plumose setae; D, arthrite of maxillule; E, coxal endite of maxillule; F, endopod of maxillule.

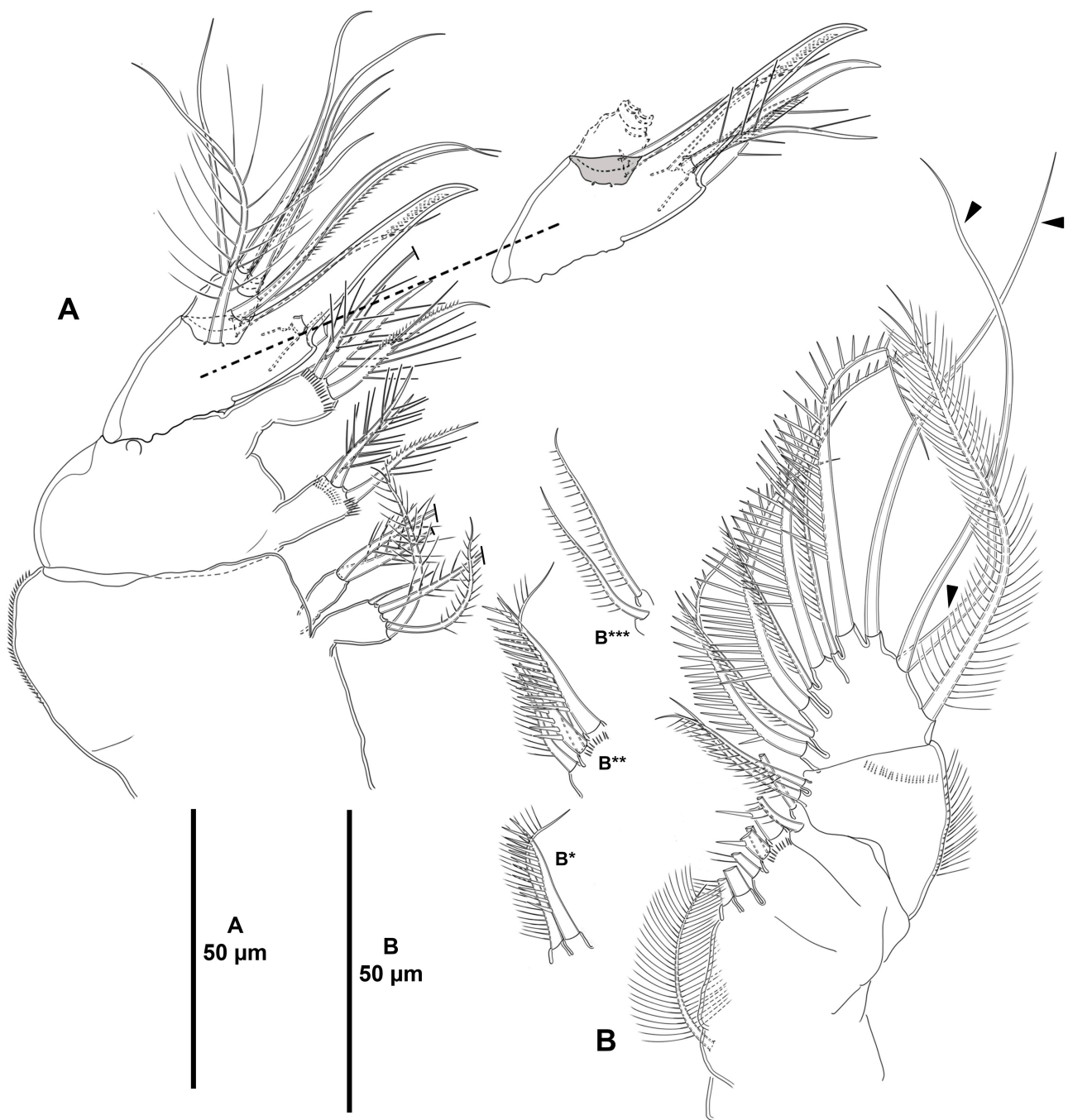


FIGURE 7. *Scottolana tama* sp. nov., female. A, maxilla; B, maxilliped, with arrowheads indicating plumose setae; B*, proximal—coxal—endite of syncoxa of maxilliped; B**, middle—coxal—endite of syncoxa of maxilliped; B***, distal—coxal—endite of syncoxa of maxilliped.

Antennule (Fig. 5A, B) presumably with six original segments. First segment unarmed, with two subdistal rows of long spinules ventrally; second to fifth segments imperfectly separated, with 28 setae in all of which eight biarticulate, and two (seemingly free) aesthetascs; sixth segment with 14 elements of which one biarticulate.

Antenna (Fig. 5C, D) biramous. Basis unornamented. Exopod relatively shorter than endopod; eight-segmented; first-seventh segments with one, eighth segment with four pinnate elements. Endopod three-segmented; first segment with two, second segment with two medial and two distal setae as figured, third segment with six pinnate well-developed setae and one small, slender, bare element.

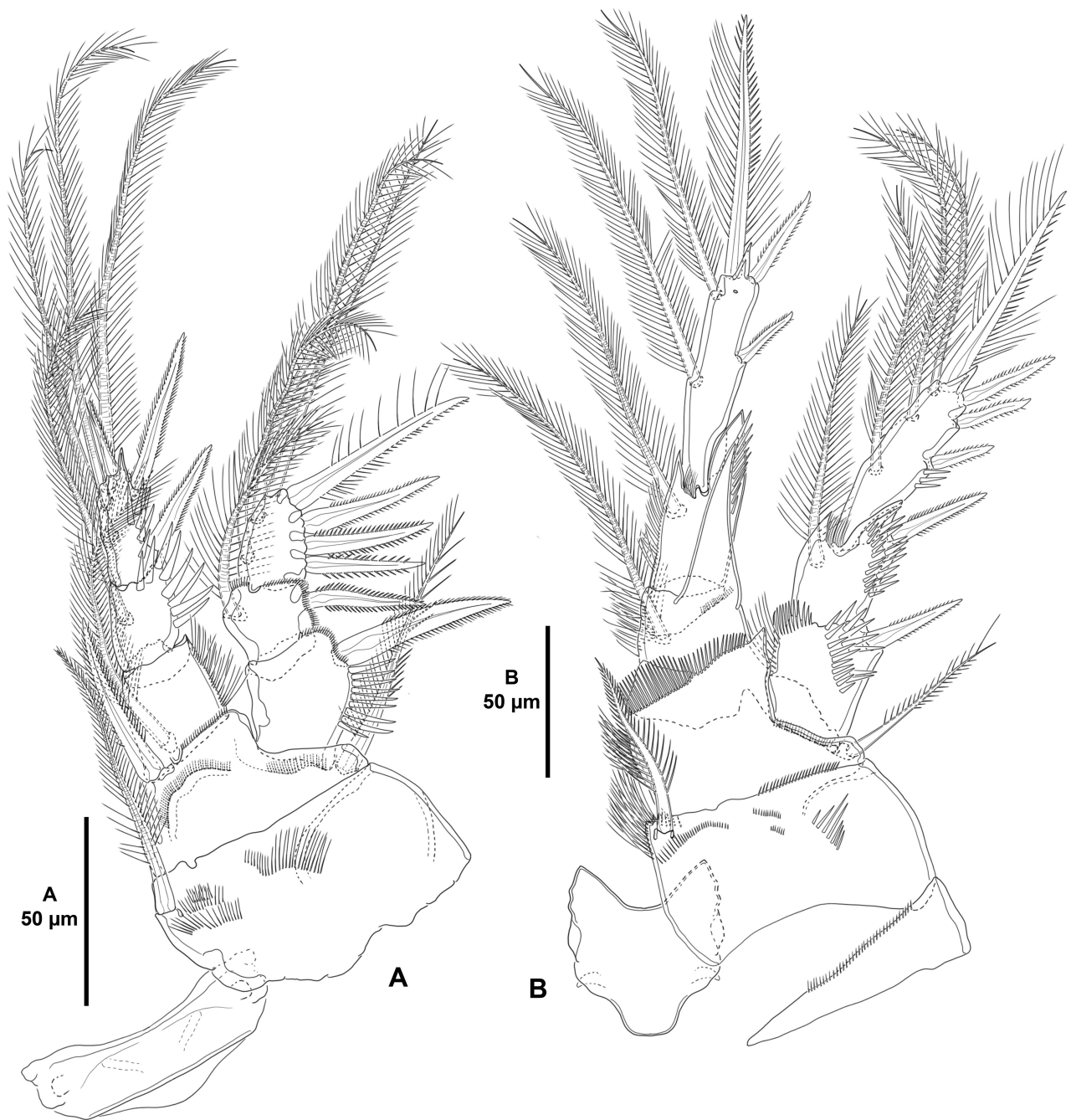


FIGURE 8. *Scottolana tama* sp. nov., female. A, P1; B, P2.

Mandible (Fig. 6A, B) with well-developed gnathobase bearing multicuspidate teeth and one pinnate seta as shown. Basis large, with two inner subdistal pinnate setae. Exopod three-segmented, bent outwards, first and third segments shortest, middle segment longest; first segment with one proximal and one subdistal seta, second segment with one proximal element, third segment with three setae; all setae plumose. Endopod two-segmented; first segment larger, with three inner subdistal setae, second segment with eight distal elements as depicted.

Maxillule (Fig. 6C–F) with praecoxa and coxa partially fused. Praecoxal arthrite with medial row of small spinules and with two surface setae, distally with eight spines and two setae as shown. Coxal endite with short row of subdistal spinules and six setae; with two long plumose epipodal setae. Basis with row of long inner spinules, seemingly with two ill-defined endites of which proximal with three, distal with five elements. Exopod large, slightly bent outwards, one-segmented; with five inner relatively short setae, five distal very long elements, and one

outer reduced seta; all elements plumose. Endopod shorter than exopod, two-segmented; first segment larger, with five inner elements as shown; second segment with six plumose setae.

Maxilla (Fig. 7A) with large praecoxa bearing two endites; proximal endite larger than distal, with three long pinnate elements and one small bare seta; distal endite with two pinnate setae. Coxa shorter than praecoxa; with two endites of which proximal somewhat shorter, each endite with subdistal small spinules and three setae as shown. Allobasis drawn out into strong unipinnate claw accompanied by five elements of which one a strong spinulose spine nearly as long as claw. Endopod two-segmented; first segment with five, third segment with four setae.

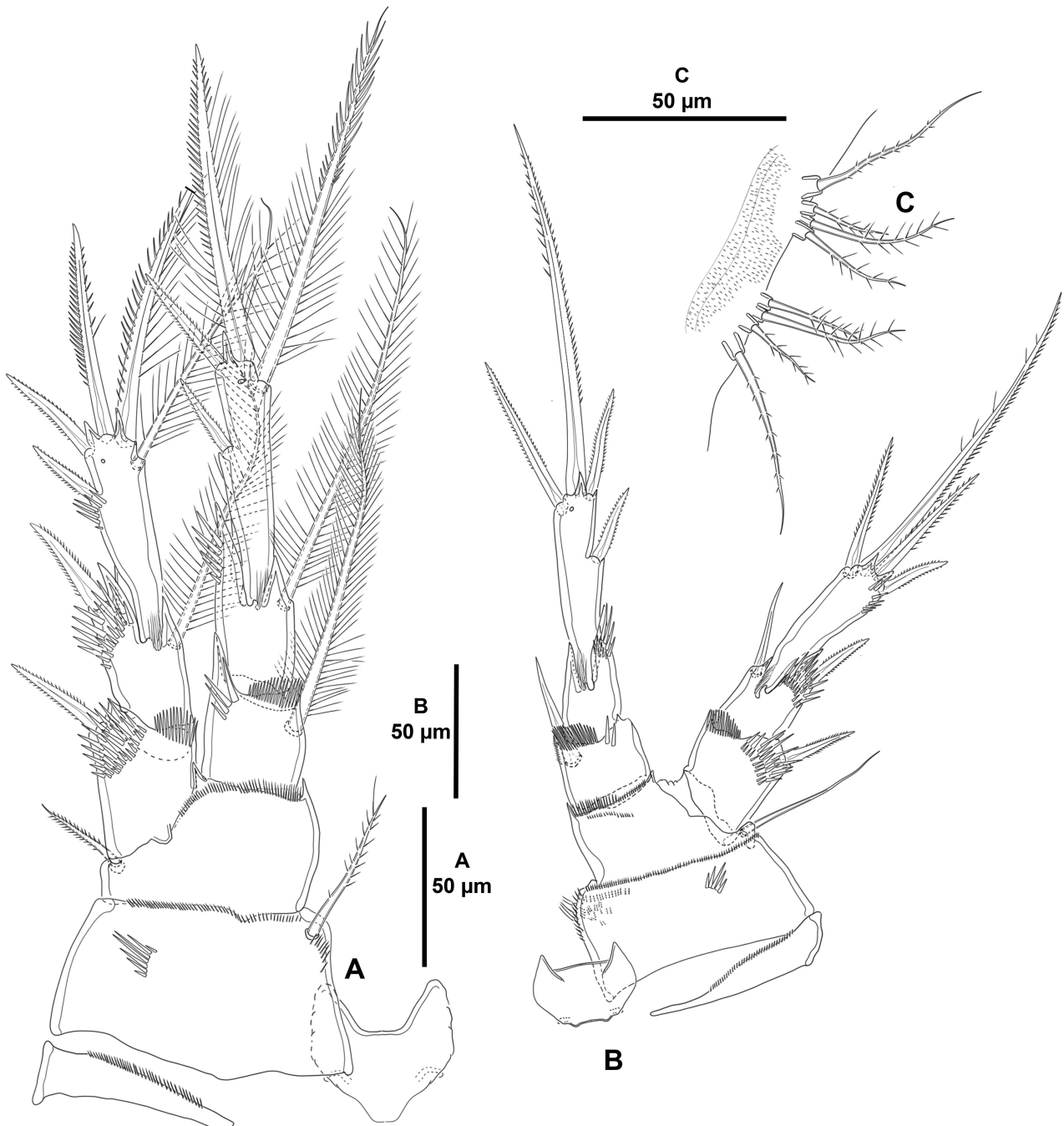


FIGURE 9. *Scottolana tama* sp. nov., female. A, P3; B, P4.

Maxilliped (Fig. 7B) phyllopodial. Praecoxa and coxa fused forming syncoxa; with one —praecoxal— proximal seta, and three —coxal— endites of which proximal with two (one unipinnate, one strongly spinulose), medial with four (two unipinnate, two strongly spinulose), distal with two unipinnate setae. Basis with slender long spinules

along outer margin and small subdistal spinular ornaments as figured, with two unipinnate setae. Endopod one-segmented, as long as basis; with 11 setae arranged as follows: innermost element strongly spinulose, three pairs composed of one inner unipinnate seta and one strongly spinulose element each, and four outer plumose elements.

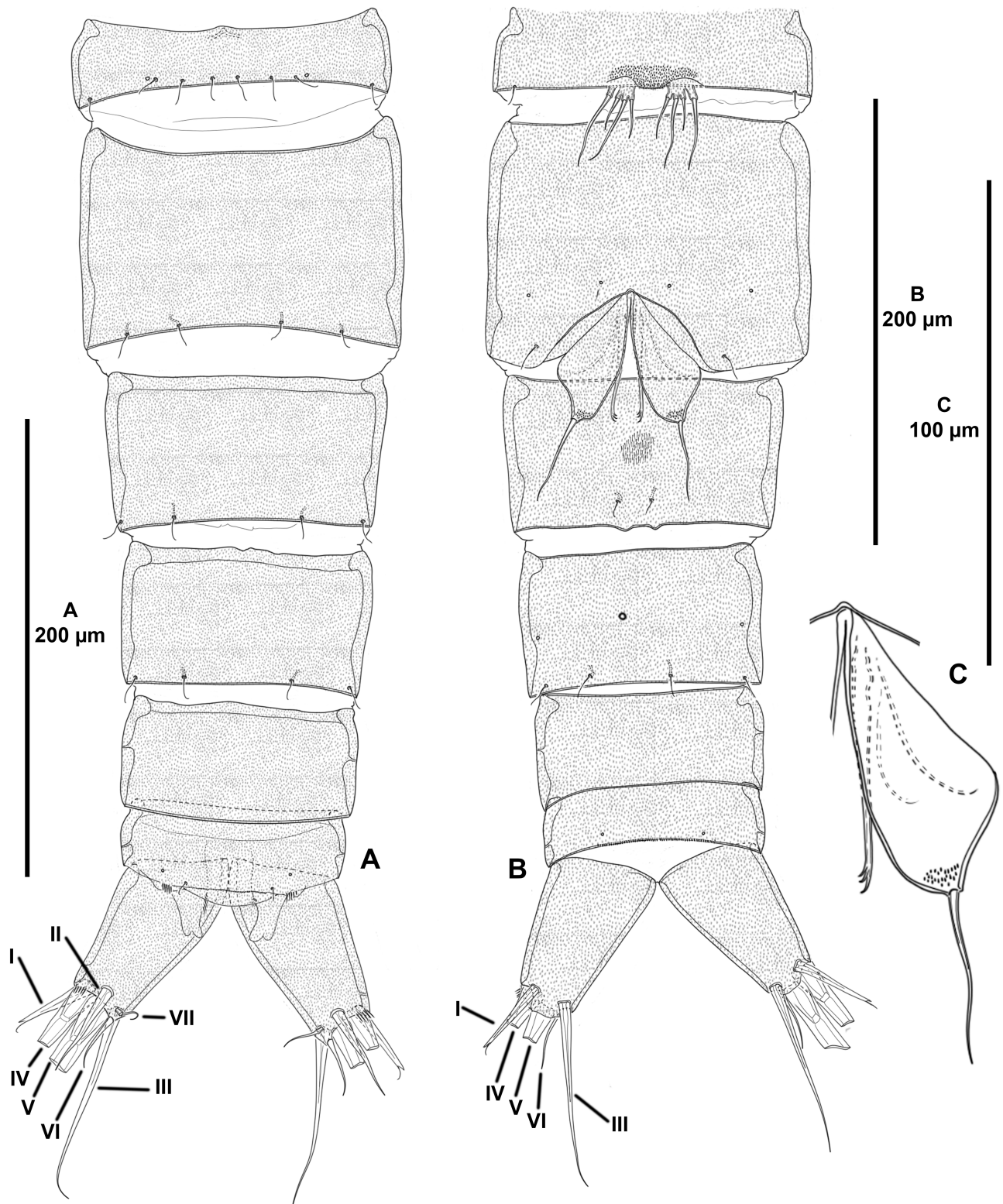


FIGURE 10. *Scottolana tama* sp. nov., male. A, urosome, dorsal, with caudal setae indicated with Roman numerals; B, urosome, ventral; C, P6.

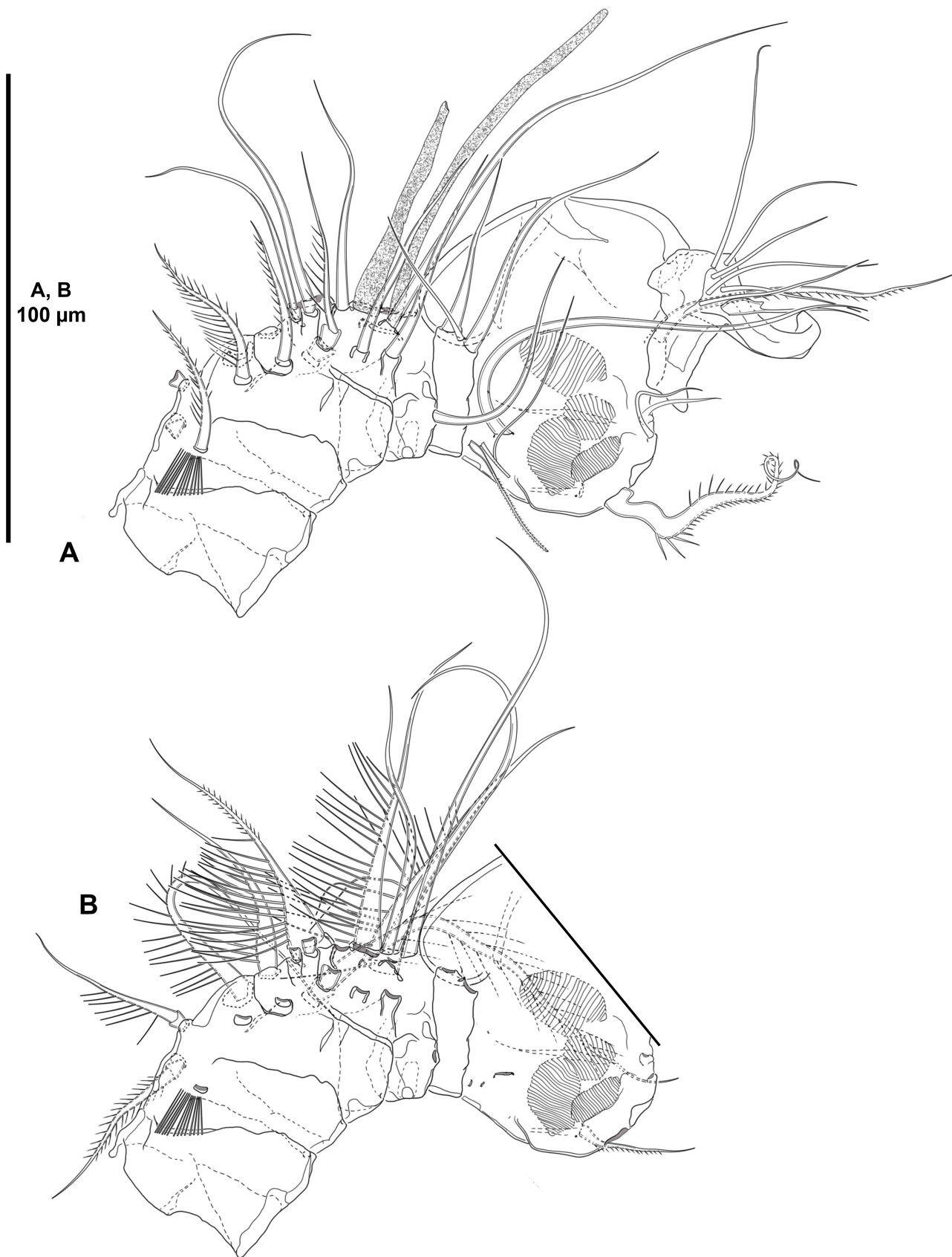


FIGURE 11. *Scottolana tama* sp. nov., male. A, antennule, with anterior setae; B, proximal segments of antennule, with posterior setae.

P1 (Fig. 8A) with intercoxal sclerite transversely elongate. Coxa and basis with spinular ornamentation as figured, the former with inner long pinnate seta, the latter with outer pinnate seta and inner pinnate spine. Exopod three-segmented of which EXP1 largest; EXP1–2 with spinular ornamentation as shown, EXP3 seemingly without spinular ornamentation; EXP1 with outer spine, without inner armature; EXP2 with outer spine and inner seta; EXP3 with three outer spines, two distal elements (one distal outer spine, one distal inner seta), and two inner setae. Endopod with three segments of similar lengths, but ENP1 larger, ENP3 reaching beyond EXP3; ENP1 with long outer setules, with one proximal inner seta; ENP2 with strong outer spinules, with one medial inner seta; ENP3 with strong outer spinules, with two outer spines, two apical elements (one distal outer flagellate short spine, one distal inner seta), and two inner setae.

P2 (Fig. 8B) with U-shaped intercoxal sclerite with two distal pointed tines. Praecoxa triangular, transversely elongate, with small spinules along distal margin. Coxa large, with spinular ornamentation as figured, with long distal inner setules, with inner pinnate seta. Basis with long inner setules, with anterior spinules close to insertion of endopod and with posterior small spinules close to insertion of exopod, with outer pinnate seta as long as EXP1 and EXP2 combined. Exopod three-segmented, as long as but inserted at a lower level than endopod so that exopod appears to be shorter than endopod; EXP1 and EXP2 subquadrate, EXP3 elongate, longest; EXP1 with patch of strong outer spinules, with longitudinal row of inner setules, and with coarsely incised distal inner hyaline frill, with outer spine, without inner armature; EXP2 with patch of strong outer spinules, with finely incised distal inner hyaline frill, with outer spine and inner seta; EXP3 with few outer spinules proximally, with three outer spines, two apical elements (one distal outer spine, one distal inner seta), and two inner setae. Endopod three-segmented; ENP1 shortest, with posterior row of minute spinules close to outer margin, with long inner setules, with distal outer long apophysis reaching beyond tip of ENP2, with inner seta; ENP2 with longitudinal row of strong spinules on distal outer long apophysis, the latter reaching proximal third of ENP3, with long inner setules, distal inner hyaline frill finely incised, with inner seta; ENP3 longest, without spinular ornamentation, with subdistal medial pore, with one outer spine, two distal elements (one distal outer spine, one distal inner spiniform element), and two inner setae.

P3 (Fig. 9A) with intercoxal sclerite, praecoxa and coxa largely as in P2, the latter with inner pinnate seta. Basis with transverse row of small spinules close to insertion of endopod, outer seta visibly shorter than EXP1. Exopod three-segmented, relative length of exopod and endopod as in P2; EXP1 and EXP2 largely as in P2; surface ornamentation of EXP3 as in P2, with subdistal outer pore, with armature consisting of two outer, two distal elements (one distal outer spine, one distal inner spiniform element), and one inner seta. Endopod three-segmented; ENP1 shortest, with few outer strong spinules at base of outer distal apophysis, distal inner hyaline frill coarsely incised, with inner seta; ENP2 largely as in P2 but distal outer apophysis less developed, with inner seta; ENP3 longest, without spinular ornamentation, with subdistal medial pore, with one outer spine, two distal elements (one distal outer spine, one distal inner spiniform element), and one inner seta.

P4 (Fig. 9B) with intercoxal sclerite as depicted. Praecoxa as in P2 and P3. Coxa with spinular ornamentation similar to that of P3, unarmed. Basis with spinular ornamentation as shown, with bare outer seta as long as EXP1 and EXP2 combined. Exopod three-segmented, relative length of exopod and endopod as in P2 and P3; EXP1 largely as in P2 and P3, with outer spine, without inner armature; EXP2 largely as in P2 and P3, with outer spine, with bare inner spiniform element visibly shorter than in P2 and P3; EXP3 with few subdistal outer spinules, with one outer spine, two distal elements (one distal outer spine, one distal inner spiniform element), and one inner spiniform element. Endopod three-segmented, relative length of segments as in P3; ENP1 with few medial spinules subdistally, outer distal apophysis poorly developed, distal inner hyaline frill coarsely incised, with inner short spiniform element; ENP2 largely as in P2 but distal outer apophysis somewhat less developed, unarmed; ENP3 longest, without spinular ornamentation, with subdistal medial pore, with one outer spine, two distal elements (one distal outer spine, one distal inner spiniform element), and one inner spiniform element.

Armature of swimming legs as in the differential diagnosis above.

P5 (Fig. 9C) incorporated into somite, with four pinnate setae of different lengths as shown, outermost basal.

P6 (Fig. 3B) represented by one seta on each side of genital field, the latter midventral in genital somite proximally, large, with paired copulatory pores covered by flaps; largely as in *S. antillensis*.

Description of male. Habitus (Fig. 2B) semicylindrical, largely as in female except for genital and third urosomites separated; total body length measured from anterior tip of rostrum to posterior margin of caudal rami ranging from 800 μm to 940 μm (mean= 832 μm ; n= 5). Urosome (Figs. 2B, 10A, B) tapering posteriad; consisting of P5-bearing somite, subquadrate genital somite, three free somites, and anal somite with caudal rami; with sensilla and pores as shown. General shape of caudal rami (Fig. 10A, B) as in female; all setae displaced (sub)distally; seta I

close to outer distal corner, ventral to seta II, the latter medially on dorsal surface; seta III long, arising close to inner distal corner; principal setae IV and V with fracture planes; seta VI slender, short, arising on inner distal corner; dorsal seta VII biarticulate, close to inner distal corner. Sexual dimorphism expressed in the unmodified condition of the caudal setae, A1, and P6.

Antennule (Fig. 11A, B) chirocerate; seemingly eight-segmented. First segment unarmed, ventrally with set of long spinules distally; second to fifth segments imperfectly separated, with 22 setae and two aesthetascs as depicted; sixth segment short, with three setae; seventh segment globular, with corrugated pads ventrally, with seven setae as depicted; last segment as shown, with seven setae one of which modified.

Antenna and postantennal mouthparts, P1–P5 as in female.

P6 (Figs. 2C, 10B, C) sexually dimorphic, similar to that of *S. antillensis*; each leg consisting of a triangular plate closing off genital pores, with distal patch of minute spinules, with one distal smooth seta; genital area with additional slender long elements as long as plates of P6, with clawed distal part.

Genus *Canuellina* Gurney, 1927

Type species: *Canuellina insignis* Gurney, 1927.

Other species: *Canuellina canalis* Por, 1969; *C. femur* Por, 1967; *Canuellina secunda* (Coull, 1971); *C. pacifica* sp. nov.; *C. tuba* Por, 1983.

Canuellina pacifica sp. nov.

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(Figs. 12–23)

Material examined. ♀ holotype preserved in alcohol (ICML-EMUCOP-020623-01), ♂ allotype partially dissected (habitus preserved in alcohol; right A1, right P1–P3, left P4 dissected and mounted on one slide each) (ICML-EMUCOP-020623-04), two ♀ paratypes (ICML-EMUCOP-020623-02–03), June 2, 2023, from the type locality (stn 2, see below); three ♀ paratypes dissected and mounted on eight, 11, and nine slides (ICML-EMUCOP-020223-22–24), February 2, 2023, from stn 6 (see below); Leonardo García-Vázquez leg.

Type locality. North-western Mexico, northern Sinaloa state, Ohuira Bay, stn 2 (25.6°N, 109.02°W); sand 79.59%, silt 14.20%, clay 6.21%, C_{org} 0.60%.

Other sites: North-western Mexico, northern Sinaloa state, Ohuira Bay, stn 6 (25.56°N, 108.98°W); February 2, 2023; sand 27.34%, silt 49.06%, clay 23.6%, C_{org} 2.37%.

Etymology. The species name refers to the region where the material was collected.

Differential diagnosis. Canuellidae. P5-bearing somite with dorsal pattern of chitinized plates. Caudal rami with seven setae of which six unmodified, one transformed into triangular blunt, hyaline spiniform dorsal element close to outer subdistal margin. Antennary basis with one seta. Distal inner seta on P3EXP3 nearly half as long as the distal outer seta; distal inner element on P3ENP3 shorter than distal outer seta; distal inner seta on P2EXP3 visibly shorter than distal outer element; P2ENP2 with long stiff inner seta parallel to inner margin of outer projection. Female P5 separated from somite, pair of legs fused medially, each with four setae. Male P6 with four elements of different lengths, three outermost ones sclerotized, innermost shortest.

Description of female. Habitus (Fig. 12A) semicylindrical; total body length measured from anterior tip of rostrum to posterior margin of caudal rami ranging from 1120 µm to 1260 µm (mean= 1202.5 µm; n= 4), with maximum width at the posterior margin of cephalothorax. General body shape largely as in *C. secunda*. Rostrum (Fig. 15A) not fused to cephalothorax; large, broadly triangular, with rounded tip; with one subapical somewhat thickened sensilla on each side. First pedigerous somite fused to cephalosome. Urosome (Figs. 12A, 13B, D, 14A) tapering posteriad, hyaline posterior fringe of urosomites smooth, consisting of fifth pedigerous somite, genital double-somite, two free somites, and anal somite; dorsal and ventral surface of urosomites with sensilla and pores as shown. P5-bearing somite (Figs. 13B, 14B) with dorsal pattern of chitinized plates as shown. Genital somite and third urosomite fused dorsally and ventrally forming genital double-somite (Figs. 12A, 13B, D, 14A, C), with lateral internal cuticular band indicating former division between somites, slightly longer than wide, with genital area

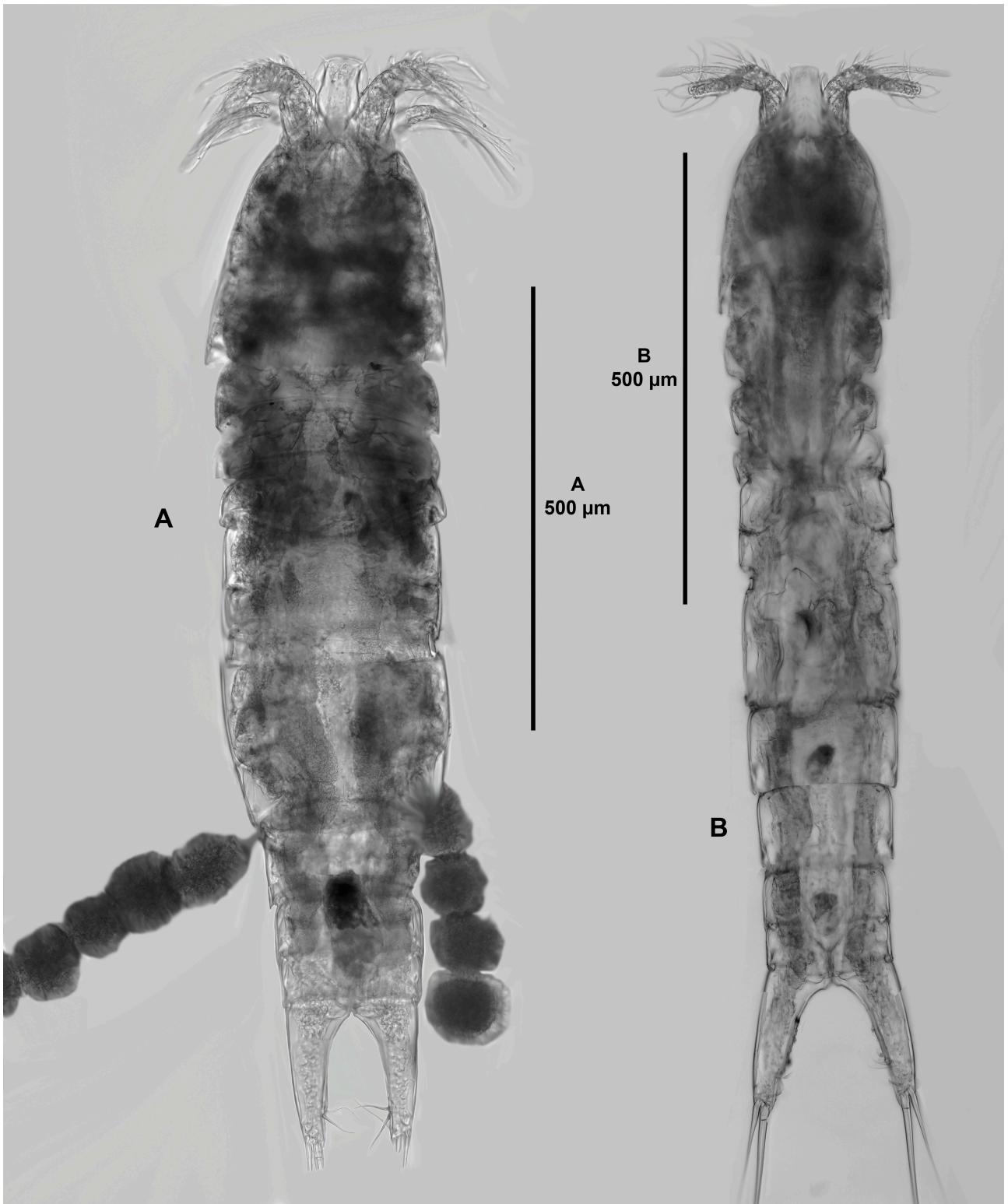


FIGURE 12. *Canuellina pacifica* sp. nov. A, female, habitus, dorsal, microphotograph; B, male, habitus, dorsal, microphotograph.

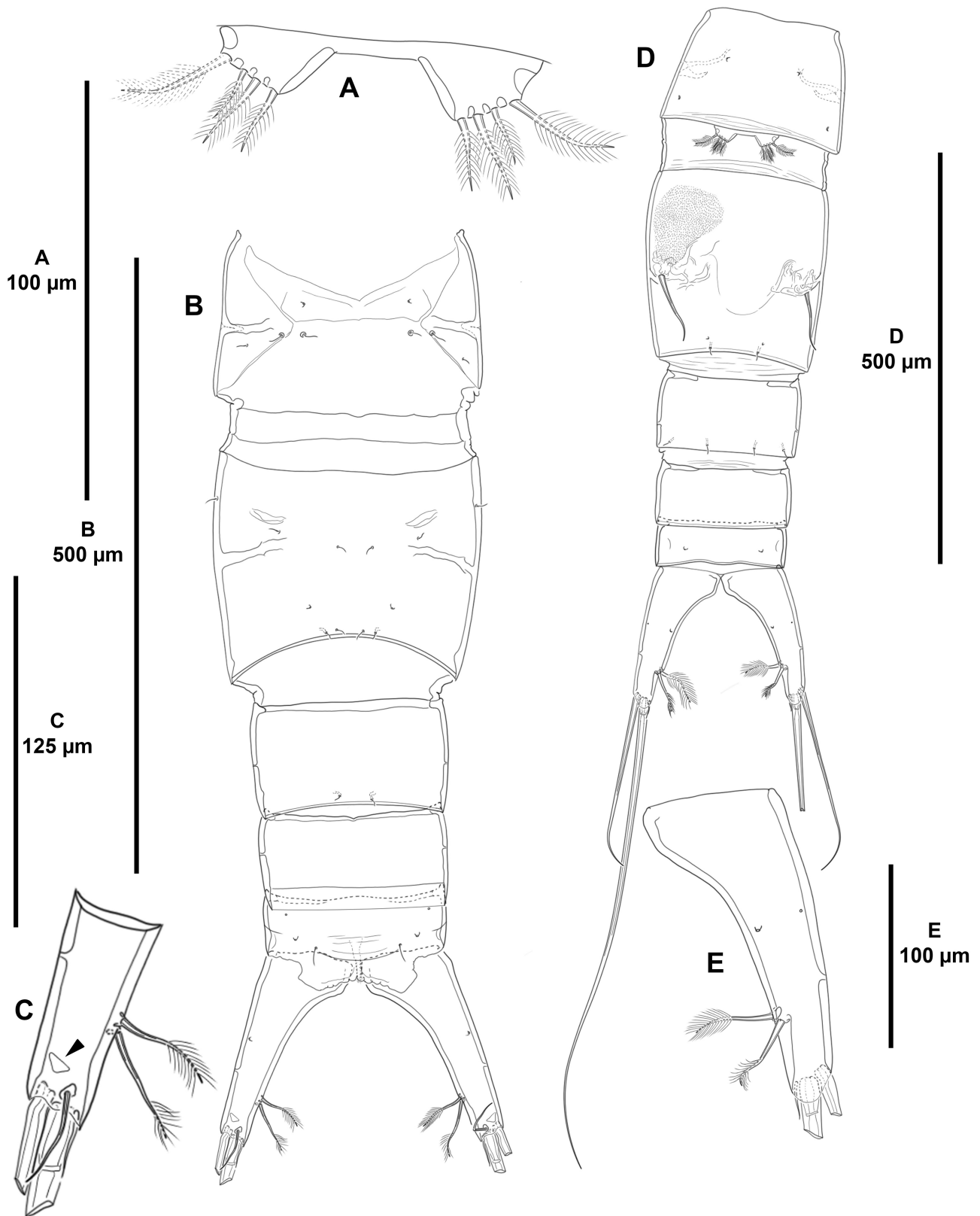


FIGURE 13. *Canuellina pacifica* sp. nov., female. A, P5; B, urosome, dorsal; C, distal part of left caudal ramus, with arrowhead indicating hyaline spiniform blunt element; D, urosome, ventral; E, left caudal ramus, ventral.

situated lateroventrally in the middle of genital double-somite, with one side covered with minute spinules as depicted. Fourth urosomite longer than fifth. Anal somite shorter than preceding somite, with caudal rami. Caudal rami (Figs. 13B–E, 14D) largely as in *C. secunda*, rami visibly longer than fifth and anal somites combined, about 2.3 times as long as wide, proximal margin wider and abruptly tapering posteriad; inner margin concave, outer margin nearly straight; distal margin extended ventrally into a rounded hyaline outgrowth; with pores as shown; homology of setae difficult to determine; setal complement as in *C. secunda*, with two inner plumose elements on distal fourth, one medial subdistal dorsal seta, one short distal inner seta, and two principal distal setae of which inner with fracture plane, and additionally with triangular blunt, hyaline spiniform dorsal element close to outer subdistal margin (Figs. 13B, C, 14D). With two uniseriate egg sacs with eight eggs each.

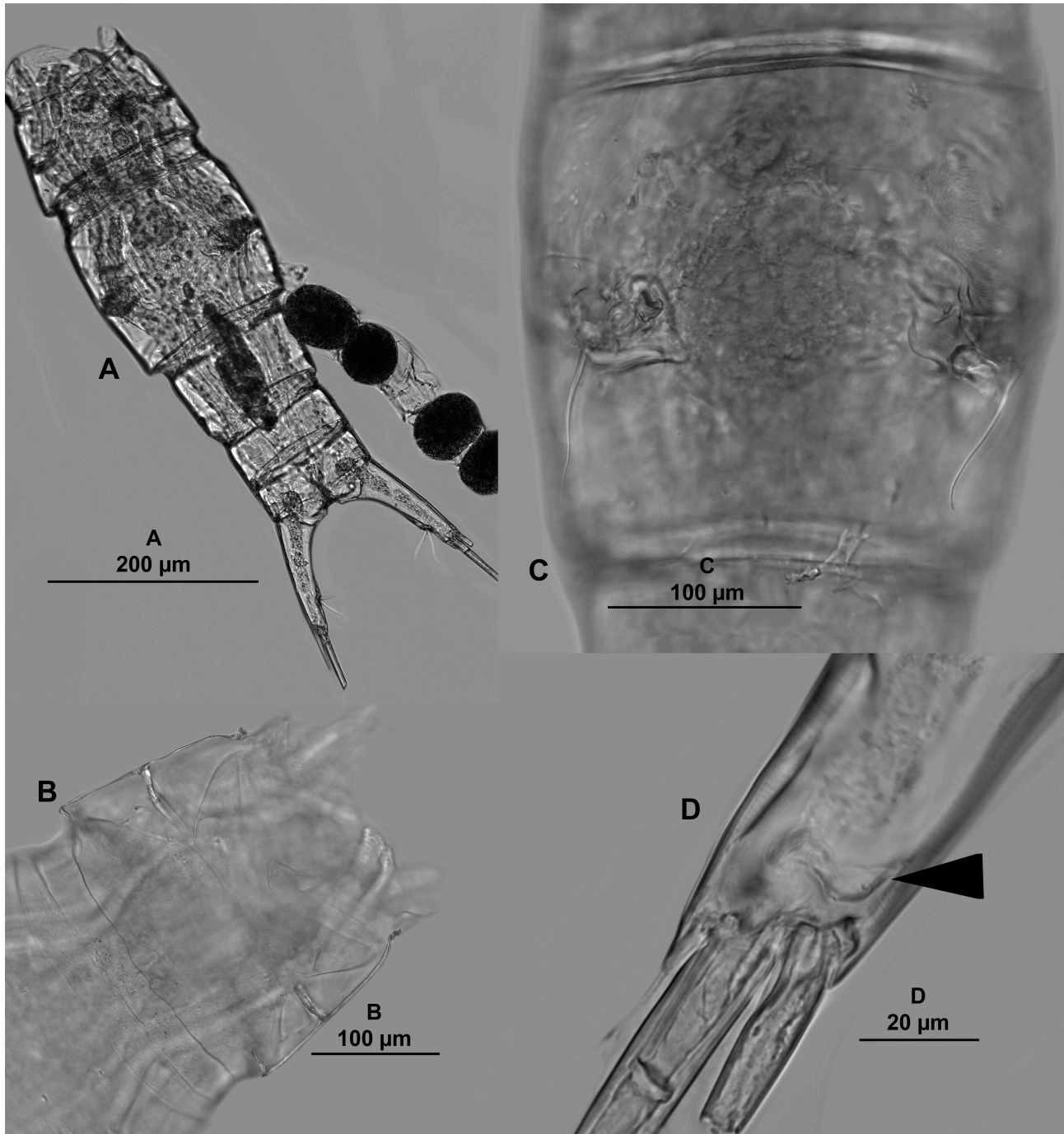


FIGURE 14. *Canuellina pacifica* sp. nov., female. A, urosome, dorsal, microphotograph; B, P5-bearing somite, dorsal, microphotograph; C, genital double-somite showing P6, ventral, microphotograph; D, distal part of caudal ramus, with arrowhead indicating hyaline spiniform blunt element, microphotograph.

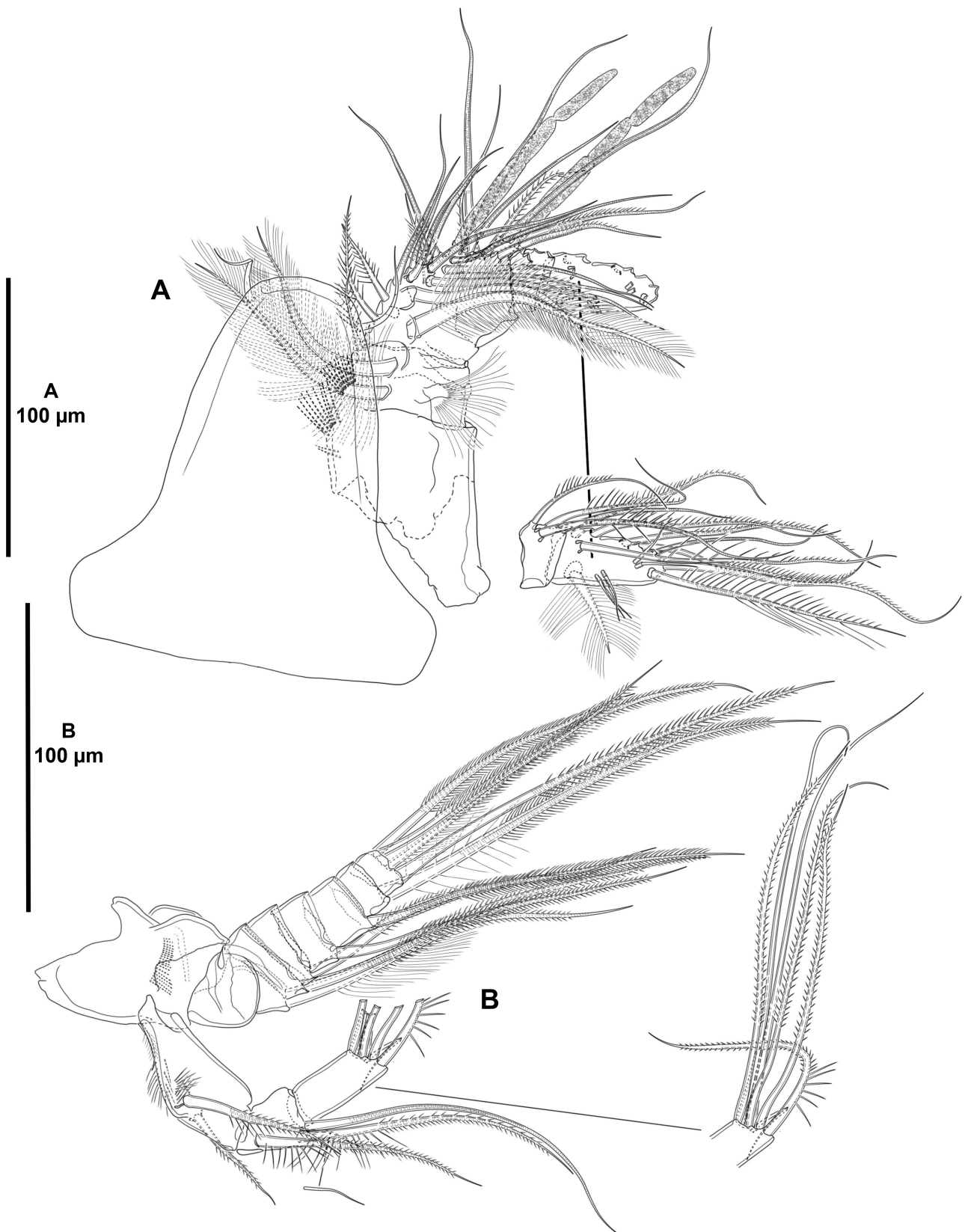


FIGURE 15. *Camuellina pacifica* sp. nov., female. A, rostrum and antennule; B, antenna.

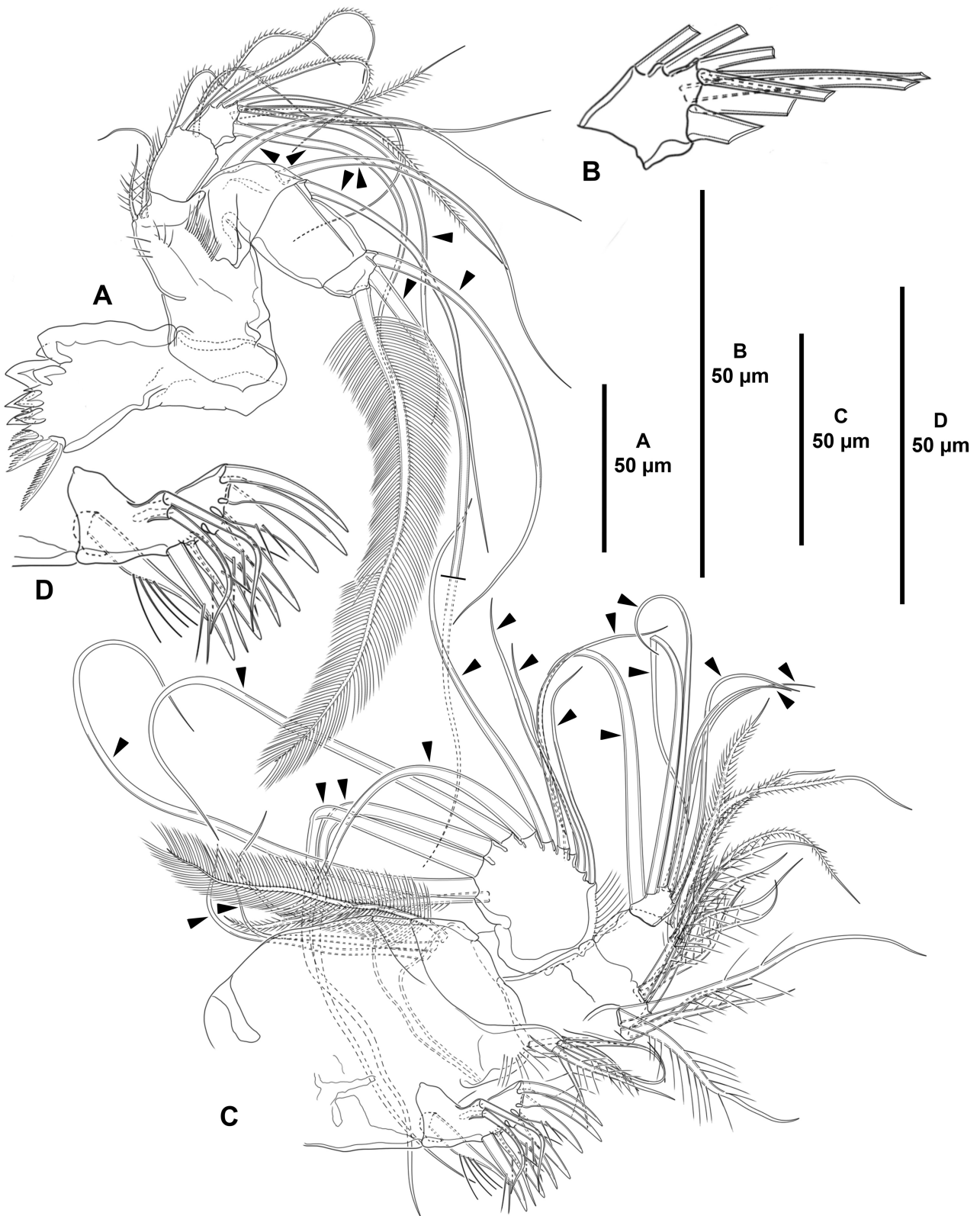


FIGURE 16. *Canuellina pacifica* sp. nov., female. A, mandible, with arrowheads indicating plumose setae; B, distal segment of endopod of mandible; C, maxillule, with arrowheads indicating plumose setae; D, arthrite of maxillule.

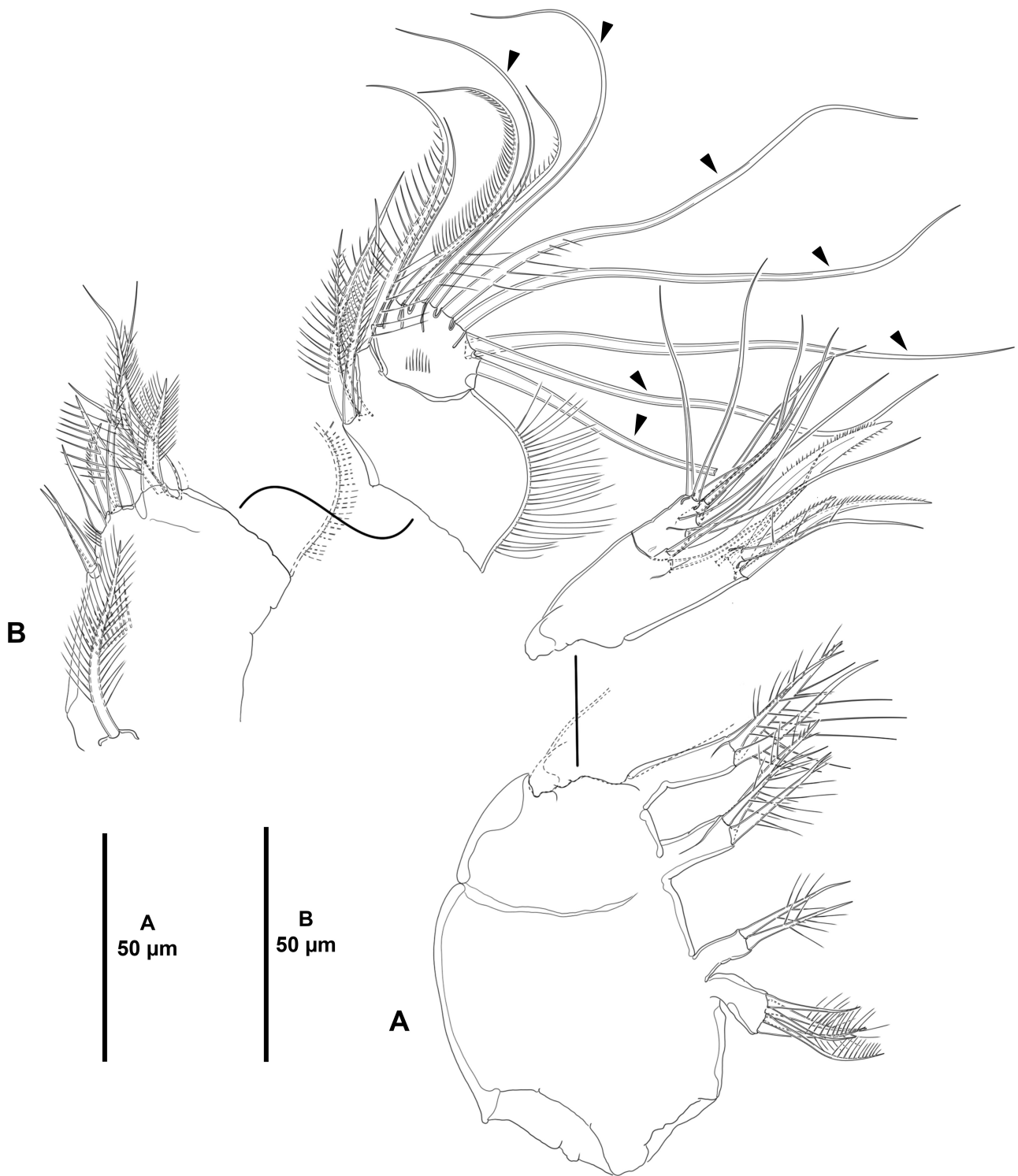


FIGURE 17. *Camuellina pacifica* sp. nov., female. A, maxilla; B, maxilliped, with arrowheads indicating plumose setae.

Antennule (Fig. 15A) presumably with seven original segments. First to fifth segments imperfectly separated forming large first composite segment with two proximal spinular rows, with set of medial inner long setules, with 26 setae in all and two seemingly free aesthetascs; penultimate segment distinct, with four setae; last segment distinct, with 14 setae as shown of which proximal outer stout and plumose, three medial outer and two subdistal biarticulate.

Antenna (Fig. 15B) biramous. Basis with spinular row medially, with short outer seta. Exopod seven-segmented; first-sixth segments with one, seventh segment with four pinnate elements. Endopod three-segmented; first segment with outer spinules as shown, with two medial setae; second segment seemingly unornamented, with one proximal

and two distal elements; third segment with seven setae (six long of which two bare and four pinnate as depicted, and one short naked seta).

Mandible (Fig. 16A, B) with well-developed gnathobase bearing multicuspidate teeth and several (five?) pinnate spines of which ventral longest. Basis large, with spinular rows as shown, with two inner subdistal setae. Exopod three-segmented, bent outwards; first segment with two setae (one medial, one subdistal); second segment with one proximal element; third segment with three setae; all endopodal setae plumose. Endopod two-segmented; first segment larger, with three pinnate inner setae, second segment with eight elements of which two outer plumose, two medial seemingly unornamented, the other setae pinnate.

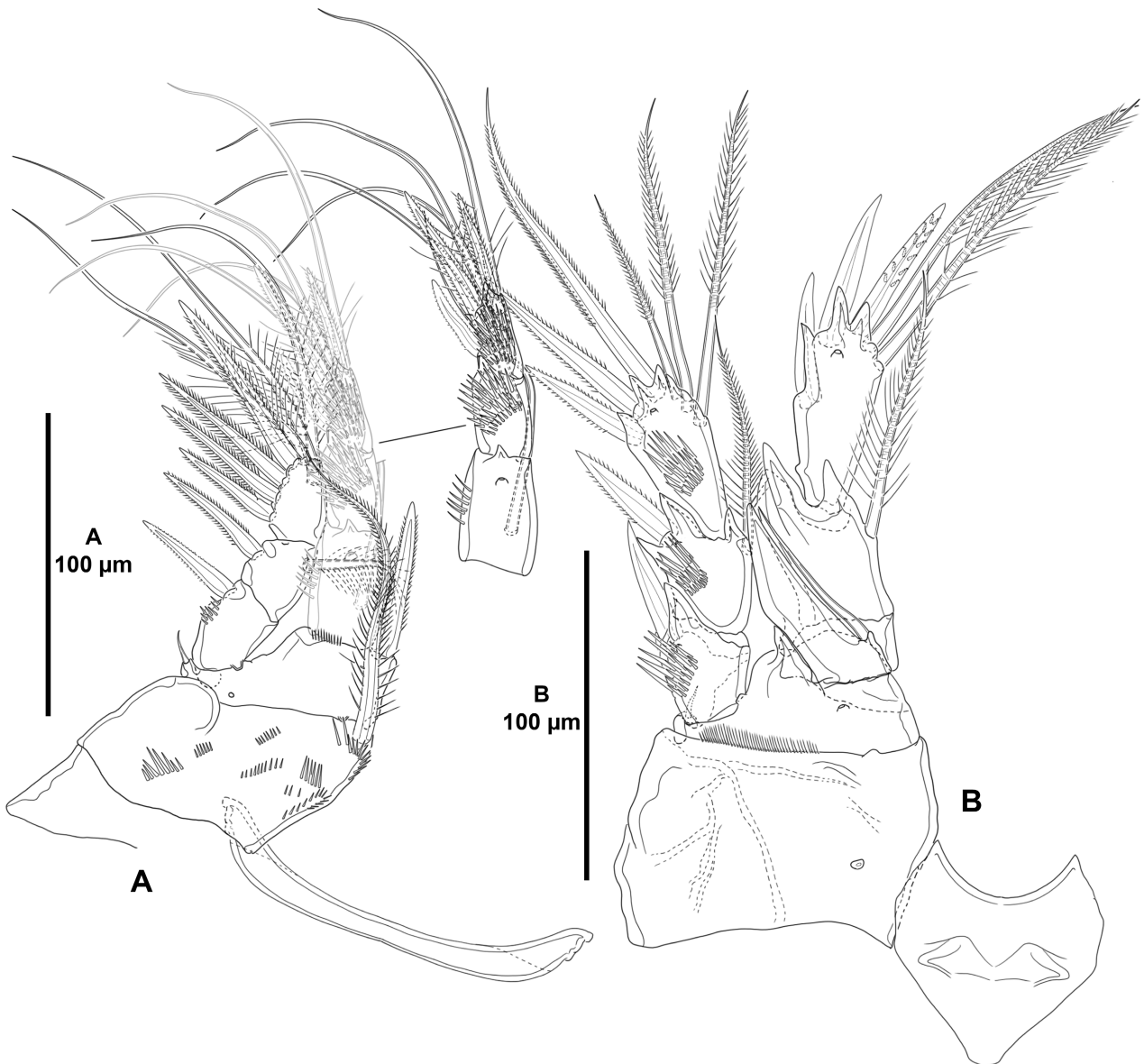


FIGURE 18. *Canuellina pacifica* sp. nov., female. A, P1 (setular ornamentation of exopodal and endopodal setae omitted for clarity); B, P2.

Maxillule (Fig. 16C, D) with praecoxa and coxa partially fused. Praecoxal arthrite narrow, seemingly unornamented; proximally with one thick seta with long slender pinnae, distally with seven spines and one seta, with two setae arising from short setophore. Coxal endite with row spinules and five setae; with three long plumose epipodal plumose setae. Exopod massive, bent outwards, one-segmented; with 11 setae of which ten inner and distal long and plumose, outermost shorter and bipinnate. Endopod three-segmented; first segment with four medial and four distal pinnate setae; second segment with five pinnate elements, third segment with six plumose setae.

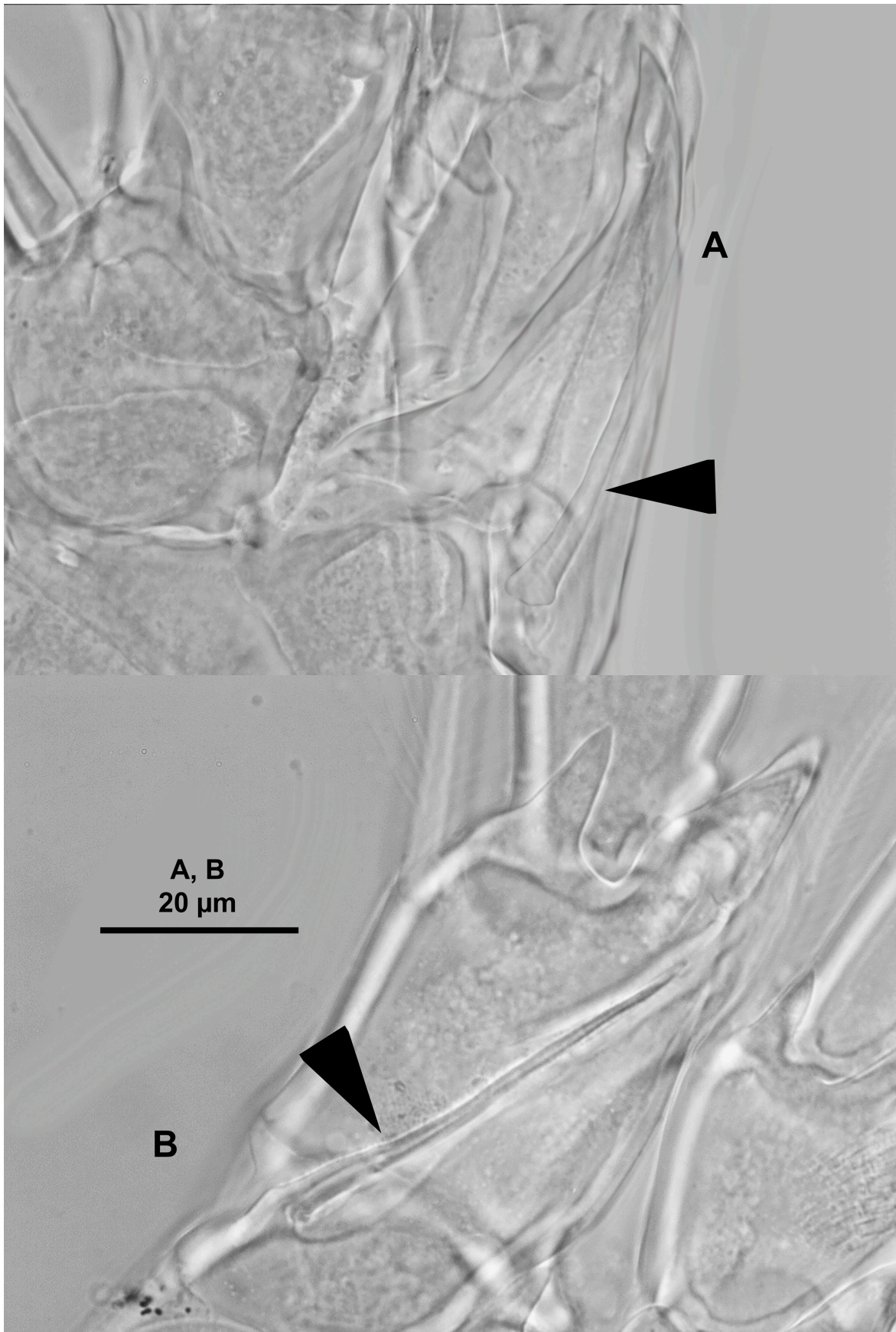


FIGURE 19. *Canuellina pacifica* sp. nov., female. A–B, endopod of P2, with arrowheads indicating long stiff inner seta parallel to inner margin of outer projection, microphotograph.

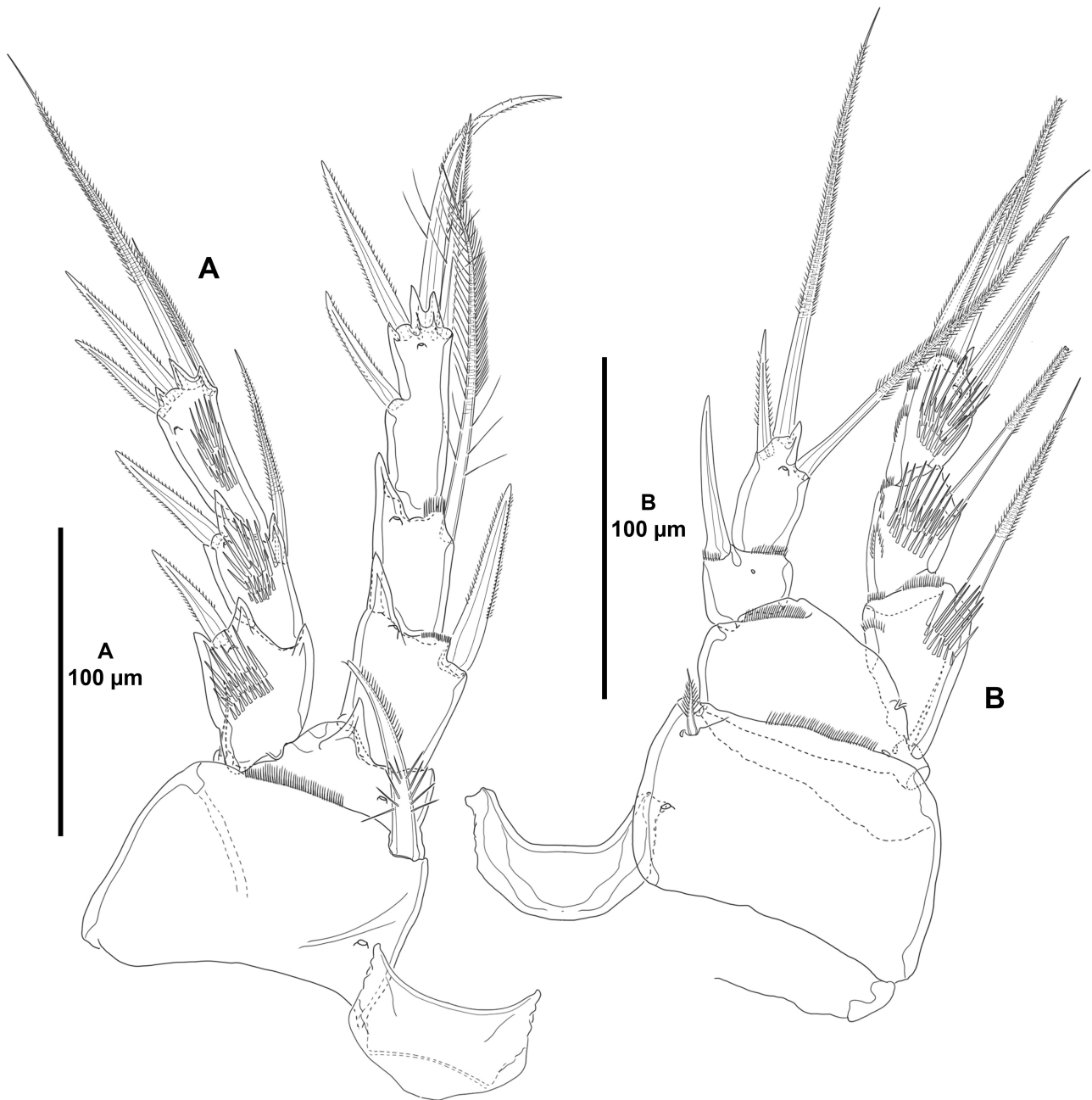


FIGURE 20. *Canuellina pacifica* sp. nov., female. A, P3; B, P4.

Maxilla (Fig. 17A) with praecoxa and coxa imperfectly separated forming large syncoxa, seemingly unornamented; with four endites, of which two praecoxal close-set (proximal with five, distal with two setae), and two coxal separated (each with three setae). Allobasis drawn out into strong pinnate claw accompanied by three setae and two spines. Endopod seemingly one-segmented, with nine setae.

Maxilliped (Fig. 17B) phyllopodial. Praecoxa and coxa fused forming large syncoxa with one medial and one subdistal row of spinules, with one (praecoxal) proximal seta, and three sets (endites) of setae with two medial, four subdistal, and three distal elements. Basis with longitudinal row of outer long spinules; with three spinulose medial inner setae, and one spinulose inner element arising from distal long setophore. Endopod one-segmented, with ten setae arranged in four groups with two, two, three, and three setae, of which outermost seven plumose, the other pinnate.

P1 (Fig. 18A) with intercoxal sclerite transversely elongate. Coxa and basis with spinular ornamentation and with pores as figured, the former with inner long bipinnate seta, the latter with reduced outer naked seta and inner

pinnate spine. Exopod with three subequal segments, reaching tip of ENP2; EXP1 with few, EXP2 without outer spinules, the former with outer spine and without inner armature, the latter with outer spine and inner seta; EXP3 unornamented, with three outer spines, two distal elements (one distal outer spine, one distal inner plumose seta), and two inner plumose setae. Endopod three-segmented, first segment longest, third segment shortest; ENP1 with short longitudinal row of outer spinules and medial subdistal pore, with one inner plumose seta; ENP2 and ENP3 with anterior patch of spinules as shown, the former with one inner plumose seta, the latter with two outer spines, two distal elements (one distal outer spine, one distal inner plumose seta), and two inner plumose setae.

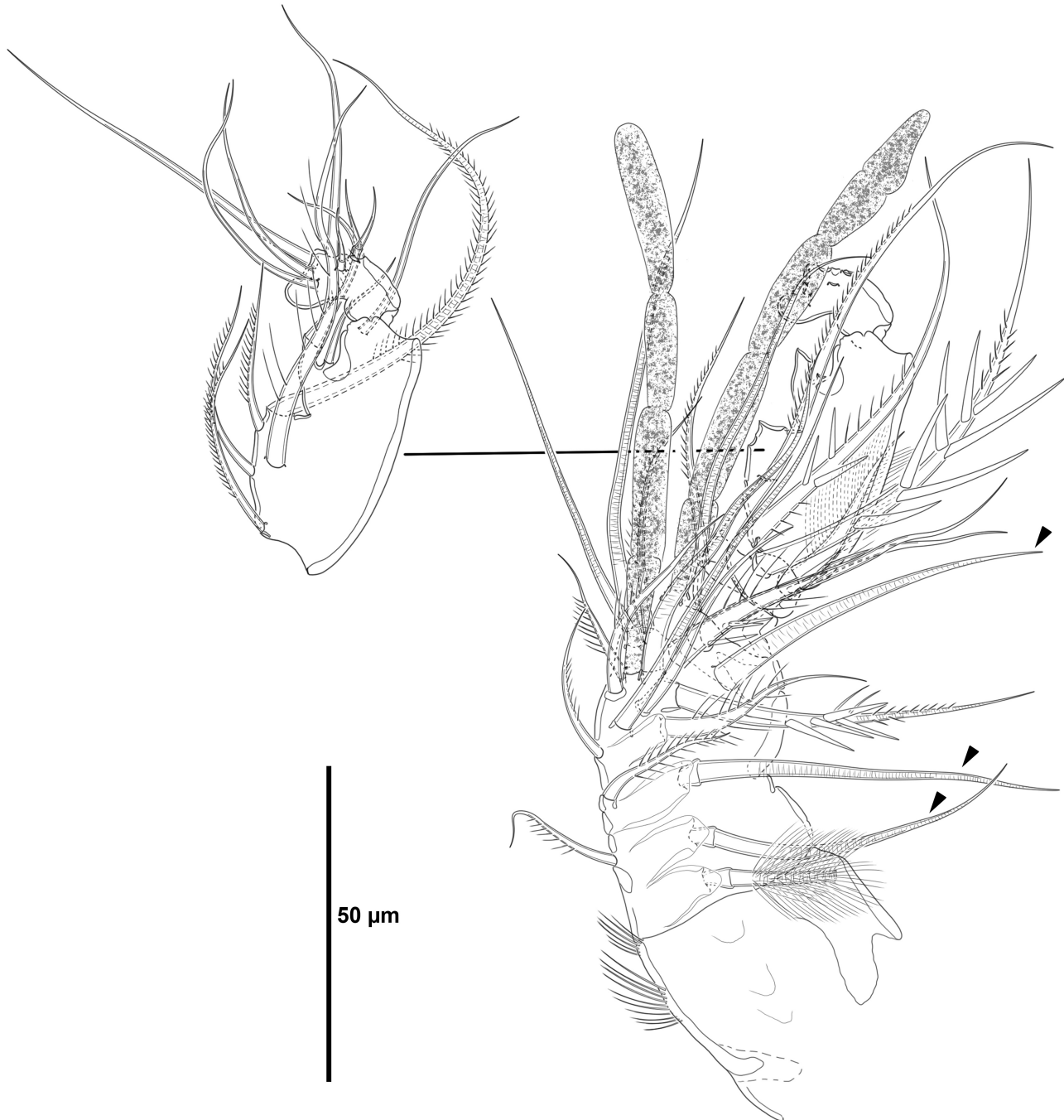


FIGURE 21. *Canuellina pacifica* sp. nov., male. Antennule, with arrowheads indicating plumose setae.

P2 (Figs. 18B, 19A, B) with U-shaped intercoxal sclerite with two distal pointed tines, proximal part triangular. Coxa large, with spinular ornamentation as figured, with medial inner pore, unarmed. Basis as shown, with medial pointed projection distally between rami; with medial pore close to base of endopod; with reduced outer seta. Exopod three-segmented, inserted at a lower level than endopod and reaching distal third of ENP3; EXP1 shortest,

EXP3 longest; exopodal segments with anterior patch of spinules as shown; EXP1 with outer spine, without inner armature; EXP2 with outer spine and inner seta; EXP3 with two outer spines, two apical elements (one distal outer spiniform element, one distal inner plumose seta), and two inner plumose setae. Endopod three-segmented, first segment shortest, third segment longest; ENP1 with outer pointed projection reaching tip of ENP2, unornamented, with long stiff inner seta parallel to inner margin of outer projection; ENP2 with outer and inner distal pointed projections, unornamented, with inner seta as shown; ENP3 with medial subdistal pore, with distal pointed outgrowths as depicted, with two outer naked spines, two distal elements (one distal outer spine with hook-like spinules, one distal inner seta), and one inner seta.

P3 (Fig. 20A) with U-shaped intercoxal sclerite with two distal pointed tines, proximal part of sclerite attenuated. Coxa large, with spinular ornamentation as figured, with medial inner pore, with strong inner spiniform element. Basis largely as in P2; with medial inner pore close to base of endopod; with outer seta comparatively longer than in P2. Exopod three-segmented, inserted at a lower level than endopod and reaching middle of ENP3; EXP1 largest, EXP3 elongate; exopodal segments with anterior patch of spinules as shown; EXP1 with outer subdistal pore, with outer spine, without inner armature; EXP2 with outer subdistal pore, with outer spine and inner bipinnate seta; EXP3 with subdistal outer pore, with four elements displaced distally (two outer spines, one distal outer and one distal inner seta). Endopod three-segmented, first segment shortest, third segment longest; ENP1 with outer pointed projection reaching middle of ENP2, without spinular ornamentation, with subdistal outer pore and distal inner hyaline frill, with inner spine; ENP2 with outer distal pointed projection, unornamented, with subdistal outer pore, with distal inner hyaline frill, with inner seta; ENP3 with distal pointed outgrowths as depicted, unornamented, with medial subdistal pore, with two outer spines, and two distal elements (one distal outer spine, one distal inner spiniform element).

P4 (Fig. 20B) with intercoxal sclerite as depicted. Coxa with spinular ornamentation and medial inner pore similar to that of P3, with short inner seta. Basis with transverse spinular row distally close to insertion site of endopod, with proximal outer pore, with long outer seta. Exopod three-segmented, inserted at a lower level than endopod, much longer than the latter; EXP1 largest, EXP2 and EXP3 subequal in length; exopodal segments with anterior patch of spinules as shown; EXP1 with small spinules distally and medially close to inner margin, with long outer spine, without inner armature; EXP2 with small spinules along inner margin as shown, with outer long spine, without inner armature; spinular ornamentation of EXP3 largely as in EXP2, with subdistal outer pore, with two outer spines and two distal elements (one distal outer long seta, one distal inner shorter spiniform element). Endopod two-segmented, reaching tip of EXP2, first segment shortest; ENP1 with small outer distal spinules, with medial pore, with inner strong, bare spine; ENP2 with outer distal pointed projection, unornamented, with outer subdistal pore, with three elements (one outer and one distal seta, one inner spine).

Armature of swimming legs as in the differential diagnosis above.

P5 (Fig. 13A, D) separated from somite, pair of legs fused medially forming transversely elongated plate, with four plumose setae of different lengths as shown, of which outermost (basal) longest.

P6 (Figs. 13D, 14C) represented by one long seta on each side of genital field, close to lateral margins; genital field large, with paired copulatory pores covered by flaps.

Description of male. Habitus (Fig. 12B) semicylindrical, largely as in female except for genital and third urosomites separated; total body length of the only male specimen found, measured from anterior tip of rostrum to posterior margin of caudal rami 1050 μm . Urosome tapering posteriad, consisting of P5-bearing somite, subquadrate genital somite, three free somites, and anal somite with caudal rami. General shape of caudal rami as in female, dimorphism expressed in segmentation of urosome, A1, and shape of P6.

Antennule (Fig. 21) chirocerate; seemingly eight-segmented. First segment unarmed, ventrally with set of long spinules medially and distally; second to fourth segments imperfectly separated, with 23 setae and two aesthetascs as depicted; fifth and sixth segments short, with two and three setae respectively; seventh segment elongate, with eight setae; eighth segment short, with blunt tip, with seven setae of which three biarticulate.

Antenna and postantennal mouthparts, P1–P5 (not shown) as in female.

P6 (Figs. 22, 23) large, closing off single medial genital pore; inner margin distinct and with slender setules, outer margin seemingly fused to somite; with four elements of different lengths as shown, three outermost ones sclerotized, innermost shortest.

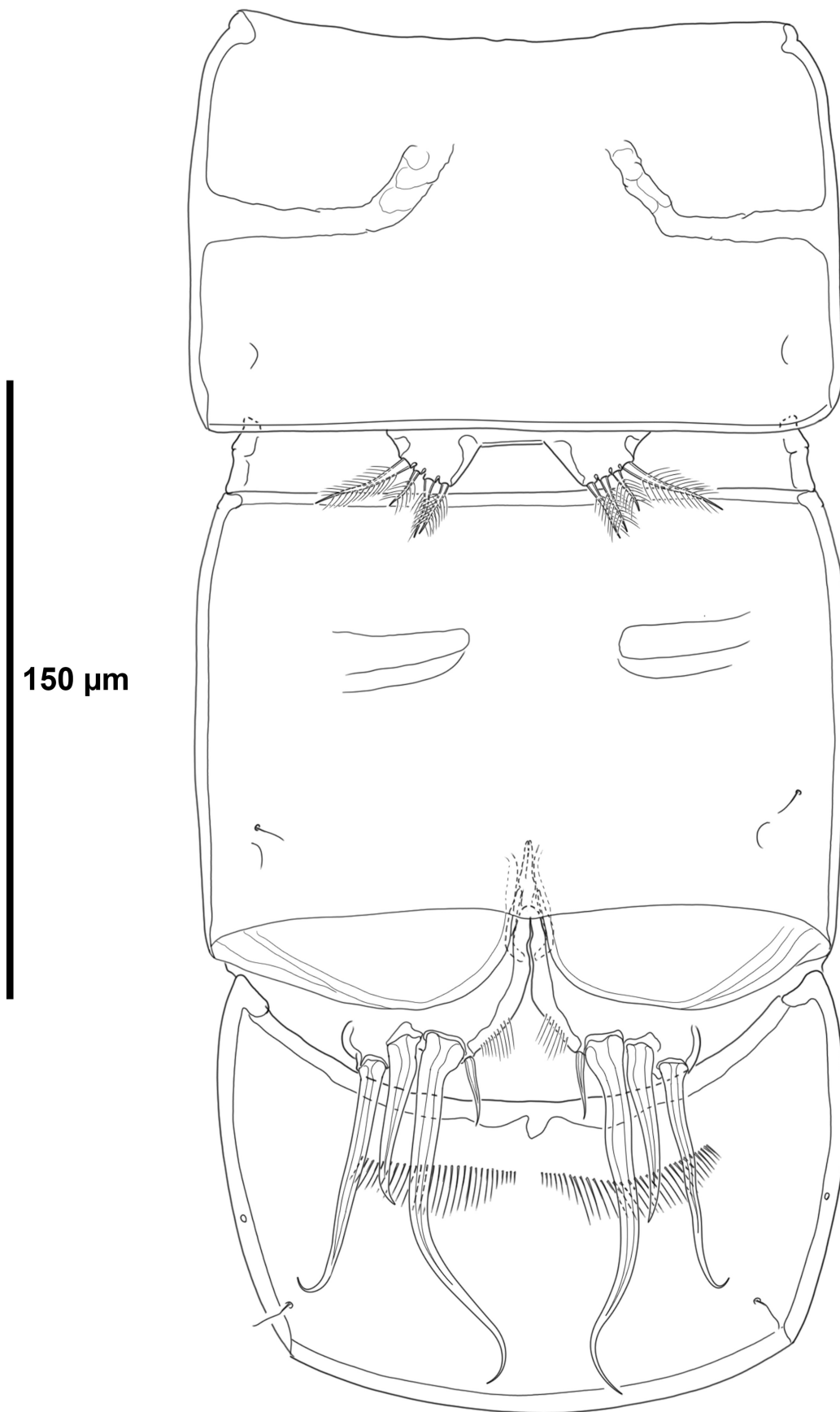


FIGURE 22. *Canuellina pacifica* sp. nov., male. P5-bearing somite, genital somite, and third urosomite, ventral, showing P5 and P6.

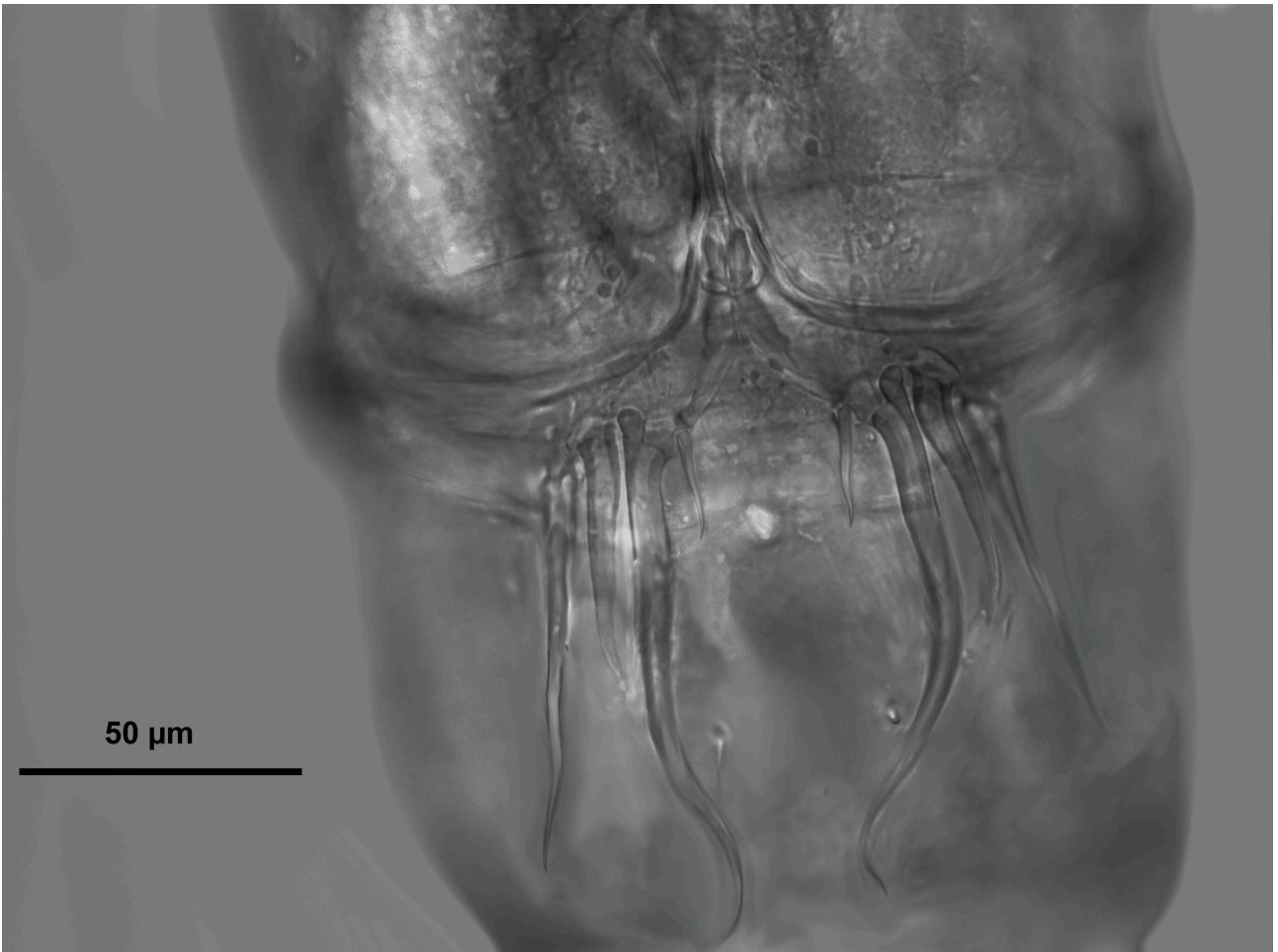


FIGURE 23. *Canuellina pacifica* sp. nov., male. P5, microphotograph.

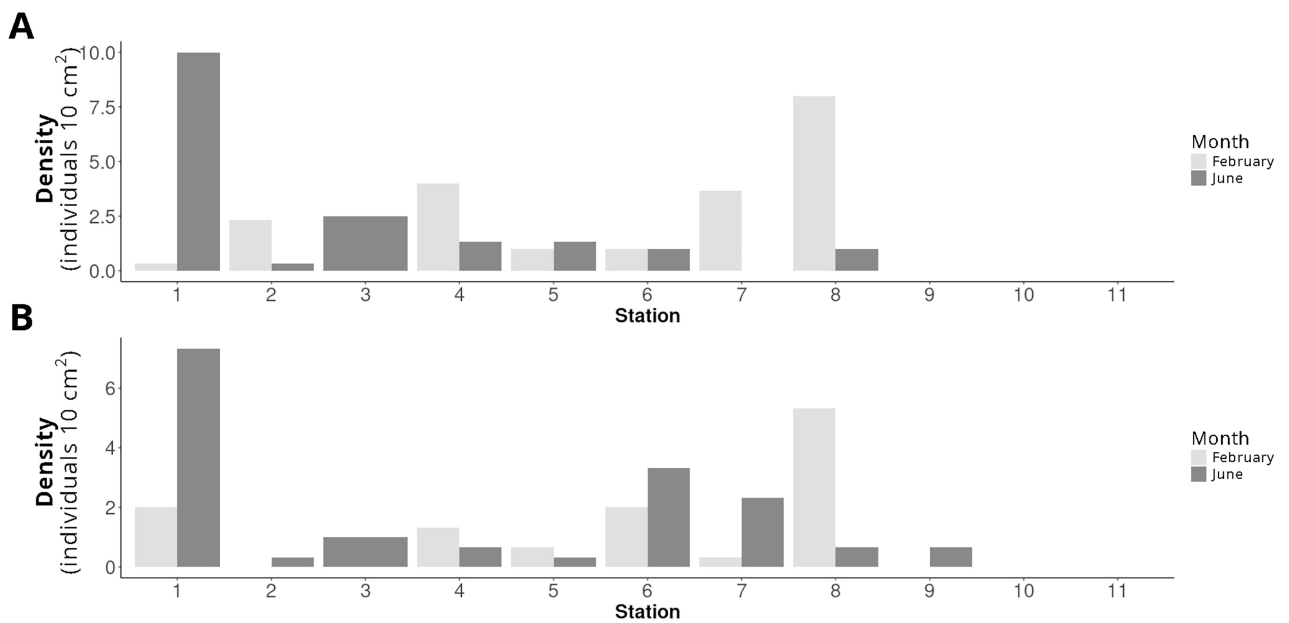


FIGURE 24. Mean densities of the most abundant species. A, *Scottolana tama* sp. nov.; B, *Longipedia corteziensis* Gómez, 2001.

Ecology and distribution

The environmental variables of bottom water exhibited significant seasonal variations; average temperature, salinity, conductivity and dissolved oxygen increased from February (18 °C, 28 PSU, 39.14 mS cm⁻¹, and 4.97 mg L⁻¹) to June (28° C, 35 PSU, 57.59 mS cm⁻¹, and 6.56 mg L⁻¹). The environmental variables in sediment (organic carbon, grain size) showed no seasonal variations.

The mean density for *S. tama* **sp. nov.** was 1.8 ind. 10 cm⁻², and 1.3 ind. 10 cm⁻² for *L. corteziensis*. The seasonal decrease in density of *S. tama* **sp. nov.** from 2 ind. 10 cm⁻² in February to 1.59 ind. 10 cm⁻² in June was insignificant. The increase in density of *L. corteziensis* from 1.16 ind. 10 cm⁻² in February to 1.51 ind. 10 cm⁻² in June was also insignificant. In Ohuira Bay, spatial variation of *S. tama* **sp. nov.** and *L. corteziensis* (Fig. 24) seems to be linked to environmental conditions. The generalised linear mixed models indicated that sand, organic carbon, and dissolved oxygen were significant for both species (AIC = 162, D2 = 44, $p < 0.001$ for *S. tama* **sp. nov.**, and AIC = 130, D2 = 43, $p < 0.001$ for *L. corteziensis*).

Discussion

In the preliminary communication of his monograph of the Harpacticoida and later in his monograph, Lang (1944, 1948) proposed to subdivide the Harpacticoida into two sections or suborders, the Polyarthra for two families (Longipediidae Boeck, 1865 and Canuellidae Lang, 1944) and the Oligoarthra with three subsections or superfamilies (Maxillipedasphalea, Exanechentera, and Podogennonta) for the rest of the harpacticoid families known at the time. The section Polyarthra included copepods with a combination of, amongst others, i) presence of an inner element (seta or spine) on the coxa of, at least, P1 (coxa without inner armature in Oligoarthra), ii) antenna with three-segmented endopod, and six- to seven-segmented exopod (endopod two-, exopod at most four-segmented in Oligoarthra), iii) maxilliped leaf-shaped with numerous long plumose setae (maxilliped not leaf-shaped, without long plumose setae), iv) without sexual dimorphism in the swimming legs of males (with sexual dimorphism in, at least, one swimming leg in the males of Oligoarthra), v) first nauplius stage not dorsoventrally depressed, without furcal setae but with maxillae (first nauplius stage dorsoventrally depressed, with furcal setae, and without maxillae in Oligoarthra). Several differences between the polyarthran and oligoarthran adults and nauplii were known, but the Langian system of Polyarthra and Oligoarthra was not challenged until the 1980's when Tiemann (1984) expressed some doubts about the monophyly of the Langian concept of Harpacticoida, and suggested separating Polyarthra from Harpacticoida, and placing it at the roots of Copepoda. Dahms (1990) compared polyarthran and oligoarthran naupliar characters and concluded that the Langian Harpacticoida, with Polyarthra and Oligoarthra, was not a monophyletic unit and proposed to remove —the monophyletic—Polyarthra from Harpacticoida, and discussed whether Polyarthra should belong to Podoplea or whether they should be excluded from Copepoda as its adelpho taxon. Huys *et al.* (1996) regarded Polyarthra as a monophyletic taxon, but considered Oligoarthra polyphyletic and without strict taxonomic significance. Exclusion of Polyarthra from Harpacticoida, and the monophyly of Oligoarthra was reinforced in Dahms (2004b), and Dahms (2004a) finally removed Polyarthra from Harpacticoida and placed the former as an underived taxon of the Copepoda. Khodami *et al.* (2017) presented appealing molecular evidence for the separation of the —monophyletic—Polyarthra from the —monophyletic—Oligoarthra, and proposed the order Canuelloida for the polyarthran families while keeping Harpacticoida s. str. for all the oligoarthran taxa. Regrettably, the paper by Khodami *et al.* (2017) was retracted a few years later (Khodami *et al.* 2020). At the beginning of 2021, the president of the International Commission on Zoological Nomenclature (ICZN) formed an *ad hoc* committee on the issue of the nomenclatural status of retracted works. The ICZN voted in favour of Declaration 46 (ICZN 2023), and an amendment to Art. 8.8 was added to the Code which shall remain in force until ratified or rejected (ICZN 1999, Art. 80.1) by the International Union of Biological Sciences (IUBS) (ICZN 1999, Art. 77). Under Art. 8.8, retraction of Khodami *et al.* (2017) (Khodami *et al.* 2020) does not affect the availability of new names and nomenclatural acts contained therein. In their paper, Bang *et al.* (2022) referred to the Langian order Polyarthra and were probably unaware of the new amendment to Art. 8.8. of the Code.

Species-groups of *Scottolana* and their relationships

Por (1967) proposed the genus name *Scottolana* for three species of *Sunaristes* Hesse, 1867, but he did not fix the type species rendering the genus unavailable. Huys (2009) made the genus available by fixing *Scottolana geei* (Mu & Huys, 2004) and diagnosing the genus [for a complete account on this issue and on the taxonomic history of the genus see Huys (2009: 20–22) and Mu & Huys (2004)]. In their work, Mu & Huys (2004) detected several lineages within *Scottolana* and proposed the *longipes*-group for *S. longipes*, *S. longipes sensu* Por (1964), *S. longipes sensu* Wells (1967), *S. longipes sensu* Wells & Rao (1987), *S. geei*, *S. uxoris* and *S. dissimilis*, characterised by two postgenital urosomites in the female and three in the male, female and male P4EXP displaced outwards, P4ENP and several armature elements (outer spine of P4EXP2 and inner seta on P4ENP1) secondarily elongate (apparent elongation of ENP due to the elongation of ENP2), male P3ENP3 with modified inner tube-pore, P2–P4 bases with posterior recurved spinous processes, caudal rami with hook-like inner extension proximally and with outer spinular patch subdistally, and seta II of the female caudal rami modified. Mu & Huys (2004) explained the reduction in number of urosomites as the result of “progenetic development defined by the early offset of somite addition at the copepodid V stage” (Mu & Huys 2004: 33) and constitutes a major evolutionary trend within the genus. Five species, *S. gomezi*, *S. jasani*, *S. huysi*, *S. daecheonensis*, and *S. wonchoeli*, were described by 2022 displaying the same reduction in urosome segmentation.

Song *et al.* (2018) included *S. jasani* and *S. huysi* to the *longipes*-group. However, these two species do not fit well in Mu & Huys’ (2004) concept of the group (the outer spine on P4EXP2 and the inner seta on P4ENP1 of *S. jasani* are not elongated, P2–P4 bases lack inner recurved processes, and the female caudal seta II is not modified; *S. huysi* seems to lack the inner modified tube-pore on the male P3ENP3).

Nazari *et al.* (2018) attributed *S. gomezi* to Mu & Huys’ (2004) *longipes*-group but they noted that some of Mu & Huys’ (2004) apomorphies for the *longipes*-group were not present in *S. gomezi*, viz. outer processes on the P2–P4 bases, inner modified tube-pore on the male P3ENP3, modified caudal seta II, patch of distal outer spinules on the caudal rami, and proximal inner hook-like projection on caudal rami, and commented on the need of a revision of Mu & Huys’ (2004) set of apomorphies for the *longipes*-group, implicitly suggesting the need of widening Mu & Huys’ (2004) concept by removing some apomorphies from their list so more species can be included. Nazari’s *et al.* (2018) view found support in Bang *et al.* (2022) when they argued that the presence of a modified inner tube-pore on the male P3ENP3 and the modification of caudal seta II should be removed from the list of apomorphies for the inclusion of *S. daecheonensis* into the *longipes*-group. Following Bang *et al.* (2022), the *longipes*-group contains *S. daecheonensis*, *S. dissimilis*, *S. geei*, *S. gomezi*, *S. huysi*, *S. jasani*, *S. longipes*, *S. longipes sensu* Por (1964), *S. longipes sensu* Wells (1967), *S. longipes sensu* Wells & Rao (1987), *S. uxoris*, and *S. wonchoeli*. There is urgent need of a strong phylogenetic analysis of the genus *Scottolana* to understand the affinities amongst its species, but we do not support the widening of the boundaries of taxa or groups of taxa so more species can be included. We believe that such boundaries need to be somewhat more restrictive to clearly reflect the phylogenetic affinities between the species of *Scottolana*. Instead, we propose the *longipes*-complex for all the species with two postgenital urosomites in the female and three in the male (*S. daecheonensis*, *S. dissimilis*, *S. geei*, *S. gomezi*, *S. huysi*, *S. jasani*, *S. longipes*, *S. longipes sensu* Por (1964), *S. longipes sensu* Wells (1967), *S. longipes sensu* Wells & Rao (1987), *S. uxoris*, and *S. wonchoeli*), which is regarded here as a synapomorphy for all the species above, and constitutes a major evolutionary trend within the genus. Some of Mu & Huys’ (2004) apomorphies for their *longipes*-group seem to have been lost secondarily in several species. Below we propose several species-groups within the *longipes*-complex based on the shape of the female caudal rami, its ornamentation, and shape and situation of its armature elements.

Geei-group. Wells (1967) gave a partial redescription of *S. longipes* from Inhaca Island (Mozambique). Mu & Huys (2004) believe that Wells’ (1967) material is not conspecific with the material from Sri Lanka upon which Thompson & Scott (1903) described the species. In fact, apart from the elongate P4ENP there is little evidence to accurately attribute Wells’ (1967) *S. longipes* to the *longipes*-group *sensu* Mu & Huys (2004). Wells & Rao (1987) gave the full description of the male of *S. longipes* from Sawai Bay, Nicobar Island (they did not find the female), and stated that the populations from Inhaca Island and Nicobar Island were closely similar. These two species will be treated here as conspecifics. From Wells’ (1967) written description and drawings it is clear that caudal seta I is spiniform and caudal seta II is not transformed in the female. The overall shape of the female caudal rami of *S. longipes sensu* Wells (1967) and, most probably, of *S. longipes sensu* Wells & Rao (1987), resemble those of

S. daecheonensis and *S. jasani*. Wells' (1967) did not show any inner process on the bases of P2–P4. However, assuming conspecificity of *S. longipes sensu* Wells (1967) and *S. longipes sensu* Wells & Rao (1987) [Wells & Rao's (1987) description and drawings are more detailed than those of Wells' (1967)], the basis of P2 lack the inner process, but it is present on the bases of P3 and P4. *Scottolana longipes sensu* Wells (1967) and *S. longipes sensu* Wells & Rao (1987) display the other apomorphies for the *longipes*-group *sensu* Mu & Huys (2004).

Song *et al.* (2018) attributed *S. jasani* and *S. huysi* to the *longipes*-group. However, these two species do not fit in the *longipes*-group *sensu* Mu & Huys (2004). *Scottolana jasani* lacks inner recurved processes on the bases of P2–P4, and the female caudal seta II is not modified. *Scottolana huysi* seems to lack the inner modified tube-pore on the male P3ENP3, P2 basis possesses an inner process, but it is absent in the bases of P3 and P4, and the female caudal seta II displays only a somewhat bulbous basal part, and a proximal small dentiform projection.

Bang *et al.* (2022) attributed *S. daecheonensis* to the *longipes*-group, but this species lacks the modified tube-pore on the male P3ENP3, the bases of P2 and P3 possess an inner projection which is absent on the basis of P4, and the female caudal setae are not modified.

The female caudal rami of *S. geei* is similar to that of the other species of this group in the short spiniform outer seta I and in the long inner seta II of the caudal rami, and is morphologically closer to that of *S. huysi* in the somewhat bulbous basal part of caudal seta II. The outer spine on P4EXP2 and the inner seta on P4ENP1 are not elongate.

The caudal rami of these species are similar, with outer seta I, inner lateral seta II, inner ventral seta III (seta I short and spiniform, setae II and III long and plumose), and dorsal seta VII situated in the proximal half of the ramus, and the other three setae displaced distally. They share also the P4EXP displaced outwards, a patch of subdistal outer strong spinules ventrally, and an inner proximal hook-like inner extension on the caudal rami. This Indo-Pacific group of species, composed of *S. longipes sensu* Wells (1967) from Inhaca Island (Mozambique) (Wells 1967), *S. longipes sensu* Wells & Rao (1987) from Nicobar Island (Wells & Rao 1987), *S. jasani* and *S. daecheonensis* from Korea (Bang *et al.* 2022; Song *et al.* 2018), *S. huysi* from Thailand (Song *et al.* 2018), and *S. geei* from China (Mu & Huys 2004), is herein regarded as the most primitive within the *longipes*-complex.

Brevifurca-group. Wells (1967) described *S. brevifurca* from Inhaca Island (Mozambique). The description given by Wells (1967) is rather brief, and he omitted any comment on the urosome segmentation. However, the elongation of the P4ENP, and the elongation of the outer spine of P4EXP2 and inner seta of P4ENP1, as shown in his figure 13E suggest that, pending the confirmation of the presence of the other apomorphies for the *longipes*-complex (see above), *S. brevifurca* could be included in that core of species. This seems to be supported by the fact that Wells (1967) believed that *S. brevifurca* might be close to *S. longipes* to such an extent that he was not able to distinguish the males of *S. longipes* from those males attached to the females of *S. brevifurca*, and he even expressed doubts about the validity of his newly described species. However, caudal setae I and II of *S. brevifurca* are not modified, and caudal seta V, described by Wells (1967) as a “chitinous knob”, is very characteristic. The general shape of the caudal rami and its setae, including the modified caudal seta V, are very similar to those of *S. gomezi* as described by Nazari *et al.* (2018) from material collected at the intertidal zone in Bandar Abbas, between the Persian Gulf and Gulf of Oman (Iran), not far from the type locality of *S. brevifurca*. Nazari *et al.* (2018) attributed *S. gomezi* to Mu & Huys' (2004) *longipes*-group but they noted that their species lacks several apomorphies for the *longipes*-group *sensu* Mu & Huys (2004) (see above). *Scottolana brevifurca* and *S. gomezi* differ in the segmentation of the mandibular exopod (both segments seemingly well-separated in *S. brevifurca*, but imperfectly separated in the Iranian species), and shape of the distal outer element on P1ENP3 (a long seta in *S. brevifurca*, but a short spine in *S. gomezi*). The shape of the female genital area and the relative length of the outer spine of P4EXP2 and inner seta of P4ENP1 seem different, but these apparent differences could be due to the different drawing skills of the authors. The shape and situation of caudal setae I, II and III are similar to those of the *geei*-group, but the transformed caudal seta V in *S. brevifurca* and *S. gomezi* is regarded here as synapomorphic for these two species and is (aut)apomorphy for the *brevifurca*-group. This group is distributed in the Indian Ocean and is herein regarded as an early offshoot of the *longipes*-complex.

Longipes-group. This group as defined here is composed of *S. longipes* from Sri Lanka (Thompson I. C. & Scott A., 1903), *S. longipes sensu* Por (1964) from the Eastern Mediterranean (Por 1964), *S. dissimilis* from Papua New Guinea (Fiers 1982), and *S. wonchoeli* from Korea (Bang *et al.* 2022), and, pending the (re)description of the female, *S. uxoris* from the Red Sea (Por 1983). Apart from the characteristics common to these species [see Mu & Huys (2004)], they share the shape of caudal seta I and III, which are similar to those of the *geei*- and *brevifurca*-

groups. However, the species of the *longipes*-group as defined here share also the synapomorphic modification of caudal seta II into a pear-shaped reduced spine, (aut)apomorphic for the *longipes*-group. Caudal seta I and the modified caudal seta II are situated halfway the outer and inner margin of the rami, respectively, in *S. dissimilis*, *S. wonchoeli*, and *S. longipes*. These setae are located in the proximal third of the rami in *S. longipes sensu* Por (1964). Caudal seta III is located subdistally on the ventral surface of the ramus. This group of species displays a disjunct distribution from the Eastern Mediterranean and Red Sea (*S. longipes sensu* Por (1964) and *S. uxoris*) to Sri Lanka, Papua New Guinea and Korea in the Indo-Pacific (*S. longipes*, *S. dissimilis*, and *S. wonchoeli*).

The other species of *Scottolana* share the plesiomorphic six-segmented urosome, and lack all the apomorphies of the *longipes*-group *sensu* Mu & Huys (2004). These species can be grouped into three groups as follows.

Glabra-group. This Indo-Pacific group is composed of *S. glabra* from Laing Island, Papua New Guinea (Fiers 1982), and *S. oleosa* and *S. rostrata* from Andaman Islands (Wells & Rao 1987). The setae on the caudal rami are all situated (sub)distally with seta I on the outer margin, seta II on the inner margin, and seta III on the ventral surface of the ramus, and none of them are modified in the female.

Bulbosa-group. This group is composed of *S. bulbosa* from Netanya, Israel, Eastern Mediterranean Sea (Por 1964), *S. bulbifera* from Possjet Bay, Sea of Japan (Chislenko 1971) and Bohai Sea, China (Mu & Huys 2004), and *S. tumidiseta* from Andaman Islands (Wells & Rao 1987). All setae are displaced (sub)distally, and setae I and II are displaced inwards. Caudal setae I and II are situated on the distal third in *S. tumidiseta*. Seta I is reduced to a spiniform element ventral to seta II, the latter with proximal part strongly bulbous and with whip-like distal part. Seta III is located (sub)distally on the ventral surface of the ramus. The strongly bulbous appearance of seta II with a whip-like distal part is regarded here as (aut)apomorphic for the *bulbosa*-group and synapomorphic for its species; the (sub)distal inner displacement of caudal seta I is regarded here as synapomorphic for the *bulbosa*- and the *antillensis*-groups. This group displays a disjunct distribution from the Eastern Mediterranean (*S. bulbosa*) to the Indo-Pacific (*S. tumidiseta* in the Indian Ocean, and *S. bulbifera* in Japan and China Seas).

Antillensis-group. This Neotropical group is composed of two species, *S. antillensis* from Jamaica (Fiers 1984), and *S. tama* **sp. nov.** from north-western Mexico (present study). The caudal setae are displaced (sub)distally; caudal seta I is short and slender and is posterior to seta II, the latter is transformed into a strong blunt short inner spine and is regarded here as synapomorphic for these two species, and (aut)apomorphic for the *antillensis*-group. The inward displacement of caudal seta I is regarded here as a synapomorphy for the *antillensis*- and the *bulbosa*-groups. Caudal seta II of *S. tama* **sp. nov.** possesses a short setule-like structure probably homologous to the whip-like distal part of caudal seta II of the *bulbosa*-group.

The description of *S. scotti* from the Malay Archipelago by Sewell (1940), and *S. inopinata* from Sri Lanka by Thompson & Scott (1903), are very brief and inaccurate. These two species were not considered in the paragraphs above and their position will remain doubtful until their redescrptions are available. These two species are regarded here as *incertae sedis* within *Scottolana*.

Justification of *S. tama* **sp. nov.**

Fiers (1984) described a new species of *Scottolana*, *S. antillensis*, from Jamaica. This species was, at the time, the only one in which the female caudal seta II is modified into a strong blunt short spine. Fiers (1984) believed that *S. antillensis* resembled most *S. bulbifera*, but differed in the free P1-bearing somite [fused to cephalosome as shown in (Chislenko 1971)], in armature formula of P4EXP3 [with four setae in *S. antillensis*, but with five elements in Chislenko's (1971) *S. bulbifera*], and shape of the spines of P3ENP [outer spine on P3EXP1 elongate, and inner seta on P3ENP1 relatively shorter in Chislenko's (1971) *S. bulbifera*]. Mu & Huys (2004) provided the full redescription of *S. bulbifera* upon material from the Bohai Sea. They showed that the P1-bearing somite is not fused to the cephalosome, and that the outer spine on P3EXP1 is visibly longer than the other outer spines of that ramus, that the inner element on P3ENP1 is relatively shorter than in *S. antillensis* and spiniform, and that the P4EXP3 possesses four elements instead of five as in Chislenko (1971) who might have confused the distal inner outgrowth of P4EXP3 with a spine. *Scottolana tama* **sp. nov.** is clearly closely related to *S. antillensis* with which conforms a Neotropical monophyletic group defined by the (aut)apomorphic caudal seta II modified into a strong blunt short spine. These two species can be separated by i) the presence of a small setule-like structure on the modified seta II in the female of *S. tama* **sp. nov.** probably homologous to the whip-like distal part of caudal seta II of the *bulbosa*-

group [Fiers (1984) inspected two females and did not observe such structure]; ii) female antennule with second to fifth segments imperfectly separated in *S. tama* **sp. nov.**, but distinctly separated in *S. antillensis* [Fiers (1984) stated that the female antennule of *S. antillensis* is similar to that of *S. dissimilis*]; iii) antennary exopod eight-segmented in *S. tama* **sp. nov.** with one seta on first and second segments, but seven-segmented in *S. antillensis* with two setae on first segment [this might be an observational error since the second segment is sometimes concealed by the first segment giving the false impression of a single segment with two setae; also, the antennary exopod of *Scottolana* was diagnosed with eight–nine setae in Mu & Huys (2004)]; iv) mandibular exopod with two setae on the first segment in *S. tama* **sp. nov.**, but with one seta in *S. antillensis*, and second endopodal segment with eight setae in *S. tama* **sp. nov.**, but with nine setae in *S. antillensis*; v) maxillary exopod with eleven setae in *S. tama* **sp. nov.**, but with ten setae in *S. antillensis*, vi) maxillary endopod two-segmented in *S. tama* **sp. nov.**, but one-segmented in *S. antillensis*; vii) the syncoxa of the maxilliped possesses nine setae (one praecoxal, eight coxal), the basis has two and the endopod 11 setae in *S. tama* **sp. nov.**, but the syncoxa possesses ten elements (one praecoxal, nine coxal), basis has three and endopod ten setae in *S. antillensis* [Fiers (1984) interpreted the praecoxa and coxa of the maxilliped as separate segments of which the praecoxa is unarmed; the division between the praecoxa and coxa in Fiers' (1984) figure 2a is reinterpreted here as an integumental fold, thus being the praecoxa and coxa fused, with one praecoxal and nine coxal elements; the distalmost basal seta in Fiers' (1984) figure 2a is reinterpreted here as the innermost proximal endopodal seta, and therefore, the endopod possesses 11 setae instead]; viii) male P6 with one distal seta in *S. tama* **sp. nov.**, but unarmed in *S. antillensis* [however Fiers (1984), only found and inspected one male whose P6 seems to have the inner cuticle interrupted [see Fiers' (1984) figure 3g], probably indicating the place where an armature element was inserted; the unarmed condition of the male P6 of *S. antillensis* still needs confirmation].

The genus *Canuellina* and justification of *C. pacifica* **sp. nov.**

Sewell (1940) proposed *Ellucana* as a new subgenus of *Canuella* Scott T. & Scott A., 1893 for *Canuella (Ellucana) longicauda* Sewell, 1940 found in weed-washings at Nicobar Island. Coull (1971) gave the subgenus *Ellucana* full genus rank, and described *E. secunda* from the North Carolina continental shelf. Additionally, he commented on the presence of this species in Barbados (Coull 1970). Coull (1971) believed that *Ellucana* and *Canuellina* were closely related by the reduction in setation of P2 and P3, and by the similar genital fields. Coull (1971) gave an ample list of differences between *E. longicauda* and *E. secunda* from which he separated both species, but probably driven by Sewell's (1940) brief description of *E. longicauda*, he suspected that, if rediscovered, the latter would prove to be conspecific with *E. secunda*. In his redescription of *E. longicauda*, Fiers (1982) rediagnosed the genus *Ellucana* and commented on the similarity between that genus and *Canuellina*. Fiers (1984) partially redescribed the female of *E. secunda* found in washings of coarse coral sand from Curaçao, and despite his list of differences, he concluded that *E. secunda* and *E. longicauda* were closely related. In his brief diagnosis of *Canuellina*, Por (1984) gave a list of species of that genus in which he included, without any reasoning, *Canuellina secunda*. By 1984, *E. secunda* was known to be distributed in Barbados, North Carolina, and Curaçao (Coull 1970, 1971; Fiers, 1984), and Yucatan, Mexico (Fiers 1984). Huys (2016) detected two lineages amongst the species included in *Ellucana* and *Canuellina* and he transferred *C. onchophora* Por, 1967 and *C. nicobaris* Wells & Rao 1987 to *Ellucana*, and *E. secunda* to *Canuellina*. These moves were based on i) the presence of normal outer spines on P4EXP2 and EXP3 in *Ellucana*, but elongated outer elements in *Canuellina*, ii) the shape of the male genital field with triangular opercula bearing a long basal styliform element and an inner uncinata spine, and a slender apical seta in *Ellucana*, but with several chitinized areas and lack of triangular opercula in *Canuellina*, and iii) male P4EXP3 sexually dimorphic in *Ellucana*, but P4EXP3 not modified in the males of *Canuellina* (Huys 2016). The male genital field is very similar in a core of species of *Canuellina*, viz. *C. canalis*, *C. femur*, and *C. tuba* (the male of *C. insignis* remains unknown). The opercula in *C. canalis*, *C. femur*, and *C. tuba* is reduced to a small plate with a distal short seta, and the inner uncinata spine and the basal styliform element are larger than in *Ellucana*. The male genital field in *C. secunda* is radically different. It is composed of P6 bearing four setae (one inner minute, one middle inner long, one middle outer half as long as the previous seta, and one outer element).

The Mexican material is clearly related to *C. secunda*. It fits all previous descriptions of the latter, but some differences were detected. These are: i) P5-bearing somite with dorsal pattern of chitinized plates in the new species, absent in *C. secunda*, ii) female and male caudal ramus with seven setae of which six unmodified, and one

transformed into triangular blunt, hyaline spiniform dorsal element close to outer subdistal margin, but caudal ramus with six unmodified setae in *C. secunda*, iii) antennary basis with one seta in the new species, but basis unarmed in *C. secunda*, iv) relative length of the distal inner seta on the P3EXP3 (nearly half as long as the distal outer seta in *C. pacifica* **sp. nov.**, but distal inner seta only slightly shorter than the distal outer element in *C. secunda*, v) relative length of the distal inner element on P3ENP3 (shorter than distal outer seta in *C. pacifica* **sp. nov.**, but visibly longer in *C. secunda*), vi) relative length of the distal inner seta on P2EXP3 (visibly shorter than distal outer element in *C. pacifica* **sp. nov.**, but as long as distal outer element in *C. secunda*), vii) P2ENP2 with long stiff inner seta parallel to inner margin of outer projection in *C. pacifica* **sp. nov.**, but ENP2 unarmed in *C. secunda*.

At present, the genus *Canuellina* is composed of *C. canalis* from the Suez Canal, Sirbonian lagoon and south Red Sea (Por 1969), *C. femur* from the Gulf of Eilat (Por 1967), *C. insignis* from Port Said (Suez Canal) (Gurney 1927), *C. tuba* from the Gulf of Eilat and Red Sea (Por 1983), and *C. secunda* known from the Gulf of Mexico and the Caribbean Sea (Coull 1970, 1971; Fiers 1984), and *C. pacifica* **sp. nov.** from the Mexican eastern tropical Pacific (present study). We believe that *Canuellina*, as currently known, is composed of two different lineages. The *canalis* lineage (*C. canalis*, *C. femur*, and *C. tuba*, and most probably, *C. insignis*) is distributed in the Red Sea and Suez Canal areas. The Neotropical *secunda* lineage (*C. secunda* and *C. pacifica* **sp. nov.**) is distributed in the Gulf of Mexico, Caribbean Sea, and north-western coast of Mexico. These lineages share the elongate outer spines on P4EXP2 and EXP3, but can be readily separated by the shape of the male P6 and genital field.

Ecology and distribution

Despite the low density of Canuelloida copepods in Ohuira Bay, their distribution showed a spatial pattern related to sediment grain size, organic carbon content, and dissolved oxygen. The reduction in sand and the increase in clay and silt content restricts the presence of copepods in the upper region of the bay (stations 9 to 11). Additionally, the increase in organic carbon at station 11 could be related to shrimp farming activities, which could alter the habitat structure and oxygen availability. Previous studies in estuaries with higher copepod densities (10 to 370 ind. 10 cm⁻²) showed a clear seasonal pattern in the copepod community, including the genera *Longipedia* and *Scottolana*, with higher densities prior to the rainy season (Ansari & Parulekar 1993). In our study, the February sampling occurred during the dry cool season, while June corresponds to the period before the rainy season (Amezcuca *et al.* 2019). However, we did not find clear temporal variations between months. It could be appropriate to explore this over a more extended period, ideally by sampling for at least two years and including at least two sampling events (i.e., replicates) within the same season.

The relatively low deviance in the model for both species suggests that ecological relationships could be relevant to seasonal variations. It has been observed that invertebrate predators regulate the populations of *Scottolana* species in Chesapeake Bay, and predation rates frequently exceed the ability of copepod populations to increase (Lonsdale 1981). However, in Ohuira Bay, the lack of knowledge about other marine invertebrates as potential predators hampers inference in this regard. The only documented ecological interactions in the area are between the ctenophore *Pleurobrachia bachei* Agassiz A. and the pelagic copepod *Microsetella norvegica* (Boeck, 1865) (Morales-Ávila *et al.* 2023).

The present study provides taxonomic descriptions of two new species of benthic copepods and ecological distribution notes for Ohuira Bay. The knowledge about macro- and meiofauna is relevant to evaluate the effectiveness of marine protected areas since species records contribute towards a complete faunal list, which is the first step for understanding distribution patterns and monitoring biodiversity.

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