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Two new Canthocamptidae (Copepoda, Harpacticoida) from sponges of the Kara and Laptev Seas

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Abstract

We studied copepods washed off the sponges from two Arctic seas: the Kara and the Laptev. We found new species in families Miraciidae, Canthocamptidae Brady, 1880, Argestidae, and Ectinosomatidae. We describe two new species of the Canthocamptidae Brady, 1880. *Heteropsyllus spongiophilus* **sp. nov.** from the Kara Sea, differs from its congeners in the armament of the swimming legs and the maxilliped. *Mesopsyllus glacialis* **sp. nov.** from the Laptev Sea, can be distinguished by the legs armament, its sexual dimorphism and the 7-segmented female antennules.

Key words: Arctic Ocean, arctic fauna, meiobenthic Copepoda, *Heteropsyllus*, *Mesopsyllus*

Introduction

We studied copepods washed off from sponges of the Arctic Kara and Laptev Seas, both typical Arctic seas with shallow depths and uniform bottom. Bottom substrates are represented by silt, thus reducing the number of ecological niches and the biological diversity of benthic copepods (Chertoprud 2018). In this regard, sponges are a component increasing the local environmental heterogeneity. They provide a rigid substrate that rises above the bottom surface and creates a flow of water near their surface.

We found new species in families Miraciidae Dana, 1846, Canthocamptidae Brady, 1880, Argestidae Por, 1986, and Ectinosomatidae Sars G.O., 1903. We describe two new species of the family Canthocamptidae Brady, 1880.

Canthocamptidae is one of the largest copepod families in terms of the number of species. Members of this family has mastered various ecological niches and are found both in sea and fresh water bodies. The taxonomy of this family is rather complex. Species and genus possessing the most primitive set of characters are of the greatest interest for taxonomy. It is obvious that such representatives must be sought in the seas. These include the subfamily Hemimesochrinae Por, 1986 and the problematic genus *Heteropsyllus* Scott T., 1894.

Heteropsyllus is a fairly large genus found only in the Northern Hemisphere, with 15 distinct species. *Mesopsyllus* Por, 1960 is a basal representative of Hemimesochrinae (Huys & Thistle 1989). This genus includes only 5 species of which 3 have been described in the last 15 years. In the studied samples, we found 3 species of *Mesopsyllus*: *M. curvisetus* (Kornev & Chertoprud, 2008), *M. glacialis* **sp. nov**. and *M.* sp. 1, however, we found only one female of the latter species, so we do not present its description. The aim of this paper is to describe two new interesting species from the genera *Heteropsyllus* and *Mesopsyllus*.

Materials and methods

Sponges were collected during three multispecies trawl surveys with the Murmansk Marine Biological Institute (MMBI) research vessel Dalniye Zelentsy in the Laptev (2014) and Kara Seas (2016). All surveys were performed with a Sigsbee trawl. Samples were preserved in 4% formaldehyde solution on the board of the research vessel, transported to MMBI, later rinsed, and transferred to 70% ethanol. A detailed description of the studied sponges is given in the work of Morozov et al. (2019).

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The copepods were collected by washing the sponges in tap water in a small plankton net (mesh size of 100 μm), and the resulting precipitate was fixed in formalin. Subsequently, the sponge washings were taken apart under a stereomicroscope. Specimens were dissected under a stereomicroscope, with each element being placed under a separate cover slip. Rough drawings were generated on printed photographs of elements, and the final drawings were prepared using the free program Inkscape 1.0.

All material was deposited in Zoological museum of Kazan Federal University.

The following abbreviations were used throughout the text and in the figures: ae= aesthetasc, acr = acrothek, P1–P6 = legs 1–6, Exp1-Exp3 = first-third segments of exopod, End1-End3 = first-third segments of endopod. Nomenclature and descriptive terminology follows Huys and Boxshall (1991), terminology in genital fields follows Moura and Pottek (1998), terminology in mandibular structure follows Mielke (1984).

Taxonomic account

Order Harpacticoida Sars, 1903

Family Canthocamptidae Sars, 1906

Genus *Heteropsyllus* Scott T., 1894

Heteropsyllus spongiophilus sp. nov.

http://zoobank.org/C170192C-44F3-416C-8206-D71A6B003DDB

Etymology. The species is named so because it was found only on sponges. The specific epithet is adjective.

Type locality. Kara Sea (73.08556°N, 67.60111°E) in sample with sponges *Polymastia grimaldii* (Topsent, 1913); *Tetilla sibirica* (Fristedt, 1887); *Semisuberites cribrosa* (Miklucho-Maclay, 1870); *Suberites sp.* Depth 55 m.

Material examined. Holotype: female, dissected and mounted on 2 slides (BP 542/1-a; 542/1 -b). Allotype, male dissected and mounted on one slide (542/2). Paratypes: one female dissected and mounted on one slide (542/3), two females and one V copepodite undissected formalin-preserved (542/4).

Description. *Female*. Body short, flattened. Total body length of holotype from anterior margin of rostrum to posterior margin of caudal rami: 0.457 mm. Fixed individuals have a pink tint. Naupliar eye not discernible. Cephalothorax (Figs. 1A,B) consisting of cephalosome with fused first pedigerous somite, wider as remaining somites, largest width 0.131 mm. Rostrum (Fig. 1C) clearly separate from the cephalothorax, with one pair of sensilla. Posterior margin of cephalothorax and second-fourth pedigerous somites smooth; posterior margin of fifth pedigerous somite with serrulate hyaline frills.

Cephalothorax with 33 pairs of sensilla, one unpaired sensilla and 6 pairs of pores. Second pedigerous somite with 9 pairs of sensilla, one unpaired pore and with several rows of small spinules. Third pedigerous somite with 9 pairs of sensills and one dorsal row of small spinules. Fourth pedigerous somite with 8 pairs of sensilla and one pair of pores. Fifth pedigerous somite with 3 pairs of sensilla, one pair of pores, one dorsal row of small spinules and paired lateral rows of large spinules.

Abdomen (Figs. 2A-C) short and wide, consisting of genital-double somite, two free abdominal somites and anal somite with caudal rami. All somites except anal somite on posterior margin with serrulate hyaline frills. Genital-double somite wider than long, flattened; with rows of small spinules, on posterior margin with lateral and dorso-lateral rows of spinules; with 7 pairs of sensilla, one pair of lateral pores and one pair of ventral large tube pores. P6 fused with somite with 3 naked setae. Genital field large laterally with sieve; copulatory pore shifted to the first urosomite, copulatory duct strongly chitinized wide and long, extending proximally to pair of labyrinthic rounded ducts.

First free abdominal somite with three pairs of sensilla, one pair of lateral and one pair of ventral pores; on posterior margin with circumsomitic transverse spinular row with gap dorsally. Second free abdominal somite on posterior margin with ventro-lateral row of spinules. Anal somite with one pair of sensilla, three pairs of lateral

pores, one pair of ventral pores and row of spinules postero-laterally. Anal operculum long with lots (holotype with 18) posterior spinules.

Caudal rami (Figs. 2A-C) square, length/width ratio 1, with one dorsal and two ventral pores; with one row of spinules on interior margin and row of spinules at base of setae I-III. Seta I small, located between setae II and III. Apical setae IV and V (Fig. 1D) long, with spinules, length 0.137 mm and 0.321 mm respectively. Seta VII triarticulated.

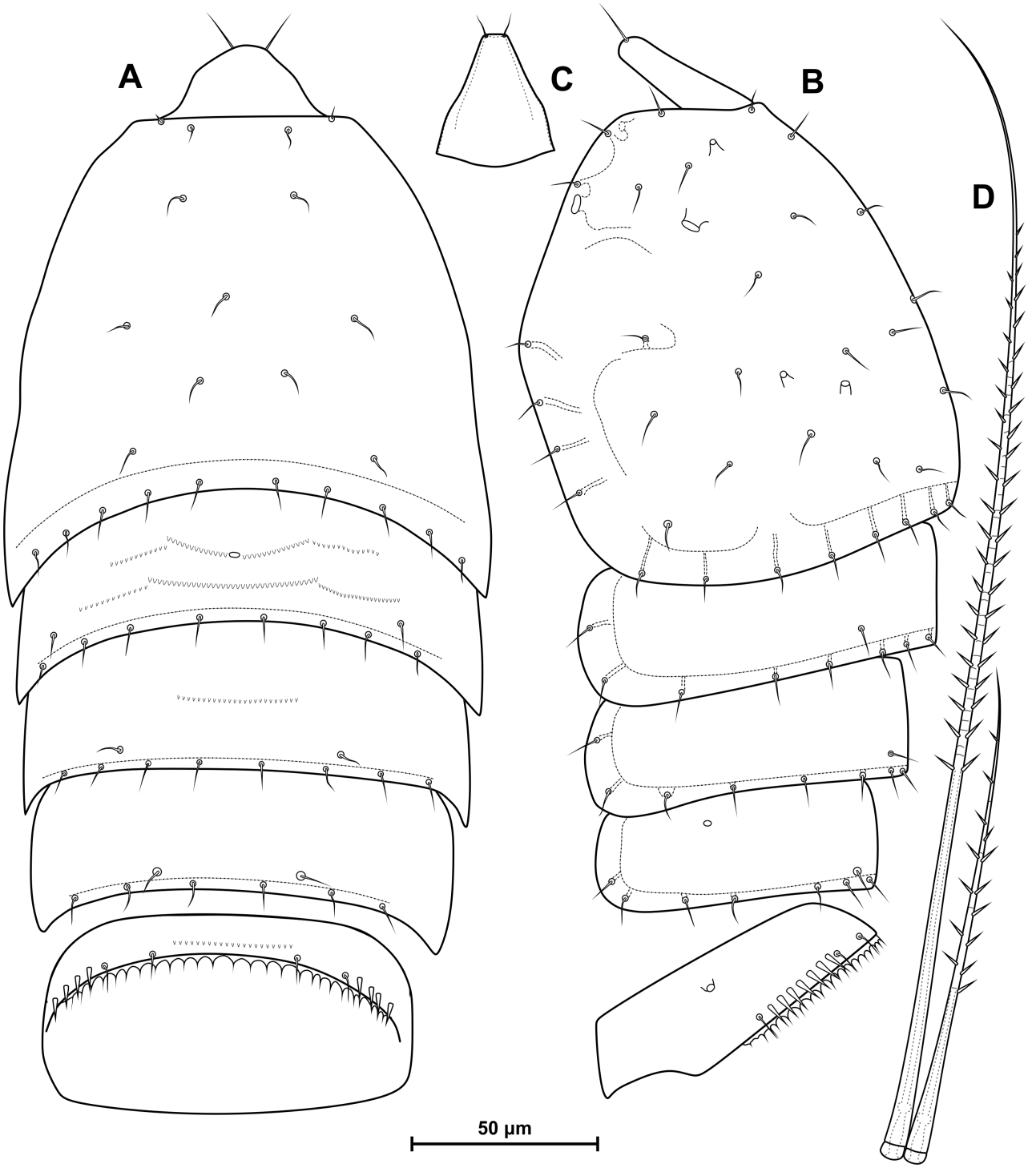

FIGURE 1. *Heteropsyllus spongiophilus* sp. nov. Female holotype: A, cephalothorax and thoracic somites, dorsal; B, cephalothorax and thoracic somites, lateral; C, rostrum, frontal; D, apical setae of caudal rami, dorsal.

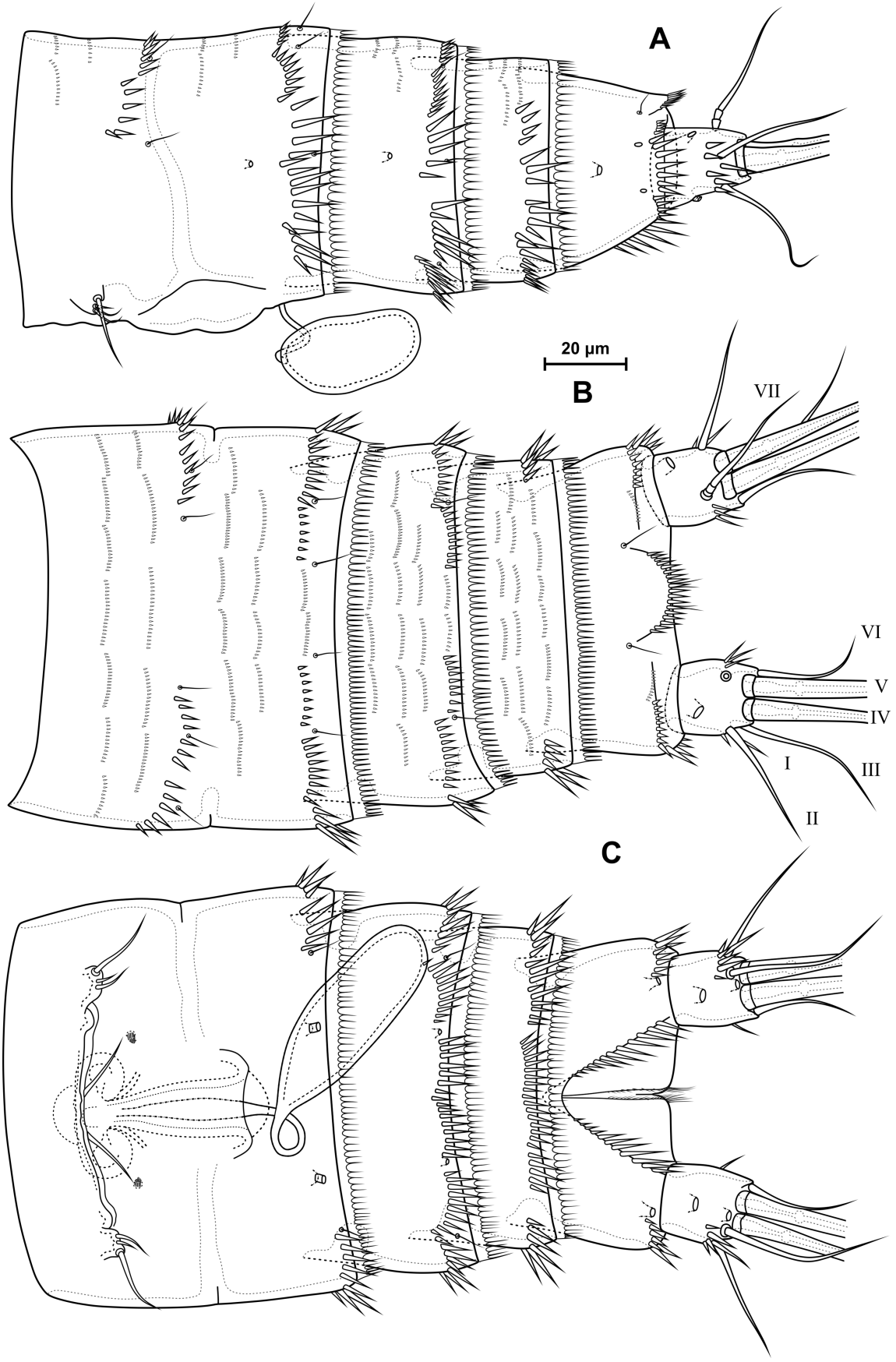

FIGURE 2. *Heteropsyllus spongiophilus* sp. nov. Female paratype: A, abdomen, lateral; B, abdomen, dorsal; C, abdomen, ventral.

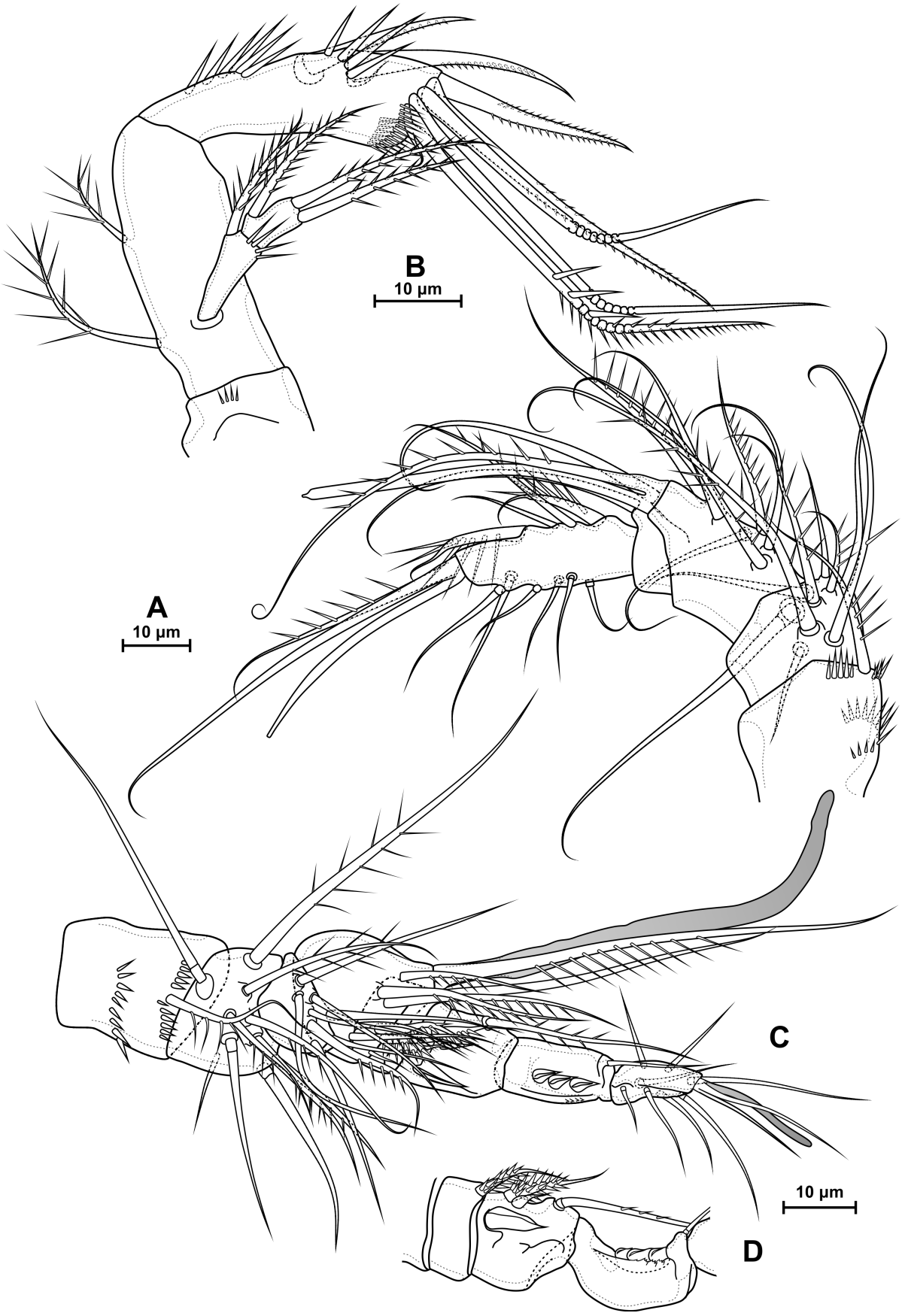

FIGURE 3. *Heteropsyllus spongiophilus* sp. nov. Female holotype: A, antennule; B, antenna. Male allotype: C, antennule, anterior; D, antennule, segments 6-8, dorsal.

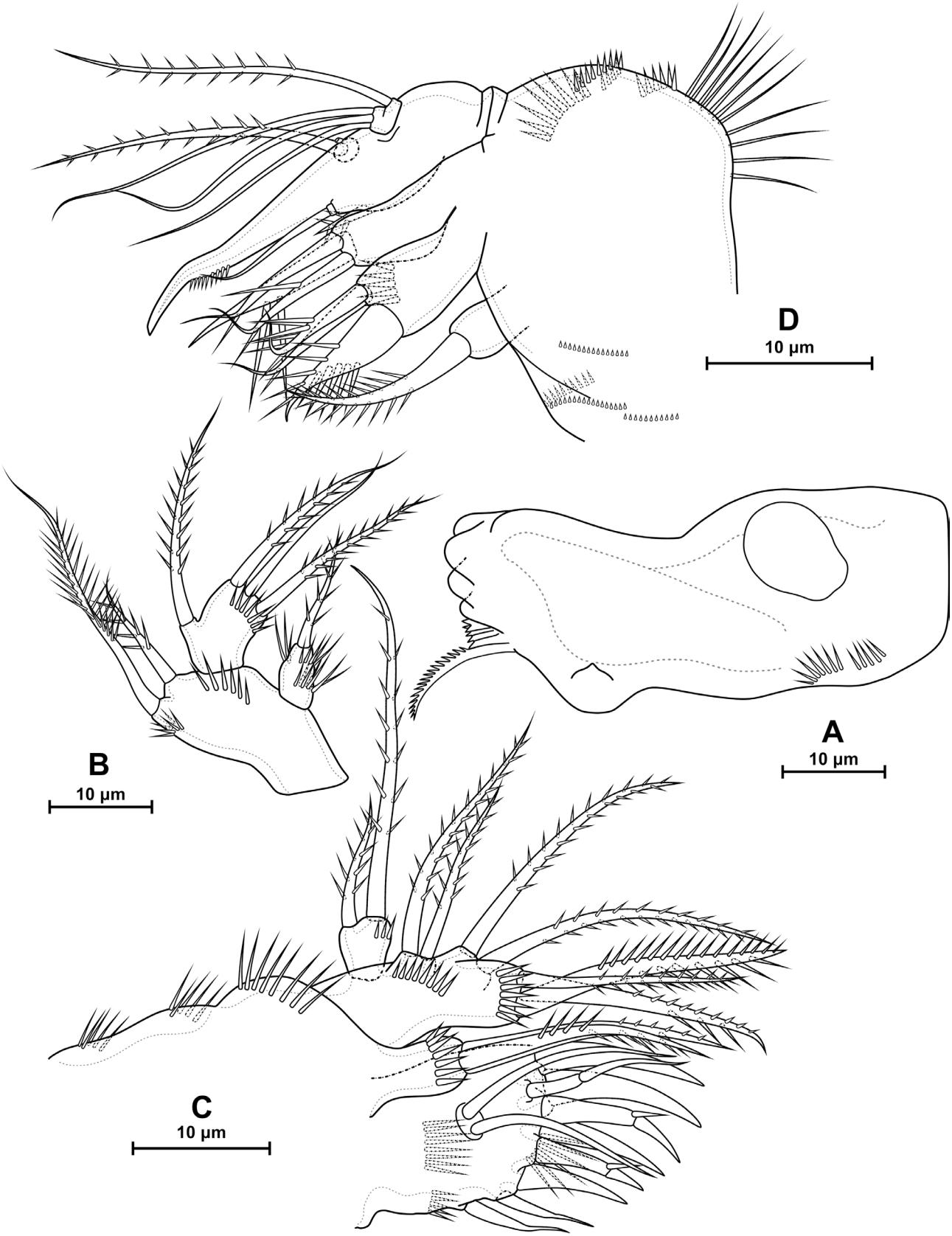

FIGURE 4. *Heteropsyllus spongiophilus* sp. nov. Female holotype: A, mandible, coxa; B, mandible, palp; C, maxillule; D, maxilla.

Antennule (Fig. 3A): short, 5-segmented. Segment 1 square, with one unipinnate seta, with two rows of spinules proximally and two rows of spinules at base of seta. Segment 2 wide, with 4 pinnate and 5 naked setae. Segment 3 with 3 free pinnate, 4 free naked setae and fused basally pinnate seta and aesthetasc. Distal segment with 2 "pine-apple-setae" (sensu Hamond, 1971), 8 naked setae and acrothek consisting of aesthetasc and two setae fused basally. Armature formula: 1-[1],2-[9],3-[7+(1+ae)],4-[1],5-[10+acr].

Antenna (Fig. 3B) with allobasis. Coxa with one spinular row. Allobasis with two bipinnate setae. Free endopodal segment with two lateral rows of large spinules, with one free spinulose spine and fused basally small seta and spinulose spine; distally with two rows of spinules; apically with three geniculate setae, two long spines and one small seta; outermost geniculate seta fused basally to small seta. Exopod 2-segmented; first segment with one bipinnate seta and one distal spinular row; second segment with 3 bipinnate setae.

Mandible (Fig. 4A,B). Coxa with spinules proximally. Gnathobase massive, with few multicuspidate teeth, spinulose seta; pars incisiva and lacinia mobilis with 4 blunt wide teeth. Pars molaris with sharply-edged. Palp consisting of free basis, 1-segmented endopod and exopod. Basis with two rows of spinules and two pinnate setae; exopod with slender spinules and one pinnate seta; Endopod with one dorsal spinular row, one pinnate proximal seta, two distal pinnate setae and one distal naked seta.

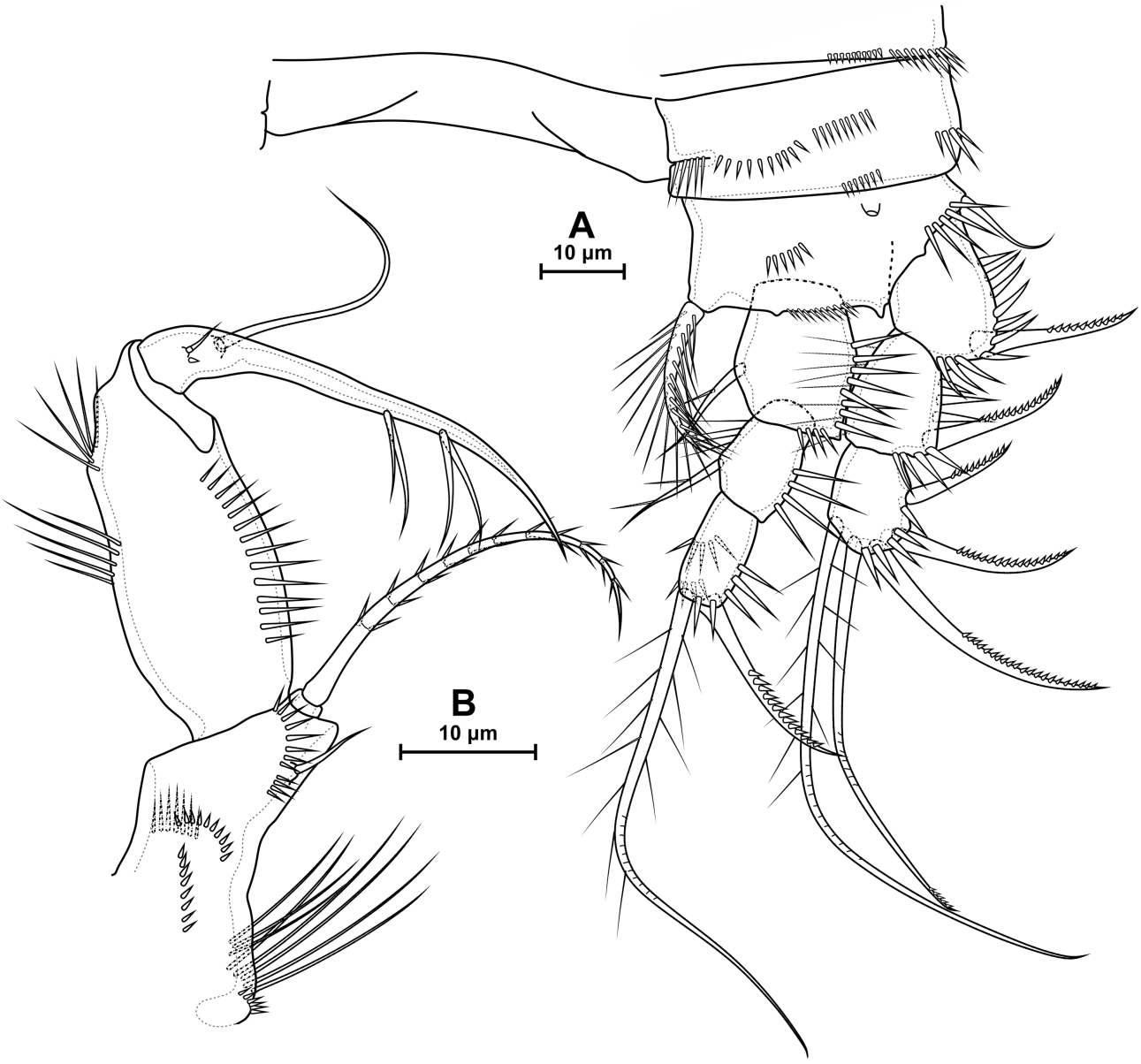

FIGURE 5. *Heteropsyllus spongiophilus* sp. nov. Female holotype: A, P1, anterior; B, maxilliped, anterior.

Maxillule (Fig. 4C). Praecoxa with 2 rows of slender spinules on outer edge. Praecoxal arthrite medially with 2 rows of spinules and two naked setae; distally with 7 strong spines and two setae. Coxa with row of slender spinules, coxal endite reaching middle of arthrite, with two spinulose setae. Basis with two rows of spinules and 5 pinnate setae. Endopod incorporated into basis, represented by protuberance with two pinnate setae. Exopod free, with spinules and two pinnate setae.

Maxilla (Fig. 4D). Syncoxa with several rows of spinules on outer and inner edge as figured, with three endites. Proximal endite with one strong bipinnate seta, middle and distal endites with three setae. Allobasis with 3 setae, one tube pore and massive distal claw. Endopod short with one pinnate proximal seta and three distal naked setae.

Maxilliped (Fig. 5B) subchelate. Syncoxa elongated with several rows of spinules as figured, distally with one small naked and one large "rat-tail" setae. Basis with one row of large inner spinules and two rows of outer slender spinules. Endopod on posterior side with one seta, on anterior side with one small seta and one small protuberance, possibly reduced seta or pore. Endopodal claw elongated, with two pairs of long slender spinules.

P1 (Fig. 5A) with 3-segmented rami. Praecoxa with row of spinules. Coxa wide, with inner fold, with spinular ornamentation as figured. Intercoxal sclerite very expanded. Basis with proximal pore, medial row of spinules, rows of spinules at base of endopod and exopod, with outer naked seta and inner strong pinnate seta. All endopodal and exopodal segments with outer spinules. First and second exopodal segments with one outer spine; third exopodal segment with tree outer spine and two apical long geniculate setae. Endopod is approximately as long as exopod. First and second endopodal segments with one inner seta, third segment with two rows of spinules on posterior side, distally with outer spine and apical long geniculate seta.

P2 (Fig. 6A). Praecoxa with row of spinule. Coxa with inner fold, with one lateral row of spinules and three closely spaced proximal rows of spinules. Basis with proximal pore, medial row of spinules, two rows of slender spinules on inner edge, rows of spinules at base of endopod and exopod; with outer bipinnate seta. All endopodal and exopodal segments with outer spinules. Exopod 3-segmented; first exopodal segment with outer spine, inner row of slender spinules and apically with frill; second segment with outer spine, inner seta, inner spinules and apical frill; third segment with three outer spines, two apical and one inner setae. Endopod 2-segmented; reaching about half of second exopodal segment; first segment with inner seta and pore, second segment with outer spine, two apical setae and two inner setae, on posterior side with spinular row.

P3 (Fig. 6B) similar to P2. Praecoxa, intercoxal sclerite and basis as in P2. Coxa with one lateral and three proximal rows of spinules and with one pore. Exopod as in P2, but third exopodal segment P3 with two inner setae. Endopod as in P2, but reaching about 1/3 of second exopodal segment and first segment without pore.

P4 (Fig. 6C) also similar to P2. Praecoxa, intercoxal sclerite, coxa and basis as in P2. Exopod as in P2, but third exopodal segment P4 with two inner setae, the distal one with strong spinules. Endopod small, reaching about 1/4 of second exopodal segment, with row of spinules on posterior side; first segment with inner seta; second segment with small naked outer spine and four bipinnate setae.

Armature of swimming legs as follows:

	endopod	exopod
P1	1; 1; 0,1,1	0; 0; 0,2,3
P2	1; 2,2,1	0; 1; 1,2,3
P3	1; 2,2,1	0; 1; 2,2,3
P4	1; 2,2,1	0; 1; 2,2,3

P5 (Fig. 8A) with separate right and left baseoendopods. Baseoendopod elongated, reaching about midlength of exopodal segment; with spinular rows on inner and outer side of endopodal lobe and at base of exopod and outer seta; outer seta of basis naked. Endopodal lobe with two pores and five setae. Exopod elongated, length/width ratio 3.45; with long spinules on inner and outer side; with 5 naked setae.

Male. Total body length from tip of rostrum to posterior margin of caudal rami: 0.354 mm. Sexual dimorphism expressed in the antennule, P2–P6, genital segmentation and ornamentation. Abdomen (Figs. 7A-C) narrower than female. Ornamentation and sensilla of somites 1, 3-5 as in female, but spinules larger. Somite 2 also as in female, but with on posterior margin circumsomitic transverse spinular row with gap dorsally. P6 fused with first abdominal somite, with three bare setae (Fig. 7C). Anal operculum with a lot of spinules (allotype with 26). Caudal rami as in female.

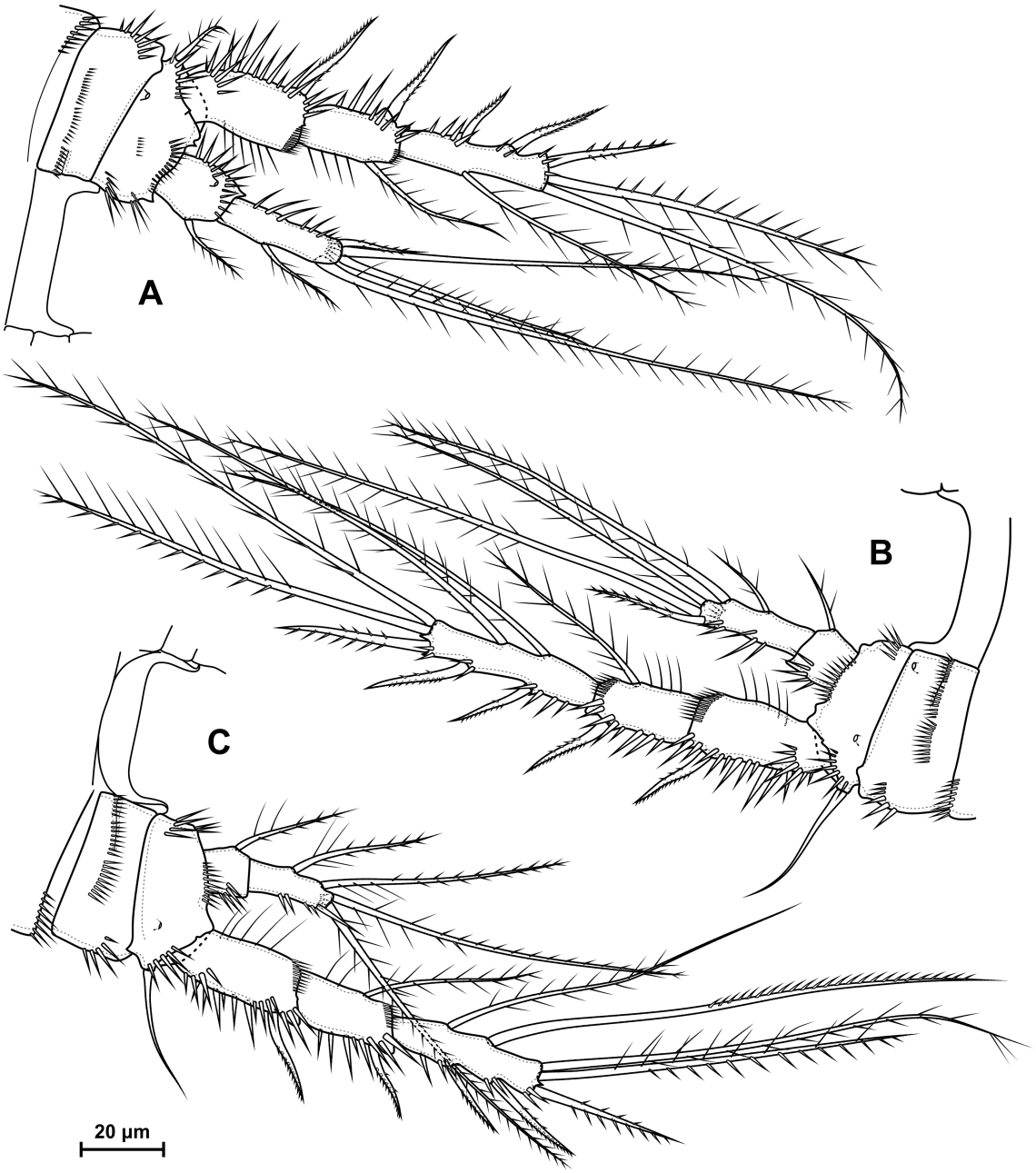

FIGURE 6. *Heteropsyllus spongiophilus* sp. nov. Female holotype: A, P2, anterior; B, P3, anterior; C, P4, anterior.

Antennule (Figs. 3C,D) 9-segmented, haplocer with geniculation between segments 7 and 8. "Pineapple-setae" located on 5 – 7 segments. Segment 1 with four rows of spinules. Segment 5 with large aestetasc fused at base with long unipinnate seta. Segment 7 with one modified lamellar seta one short modified seta. Segments 7 – 9 with articular surfaces. Segment 8 with three identical modified lamellar setae with thin tip. Segment 9 with acrothek consisting of small aestetasc and two setae. Armature formula: 1-[1],2-[10],3-[8],4-[2],5-[6+(1+ae)],6-[2],7-[2+2 modified],8-[1+3 modified],9-[8+acr].

P2 (Fig. 9A) almost like P2 female. Differences in shape of distal segments of endopod and exopod, in shape of intercoxal sclerite and length of endopodal setae.

P3 (Fig. 9B). Praecoxa, coxa, basis, first endopodal segment and segments 1–2 of exopod as in female. Distal

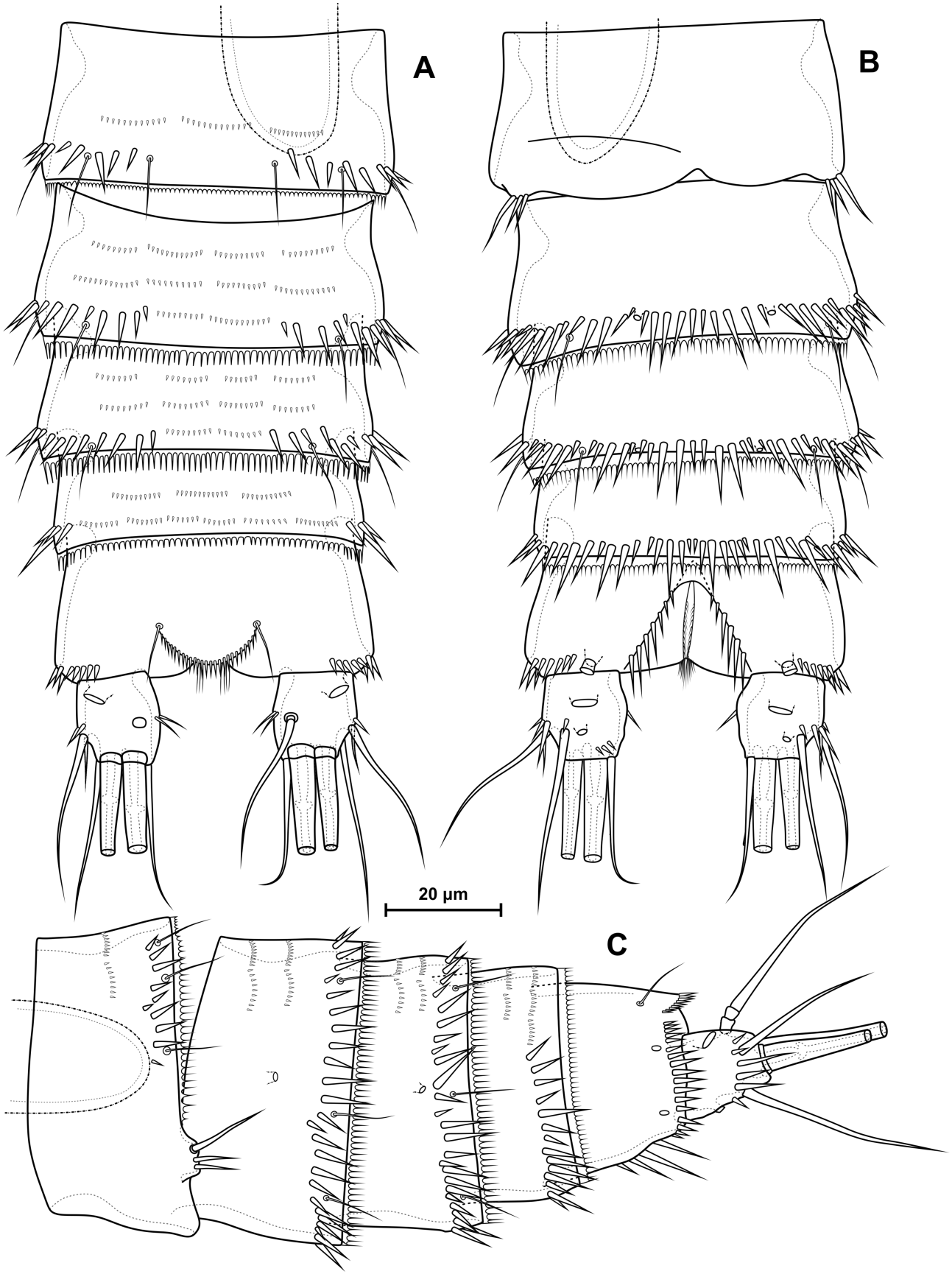

FIGURE 7. *Heteropsyllus spongiophilus* sp. nov. Male paratype: A, abdomen, dorsal; B, abdomen, ventral; C, abdomen lateral.

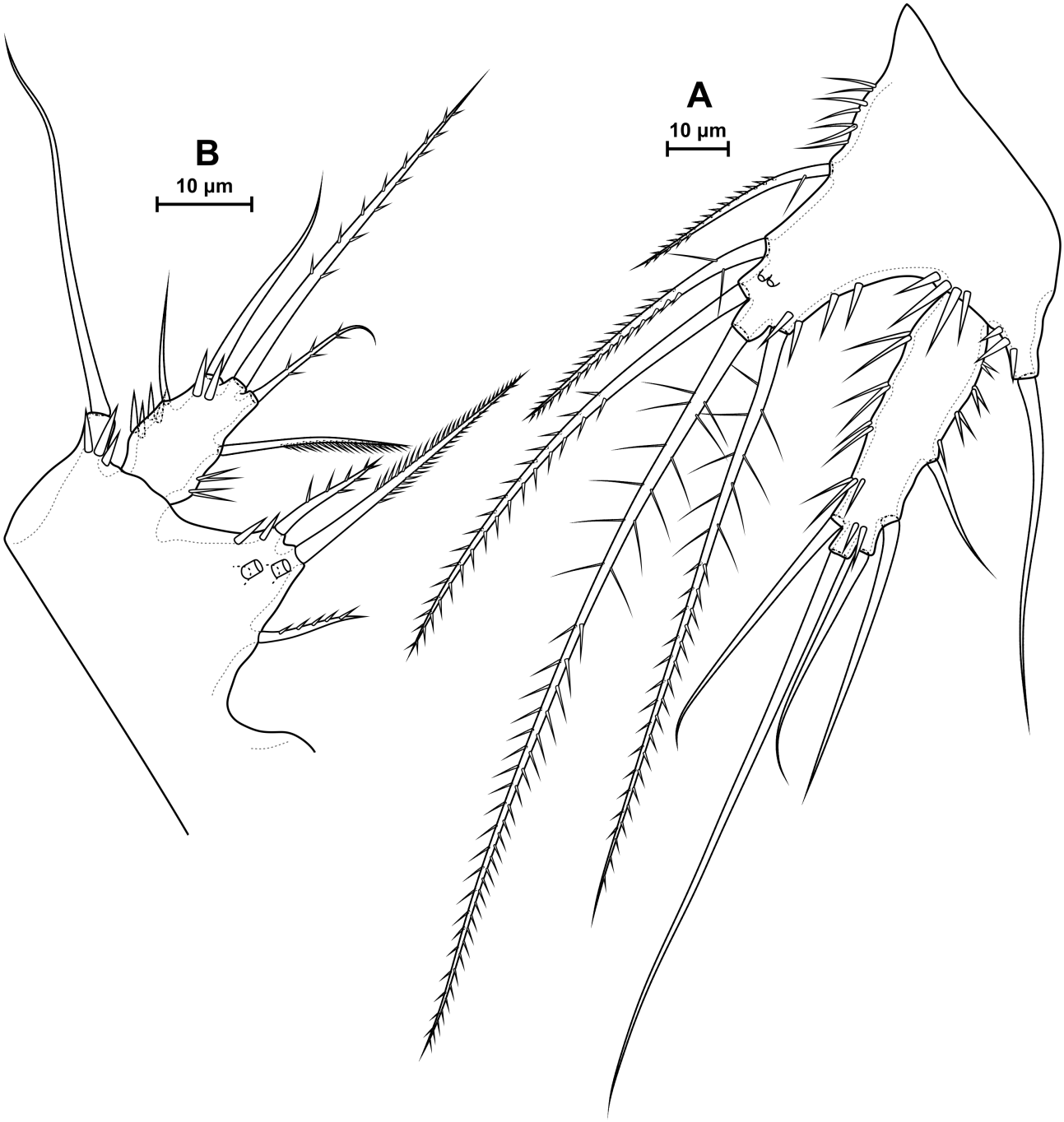

FIGURE 8. *Heteropsyllus spongiophilus* sp. nov. Female paratype: A, P5, anterior. Male allotype: B, P5, anterior.

exopodal segment shorter, inner setae with very close bases. Distal endopodal segment modified; outer seta curve and wide, transformed into apophysis and shifted on front side. One of apical setae fused at base with segment.

P4 (Fig. 9C) differs from P4 female only in shape of distal segments of endopod, exopod and intercoxal sclerite. Also first segment of endopod without row of spinules.

P5 (Fig. 8B) with left and right baseoendopods fused medially; baseoendopod with two rows of spinules, two tube pores, with one outer naked seta and three endopodal pinnate setae. Exopod short (length/width ratio 1.7) with spinules on inner, outer and distal margin; with inner pectinate seta, two apical pinnate setae and two outer naked setae.

Variability. P2 of one female without inner seta.

Ecology. Probably, like most of the other harpacticoids found in washings from sponges, *H. spongiophilus* **sp. nov.** is not an obligate inhabitant of sponges. The shape of the mouthparts and swimming legs does not have any

modifications and is similar to those of other species of the genus. Sponges for this species are most likely a convenient place in terms of food and shelter. *H. spongiophilus* **sp. nov.** most likely has the same diet as *H. pseudonunni* Coull & Palmer, 1980. Preferred feeding on detritus and bacteria is described for this species (Ustach, 1982).

Remarks. Together with the new species, the genus *Heteropsyllus* has 16 species and subspecies. According to our and published data, representatives of the genus are typical components of the seas of the Arctic Basin (Chertoprud et al. 2018, Garlitska et al. 2019). Within the genus, the described species are rather well distinguished. The new species has a unique combination of morphological features. Apparently, the closest species is *H. coulli* Kornev & Chertoprud, 2008. In general, both species have a set of traits plesiomorphic for the genus, especially in the armament of P2-P4 endopods. However, they are brought together by the reduction of the inner seta of the distal segment of the P1 endopod; both species also have a similar structure of mouthparts and P5. They differ well in the number of setae on P2 endopod of females, where *H. coulli* has six setae and *H. spongiophilus* **sp. nov.** has five setae.

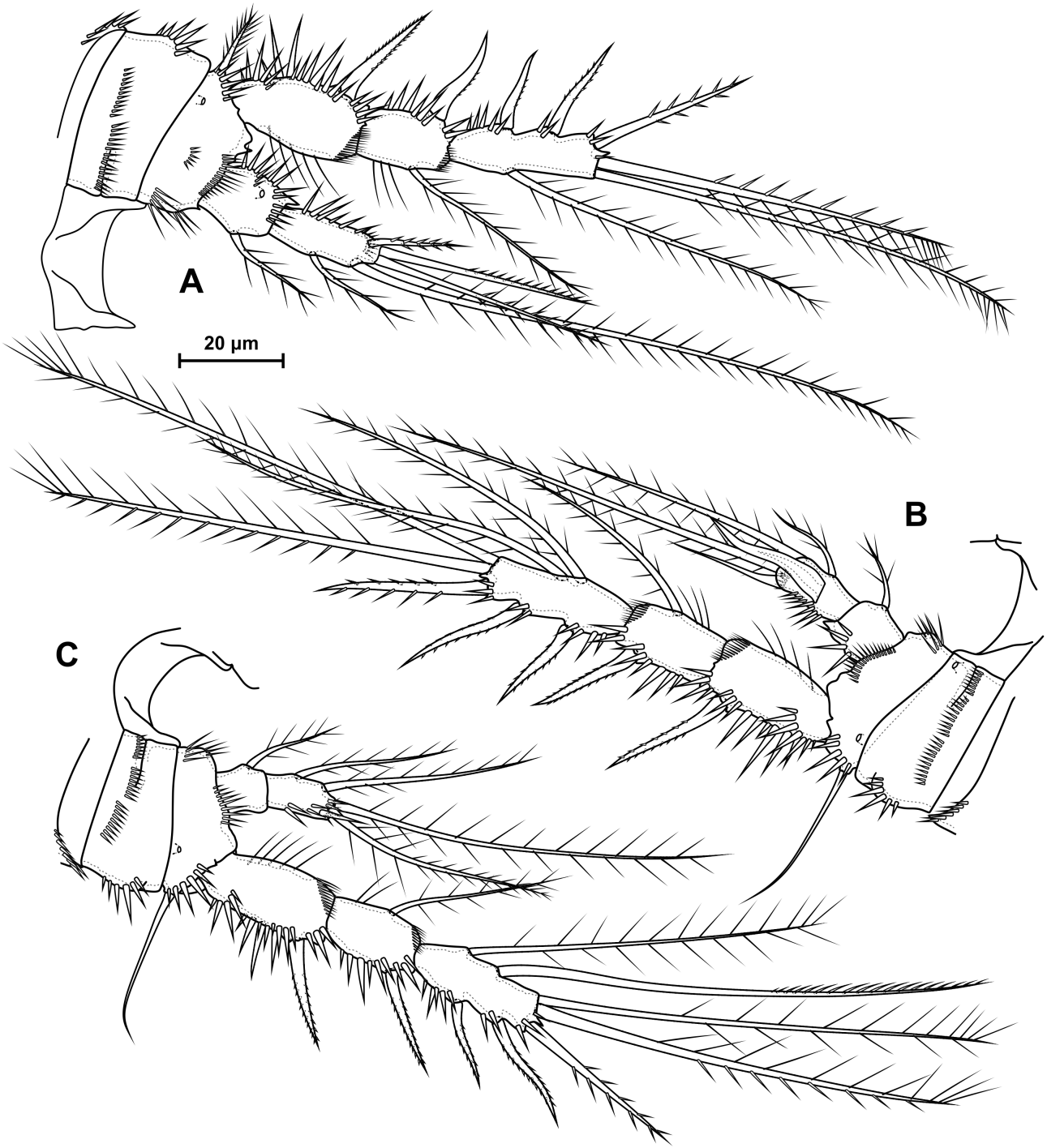

FIGURE 9. *Heteropsyllus spongiophilus* sp. nov. Male allotype: A, P2, anterior; B, P3, anterior; C, P4, anterior.

Key to the females of the genus *Heteropsyllus*:

1	P1 Exp3 with 5 setae	2
-	P1 Exp3 with 4 setae	7
2	P2 Enp2 with 6 setae. White Sea, Laptev Sea*	*H. coulli* Kornev & Chertoprud, 2008
-	P2 Enp2 with 5 setae	3
-	P2 Enp2 with 4 setae	5
3	P4 Enp2 with 5 setae, anal operculum with spinules. Kara Sea*	*H. spongiophilus* **sp. nov.**
-	P4 Enp2 with 4 setae, anal operculum naked	4
4	P1 Enp3 twice as long as Enp2; syncoxa of maxilliped with 2 setae. North Sea, Mediterranean Sea, Laptev Sea	*H. exiguus* (Sars G.O., 1911)
-	P1 Enp3 equal in length to Enp2; syncoxa of maxilliped with 1 seta. Mediterranean Sea	*H. meridionalis* Soyer, 1974
5	P3 Enp2 with 5 setae	6
-	P3 Enp2 with 4 setae. North Sea	*H. masculus* Kunz, 1971
6.	Endopodal lobe of baseoendopod P5 with 5 setae. Arctic Ocean	*H. rostratus similis* Smirnov, 1946
-	Endopodal lobe of baseoendopod P5 with 4 setae. North Sea, Kara Sea, Laptev Sea	*H. rostratus* (Sars G.O., 1920)
7	P1 Exp2 with one seta, P4 Enp1 without seta	8
-	P1 Exp2 without seta, P4 Enp1 with one seta	9
8	P1–P3 Enp1 with inner seta. Northwest Atlantic	*H. pseudonunni* Coull & Palmer, 1980
-	P1–P3 Enp1 without inner seta. Northwest Atlantic	*H. nunni* Coull, 1975
9	Endopodal lobe of baseoendopod P5 with 5 setae	10
-	Endopodal lobe of baseoendopod P5 with 4 setae. Iceland-Faroe ridge	*H. serratus* Schriever, 1983 *incertae sedis*
10	P2 Enp2 with 5 setae	12
-	P2 Enp2 with 3–4 setae	11
11	P3 Enp2 with 4 setae. North Sea, Mediterranean Sea	*H. nanus* (Sars G.O., 1920)
-	P3 Enp2 with 3 setae. Mediterranean Sea	*H. confluens* Soyer, 1974
12	Anal operculum dentate**	13
-	Anal operculum naked**	14
13	A2 exopod 2-segmented. Celtic Sea	*H. celticus* Nam & Lee, 2006
-	A2 exopod 1-segmented. Yellow Sea	*H. coreanus* Nam & Lee, 2006
14	P4 Enp2 with 4 setae. North Sea, Bay of Biscay, Black Sea, Kara Sea, Laptev Sea	*H. major* (Sars G.O., 1920)
-	P4 Enp2 with 3 setae. North Sea, Celtic Sea	*H. curticaudatus* Scott T., 1894

* Our data

** This morphological character is not the most successful. The fine serration of the anal operculum can only be seen at very high magnification. Perhaps the authors did not notice this in the original descriptions of *H. major* and *H. curticaudatus*.

Genus *Mesopsyllus* Por, 1960

Mesopsyllus glacialis sp. nov.

http://zoobank.org/E7DCBD1A-6E2E-43A0-961E-4DB9A0339052

Etymology. The species is named so because it lives in the Arctic, and its juveniles are painted bluish. The specific epithet is adjective.

Type locality. Laptev sea (75.75833°N, 124.04500°E) in sample with sponges *Polymastia grimaldii* (Topsent, 1913); *Tetilla sibirica* (Fristedt, 1887). Depth 45 m.

Material examined. Holotype: female, dissected and mounted on 2 slides (BP 543/1-a; 543/1-b). Allotype, male dissected and mounted on one slide (543/2). Paratypes: two females dissected and mounted on two slides (543/3, 543/4), 5 females, 5 males and 17 copepodites undissected formalin-preserved (543/5).

Description. *Female*. Body length of holotype: 0.439 mm. Fixed males and females colourless, but copepodites with bluish color. Naupliar eye not discernible. Cephalothorax (Figs. 10A,B) consisting of cephalosome with fused first pedigerous somite, wider as remaining somites, largest width 0.114 mm. Rostrum as in male (Fig. 10C), fused with cephalothorax, with pointed tip; with one pair of sensilla and one pore. Posterior margin of cephalothorax and all somites smooth.

Cephalothorax with 19 pairs of sensilla and 5 pairs of pores. All pedigerous and abdominal somites, except anal somite, with rows of small spinules. Second pedigerous somite with 5 pairs of sensilla and one pair of pore. Third

pedigerous somite with 6 pairs of sensilla and one pair of pores. Fourth pedigerous somite with 4 pairs of sensilla and one pair of pores. Fifth pedigerous somite with 4 pairs of sensilla, one pair of pores and dorsolateral rows of large spinules.

Abdomen (Figs. 11A-C) almost cylindrical, consisting of genital-double somite, two free abdominal somites and anal somite with caudal rami. Genital-double somite with clear border between segments; with rows of spinules ventrally, medially and on posterior margin; with 7 pairs of pores, two dorsal unpaired pores and two ventral pairs of pores. P6 right and left close; with two slender setae. Genital field with sieves; copulatory pore width on posterior margin of first of two somites; copulatory duct elliptical without labyrinthic rounded duct; seminal receptacles located on sides of duct.

First free abdominal somite with three pairs of sensilla, one dorsal unpaired pore and one pair of ventral pores; on posterior margin with ventro-lateral rows of spinules and one latero-dorsal row of spinules. Second free abdominal somite with one pair of ventral pores; on posterior margin with ventro-lateral rows of spinules. Anal somite with one dorsal pair of sensilla, one dorsal, one ventral and two lateral pairs of pores; with spinules at base of caudal rami. Anal operculum short and wide; finely serrated; one ventral side with rows of long spinules.

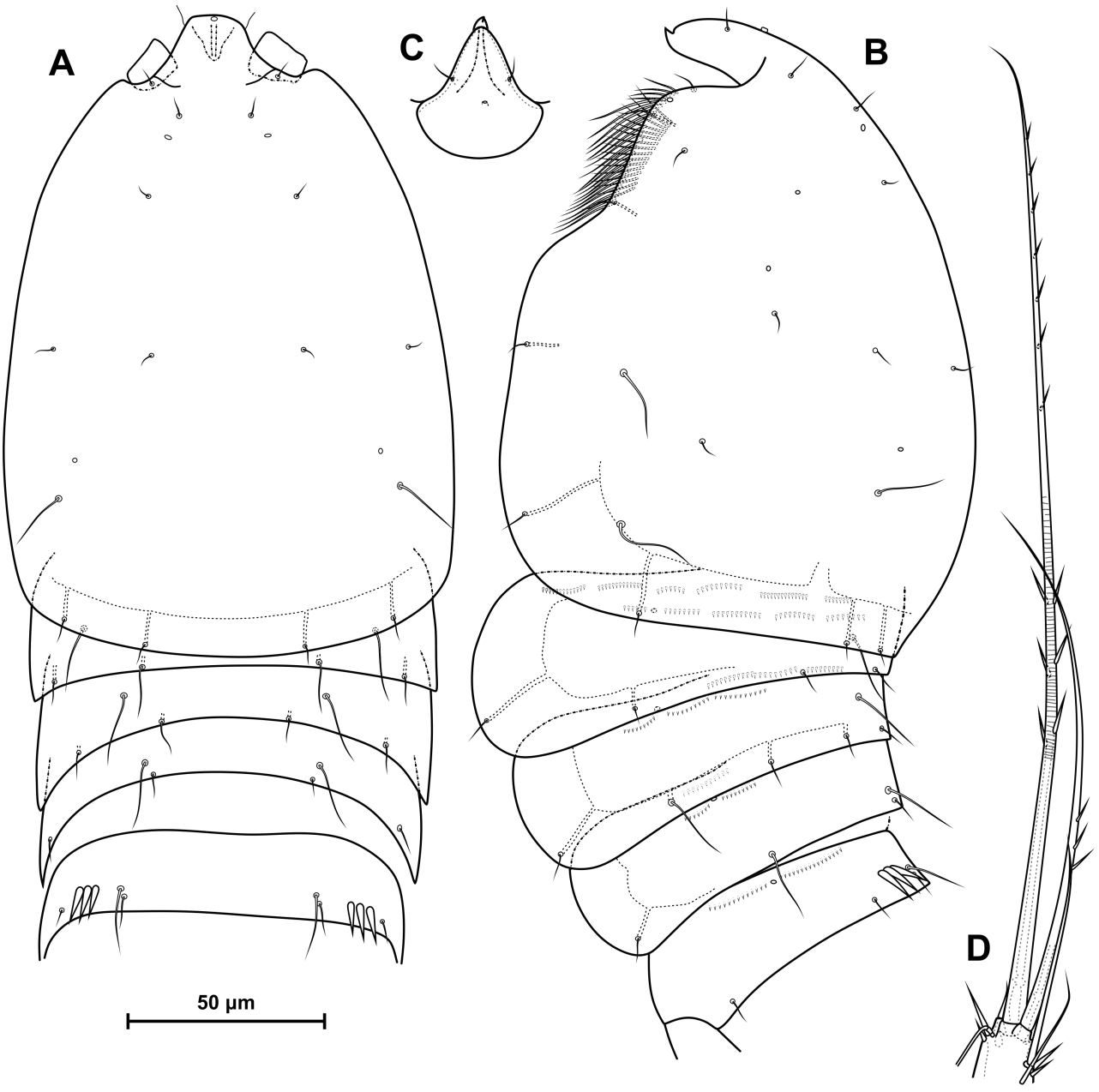

FIGURE 10. *Mesopsyllus glacialis* sp. nov. Female holotype: A, cephalothorax and thoracic somites, dorsal; B, cephalothorax and thoracic somites, lateral; D, apical setae of caudal rami, dorsal. Male allotype: C, rostrum, frontal

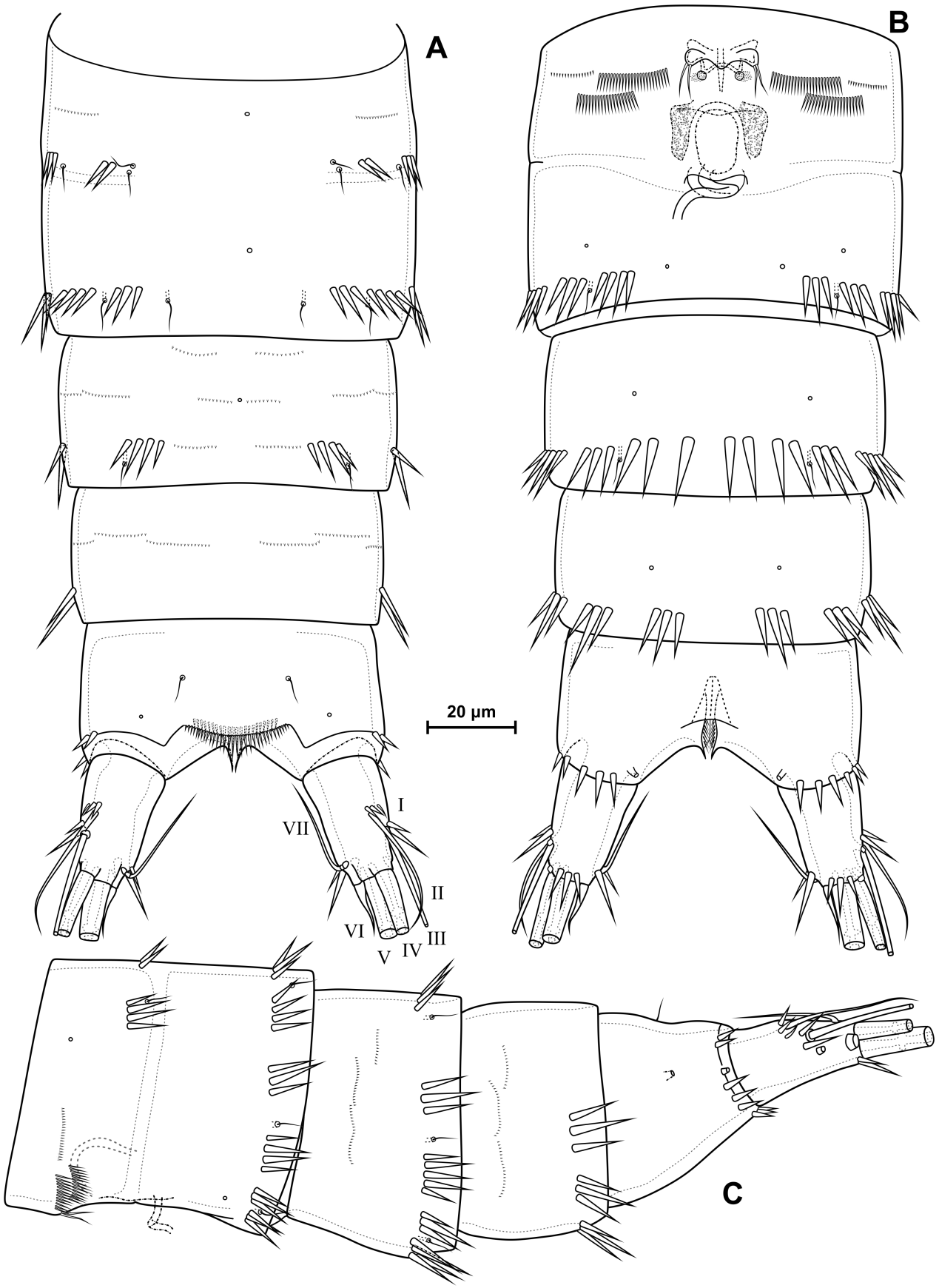

FIGURE 11. *Mesopsyllus glacialis* sp. nov. Female paratype: A, abdomen, dorsal; B, abdomen, ventral; C, abdomen, lateral

Caudal rami (Figs. 11A-C) elongated; length/width ratio 1.6, with two lateral pores; with rows of spinules at base of setae II, III and VII, with row of spinules ventrally at base of apical setae. Seta I very small, next to seta II. Apical setae IV and V (Fig. 10D) long, with spinules, length 0.137 mm and 0.252 mm respectively. Seta VII triarticulated, directed backward.

Antennule (Fig. 12A) 7-segmented. First segment with small seta and three rows of spinules. "Pineapple-setae" located on second, third and seventh segments (1, 2 and 1, respectively). Segment 4 with fused basally large aesthetasc and seta; segment 7 with acrothek consisting of aesthetasc and two bare setae. Armature formula: 1-[1],2-[9],3-[4],4-[1+(1+ae)],5-[1],6-[2],7-[7+acr].

Antenna (Fig. 13A) robust. Coxa with two spinular rows. Allobasis with clear border between basis and first endopodal segment; with one small seta and row of long spinules at its base. Free endopodal segment with two rows of large spinules and two spinulose spines; distally with two rows of spinules, apically with three robust spines and two pinnate geniculate setae. Exopod 1-segmented; with 2 setae distally and one small seta medially.

Mandible (Fig.12D). Coxa with spinules proximally. Gnathobase with strong pars incisiva, lacinia mobilis, spinulose seta and with few sharp teeth. Palp consisting of free basis and 1-segmented endopod. Basis with two rows of spinules, one inner and one outer exopodal "pineapple-setae". Endopod with row of spinules, one inner "pineapple-seta", two apical bare setae and one apical outer "pineapple-seta".

Maxillule (Fig. 13B). Praecoxa with outer spinular row. Praecoxal arthrite medially with two rows of spinules and two naked setae; distally with 9 spines. Coxa with outer spinular row; coxal endite reaching third of arthrite, with two bare setae. Basis with two rows of spinules and five bare setae. Endopod and exopod incorporated into basis, represented by two bare and one strong pinnate setae respectively.

Maxilla (Fig. 13C). Syncoxa with rows of spinules as figured, with two endites. Proximal endite with one simple seta, one stout, bluntlypointed, spinulose spine and with modified seta fused basally with endite with wide base and thin "tail". Distal endite with one simple seta, one long spine and one modified seta as on proximal endite. Allobasis with one seta and massive distal claw. Endopod not separated, with one small seta proximally and two large setae distally.

Maxilliped (Fig. 14A) subchelate. Syncoxa with three rows of spinules and pinnate seta. Basis with one row of large inner spinules and two rows of outer long spinules. Endopod on anterior side with small seta and small protuberance. Endopodal claw elongated, with two pairs of long slender spinules.

P1 (Fig. 14B) with 3-segmented rami. Praecoxa with long spinular row. Coxa with inner fold, with spinular ornamentation as figured. Intercoxal sclerite wide with two pairs of spinular rows. Basis wide, on inner side with large elliptical protrusion; with proximal pore and four spinular rows; with robust inner seta and bare outer seta. All endopodal and exopodal segments with inner and outer spinules. First exopodal segment with outer spine. Second exopodal segment with outer spine and minute inner pinnate seta. Distal segment with two spines, one pectinate seta and one geniculate long seta. Endopod is approximately as long as exopod. First and second endopodal segments with minute inner setae. Third endopodal segment with outer and inner spines and apical seta.

P2 (Fig. 15A). Praecoxa with long spinular row. Coxa with pore, outer spinular row and with rows of spinules on frontal side. Intercoxal sclerite rectangular. Basis with proximal pore, small outer seta; spinular rows located on inner side and at base of endopod and exopod respectively; inner side of basis produced into sharp spinous process. All endopodal and exopodal segments with inner and outer spinules. First exopodal segment with outer spine. Second exopodal segment with outer spine and inner minute pinnate seta. Distal exopodal segment with short inner pinnate seta, two apical long setae and three outer spines; at base of second outer spine with pore. Endopod reaching proximal part of exopod. First endopodal segment with inner minute seta and outer pore; outer margin produced into sharp process. Second endopodal segment with one inner minute seta, one inner and two apical long setae and outer spine; outer side produced into spinous process medially.

P3 (Fig. 15B). Praecoxa, coxa, basis, first and second exopodal segments and first endopodal segment as in P2. Intercoxal sclerite trapezoidal. Third exopodal segment with two inner short setae, two long apical setae and three outer spines. Second endopodal segment with inner pectinate seta, two apical pinnate setae and outer spine.

P4 (Fig. 15C). Praecoxa, coxa, first and second exopodal segments and first endopodal segment almost as in P2. Basis with proximal pore and with two inner, one distal, one medial and one outer rows of spinules; inner margin without process. Third exopodal segment with three outer spines, two apical setae, one proximal inner seta and one distal strong pectinate seta. Endopod short, reaching half of second exopodal segment. Second endopodal segment with inner pectinate seta, two apical pinnate setae and outer spine.

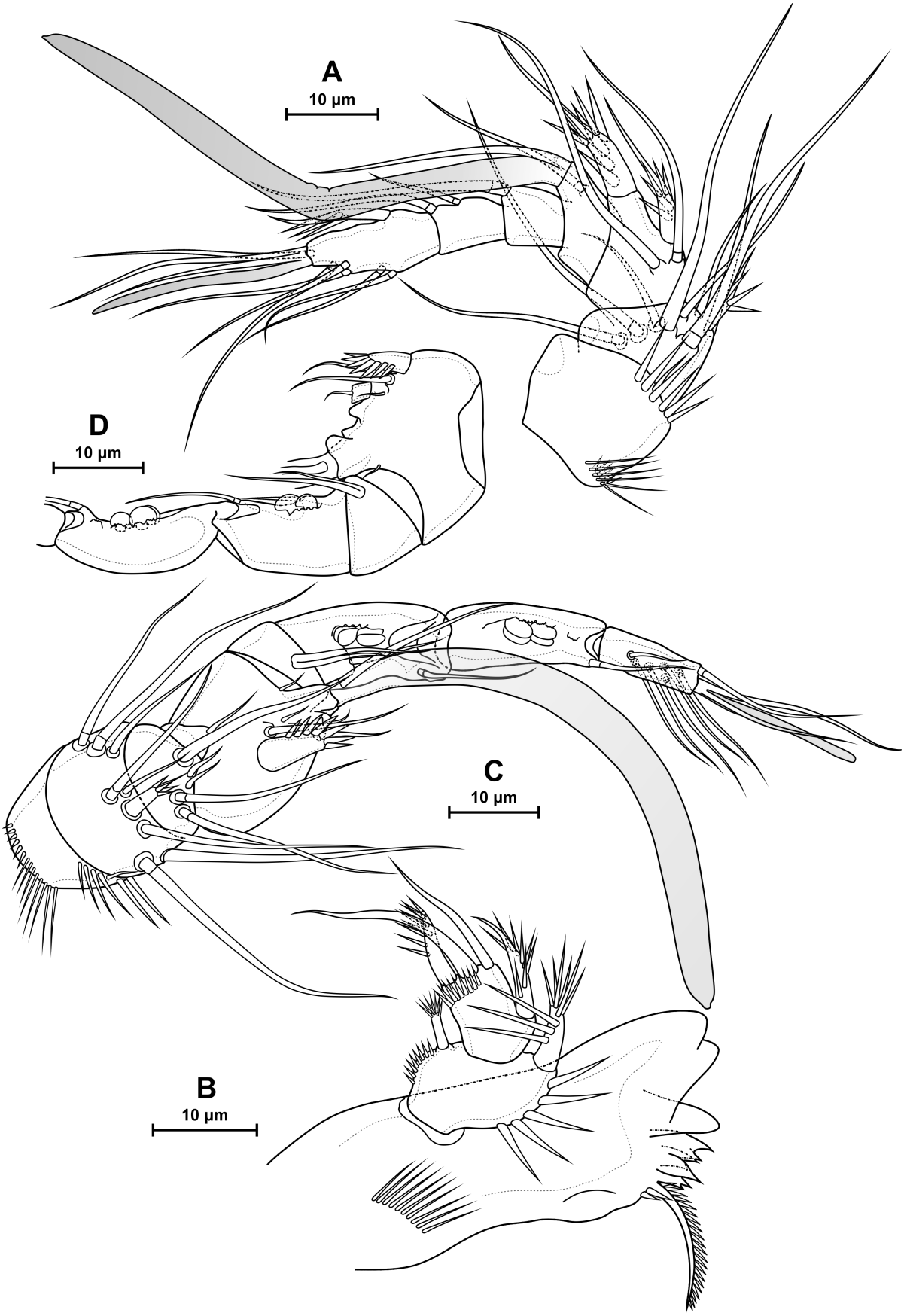

FIGURE 12. *Mesopsyllus glacialis* sp. nov. Female holotype: A, antennule; B, mandible. Male allotype: C, antennule, anterior; D, antennule, segments 5-8, dorsal

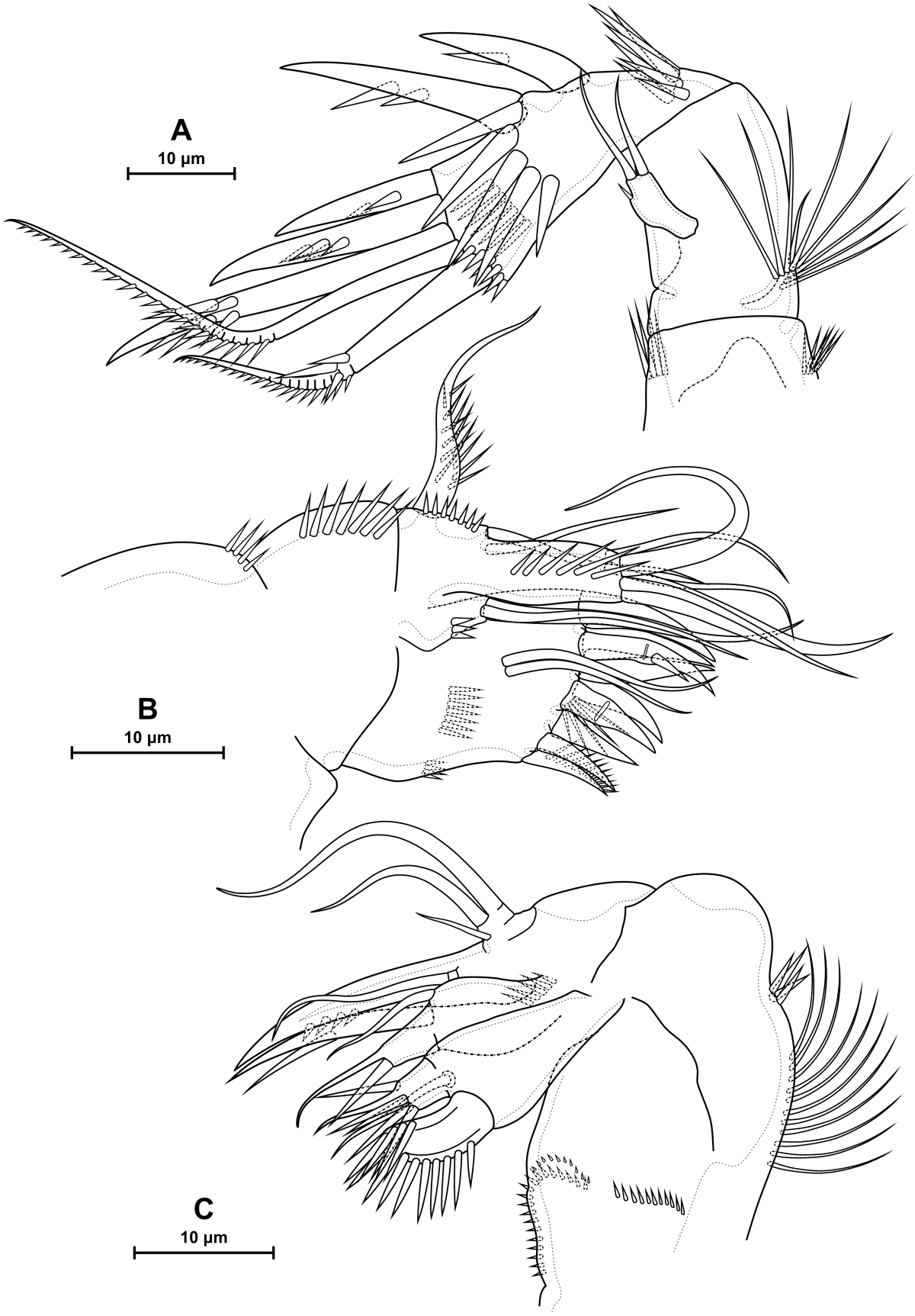

FIGURE 13. *Mesopsyllus glacialis* sp. nov. Female holotype: A, antenna; B, maxillule; C, maxilla

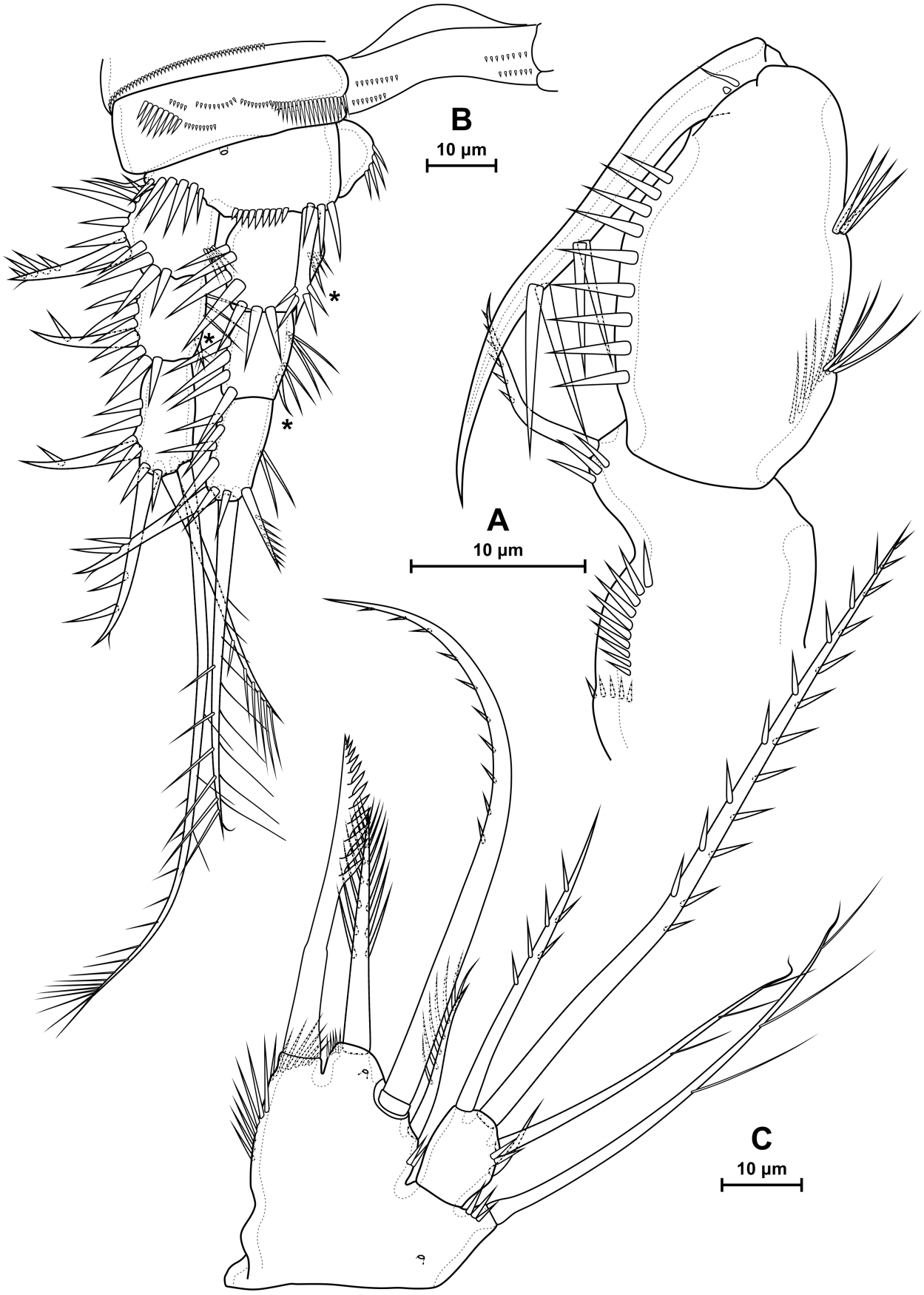

FIGURE 14. *Mesopsyllus glacialis* sp. nov. Female holotype: A, maxilliped, anterior; B, P1, anterior; C, P5, anterior. Minute setae indicated by asterisk.

Armature of swimming legs as follows:

	endopod (female)	endopod (male)	exopod
P1	1; 1; 1,1,1	1; 1; 1,1,1	0; 1; 0,2,2
P2	1; 2,2,1	1; 2,2,1	0; 1; 1,2,3
P3	1; 1,2,1	1;modified	0; 1; 2,2,3
P4	1; 1,2,1	1; 2,2,1	0; 1; 2,2,3

P5 (Fig. 14C) of characteristic shape for genus, with separate right and left baseoendopods. Baseoendopod reaching beyond end of exopod, with long pinnate outer seta and proximal pore. Endopodal lobe with distal pore, with robust pectinate inner seta, one bipinnate apical seta, long curved and small unipinnate outer setae. Exopod small, with three long pinnate setae distally and one outer bare seta.

Male. Total body length from tip of rostrum to posterior margin of caudal rami: 0.372 mm. Sexual dimorphism expressed in the antennule, P2–P6, genital segmentation. Ornamentation of abdominal somites (Figs. 17A-C) as in female, but first somite without ventral spinular rows. P6 fused with first abdominal somite, without setae. Caudal rami as in female.

Antennule (Figs. 12B,C) 9-segmented, haplocer with geniculation between segments 7 and 8. Segment 1 as in female. Segment 2 with "pineapple-seta". Segment 5 with strong modified setae, large aesthetasc and few distal protrusions; one seta robust with large spinules and fine "tail"; one seta with wide short base and fine "tail". Segment 6 with two basally fused setae. Segments 7-8 with articular surface. Segment 7 with two simple setae and two modified lamellar setae. Segment 8 with two modified mushroom-shaped lamellar setae and one distal seta. Segment 9 with acrothek. Armature formula: 1-[1],2-[9],3-[5],4-[1],5-[3+2 modified +(1+ae)],6-[2],7-[2+2 modified],8-[1+2 modified],9-[7+acr].

P2 (Fig. 17A) almost as in P2 female, except for second endopodal segment. Outer spine of second endopodal segment in form of small tip.

P3 (Fig. 17B,C). Praecoxa, coxa, basis, first and second exopodal segments as in female. Third exopodal segment as in female, but with pore at base of middle outer spine. Endopod typical for Canthocamptidae. First segment modified, with pore, inner distal corner produced into protrusion, outer distal corner produced into spinous process; on distal margin with row of small tubercles; inner seta pinnate, long. Second segment split into two pseudosegments. First one with outer spinules, distal row of flat spinules, inner minute seta and long bifurcated claw-shaped apophysis. Second one with processes on anterior surface, inner pore and two apical pinnate setae.

P4 (Fig. 18A). Praecoxa, coxa, intercoxal sclerite and exopod as in female. First endopodal segment as in female, but inner seta long and bare. Second endopodal segment with two inner unipinnate setae, two apical bipinnate setae and outer bare spine.

P5 (Fig. 18B) with left and right baseoendopods fused medially. Baseoendopod with proximal pore, long pinnate seta; endopodal lobe with inner and outer rows of spinules, inner and distal pores, with outer unipinnate and inner bipinnate setae. Exopod small, with inner robust pinnate seta, three distal pinnate setae and outer small bare seta.

Ecology. Like *H. spongiophilus* **sp. nov.**, *M. glacialis* **sp. nov.** is probably an optional inhabitant of sponges. The diet of related species has not been studied. However, the shape of the mouthparts, especially the mandible gnathobase, strongly resembles that of *Metahuntemannia* Smirnov, 1946 and *Dahmsopottekina* Özdikmen, 2009. The gnathobase has long, sharp teeth, which, according to Dahms & Pottek (1992), may indicate that the species is a predator or scavenger.

Remarks. According to Huys and Thistle (1989), *Mesopsyllus* is a basal genus of the subfamily Hemimesochrinae Por, 1986. This assumption was made on the basis of the modification of the outer seta of the male P3 endopodite. In most of their species, the subfamilies have modified setae, as in *Bathycamptus* Huys & Thistle, 1989, *Isthmiocaris* George & Schminke, 2003, and *Dahmsopottekina* Özdikmen, 2009 (Huys & Thistle 1989; Dahms & Pottek 1992; Bruch et al. 2011). In general, together with a new species and an undescribed new species from the Laptev Sea, the genus includes seven species. *Mesopsyllus glacialis* **sp. nov.**, according to the majority of variable characters within the genus, turns out to be plesiomorphic. This is the first representative of the genus with a 7-segmented antennule; it has a complete set of setae on the distal segments of P2-P3 exopods (6, 7, 7) and a complete set of setae on endopod P2 (5). It also differs from other members of the genus in the unique character of sexual dimorphism of swimming legs. Thus, the second segment of the endopod P2 of the male has a modified shape and a

greatly reduced outer seta in the form of a tip. Apophysis P3 bifurcated in the form of a claw. Therefore, on the basis of these characters, we assume that the new species is basal within the genus *Mesopsyllus*.

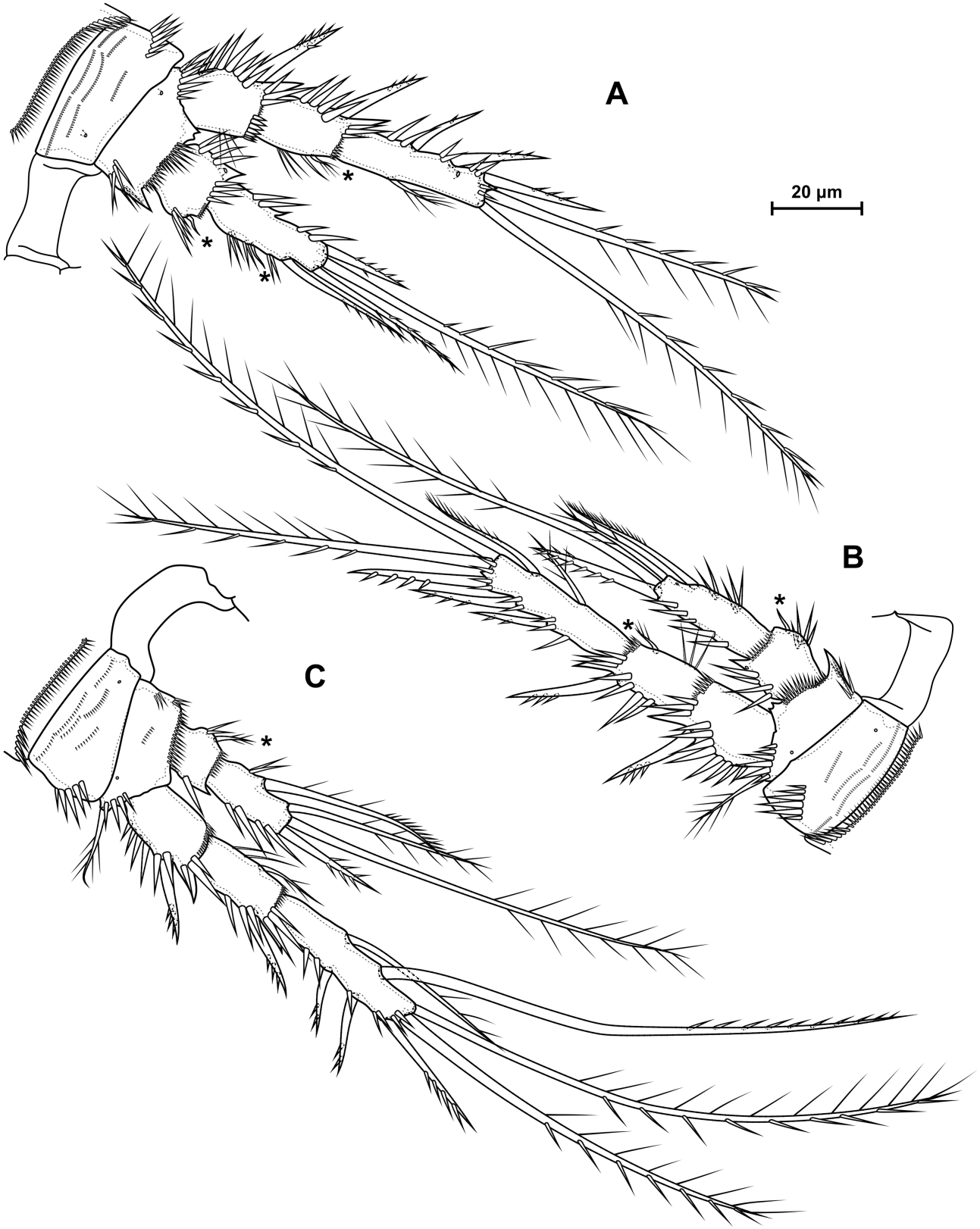

FIGURE 15. *Mesopsyllus glacialis* sp. nov. Female holotype: A, P2, anterior; B, P3, anterior; C, P4, anterior. Minute setae indicated by asterisk.

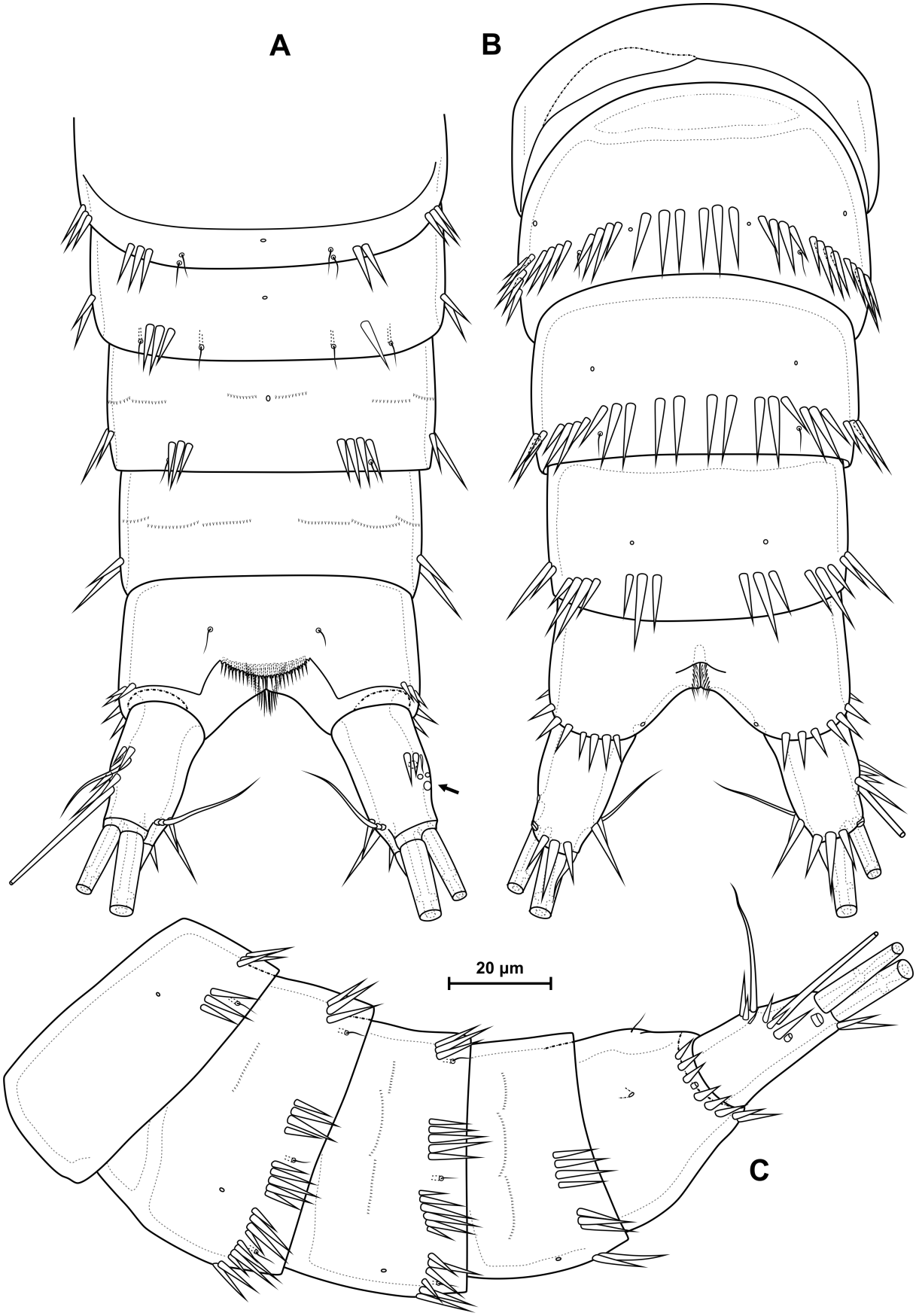

FIGURE 16. *Mesopsyllus glacialis* sp. nov. Male allotype: A, abdomen, dorsal; B, abdomen, ventral; C, abdomen lateral. Arrow is broken setae.

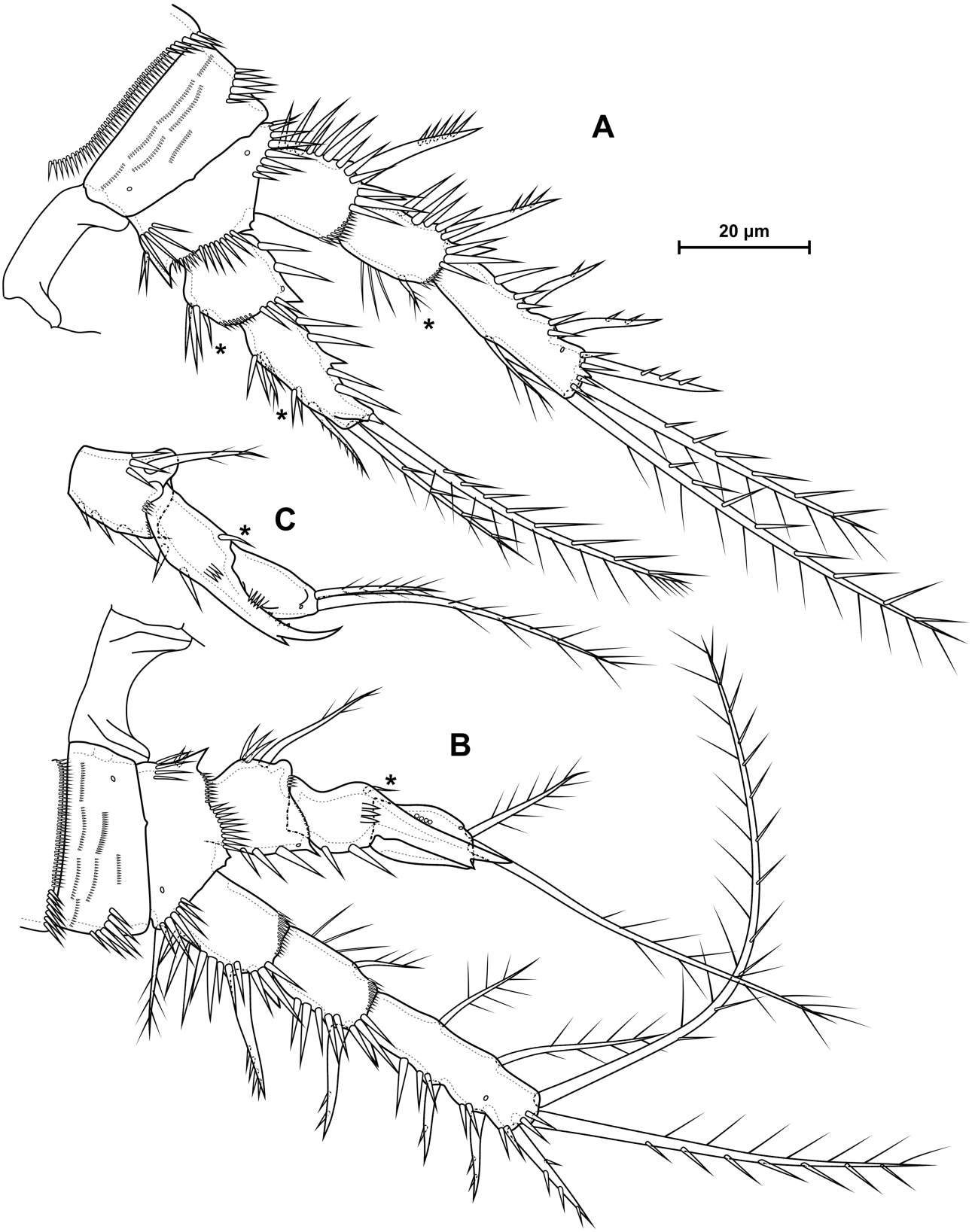

FIGURE 17. *Mesopsyllus glacialis* sp. nov. Male allotype: A, P2, anterior; B, P3, anterior; C, P3 endopod, inner side. Minute setae indicated by asterisk.

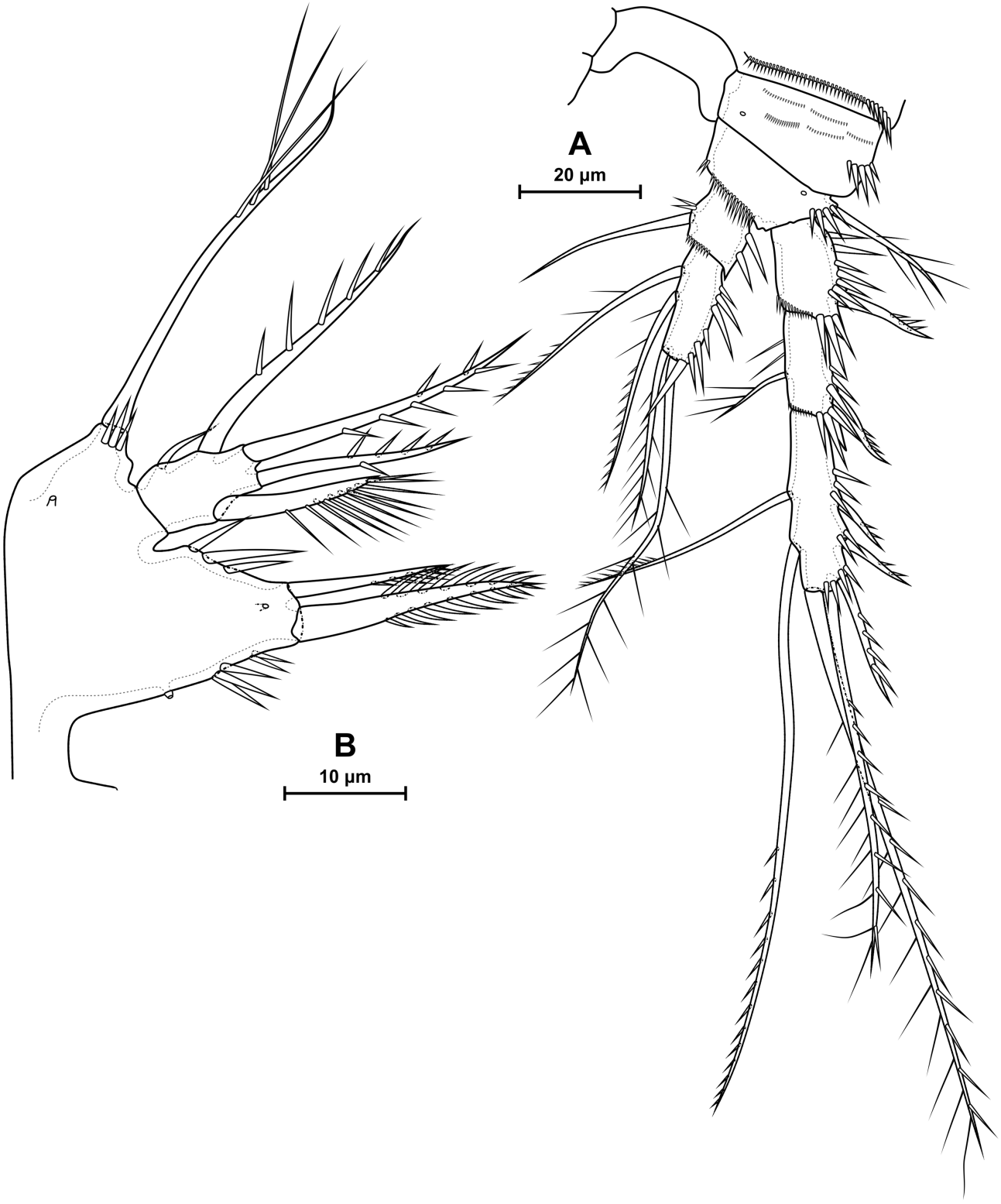

FIGURE 18. *Mesopsyllus glacialis* sp. nov. Male allotype: A, P4, anterior; B, P5, anterior.

Unfortunately, only one female was found in the second of the discovered *Mesopsyllus* species in the Laptev Sea; we did not describe it since the character of sexual dimorphism of swimming legs is too important in the taxonomy of the subfamily. In the future, it will be possible to find a male of this species. However, undoubtedly, it is also of interest because of the highest reduction of the setae of swimming legs among all representatives of the genus and is close in this parameter to the genus *Bathycamptus*, but differs in the separated baseoendopod and exopod P5.

Spine formula of P2-P4 *Mesopsyllus* sp. 1

	endopod	exopod
P2	1; 1,2,1	0; 1; 1,2,2
P3	1; 1,2,1	0; 1; 2,2,2
P4	1; 1,2,1	0; 1; 1,2,2

Key to the females of *Mesopsyllus*:

1 P2 Exp3 with 6 setae 2
- P2 Exp3 with 5 setae 5
2 P2 Enp2 with 5 setae, rostrum with smooth margin 3
- P2 Enp2 with 4 setae, rostrum with setulose margin 4
3 Antennule 7-segmented, P4 Exp3 with 7 setae, caudal rami long (l/w ratio 1.7). Laptev Sea*, Kara Sea* . . . . . *M. glacialis* **sp. nov.**
- Antennule 6-segmented, P4 Exp3 with 6 setae, caudal rami long (l/w ratio 3.7). White Sea, Laptev Sea* . . . . . *M. curvisetus* (Kornev & Chertoprud), 2008
4 P1 Endopod 3-segmented, P4 Exp3 with 6 setae. Black Sea, English Channel . . . . . *M. atargatis* Por, 1960
- P1 Endopod 2-segmented, P4 Exp3 with 7 setae. North Sea . . . . . *M. secundus* (Wells, 1965)
5 P2 Enp2 with 5 setae, P4 Exp3 with 6 setae 6
- P2 Enp2 with 4 setae, P4 Exp3 with 5 setae. Laptev Sea* . . . . . *M.* sp. 1
6 P3 Enp2 with 5 setae, P4 Enp2 with 5 setae. Bohai Sea . . . . . *M. spiniferus* Mu & Huys, 2017
- P3 Enp2 with 4 setae, P4 Enp2 with 4 setae. Bohai Sea . . . . . *M. dimorphus* Mu & Huys, 2017

* Our data

Position of *Heteropsyllus* within Harpacticoida

Heteropsyllus is a highly controversial genus of marine harpacticoids. Previously, it was most often attributed to the Cletodidae family (Lang 1948). Recently, it has usually been referred to the Canthocamptidae (Nam & Lee 2006). However, among cantocamptids, this genus is distinguished by plesiomorphic characters, like the presence of a free mandible exopod, a free maxillule exopod, the presence of three maxillary endites on the, and the presence of more than one seta on the syncoxa and endopod of the maxilliped.

The most characteristic difference is the character of dimorphism in the P3 structure, where males of *Heteropsyllus* have a slightly modified outer seta on the last segment of the endopod. In particular, this character was one of the main reasons for the isolation of *Heteropsyllus* by Kornev and Chertoprud (2008) into the separate monotypic family Heteropsyllidae Kornev & Chertoprud, 2008. However, it is currently unknown how the P3 male endopod evolved. Thus, the absence of the characteristic division of the distal segment of P3 endopod into pseudosegments, which is present in cantocamptids, may, on the contrary, turn out to be apomorphic rather than plesiomorphic. The same type of transformation can be observed in the family Laophontidae Scott T., 1904. The most basal group Esolinae Huys & Lee, 2000, with genera such as *Archilaophonte* Willen, 1995, *Esola* Edwards C., 1891, and others, already has a well-defined division of the distal segment of the male P3 endopod; however, most genera within Laophontinae Scott T., 1904 have an already undivided distal segment (Willen 1995; Huys & Lee 2000). In their phylogenetic analysis, Huys & Lee (2000) also characterize the three-segmented male P3 endopod as plesiomorphy and the two-segmented endopod as apomorphy.

In our opinion, the division of the male P3 endopodite into pseudosegments, as well as the presence of a strongly modified outer seta into apophysis, is characteristic of the common ancestor of a large number of families in Cletodidimorpha Lang, 1948 sensu Kornev & Chertoprud, 2008, excluding the families Tetragonicipitidae Lang, 1944, Normanellidae Lang, 1944 and Cletopsyllidae Huys & Willems, 1989. Already within the various groups of Cletodidimorpha, secondary fusion of pseudosegments and reverse transformation of the modified outer seta probably occurred. It is quite possible that these are neotenic transformations, as in the family Laophontidae (Huys & Lee 2000). Such transformations can be traced even within the genus *Heteropsyllus*, where *H. spongiophilus* has the most pronounced dimorphism, with a large modified apophysis, and *H. coreanus* has a small, slightly displaced thin apophysis.

Inside the Canthocamptidae, *Heteropsyllus* occupies one of the basal branches. We consider it highly likely

that *Heteropsyllus* is a basal branch of the subfamily Hemimesochrinae. Thus, Huys and Thistle (1989) state that *Heteropsyllus*, unlike typical Hemimesochrinae, does not possess pineapple-setae; however, as can be seen in this description, highly similar setae are found on the distal segment of the female antennule and on several segments of the male antennule. There is also much in common between Hemimesochrinae and *Heteropsyllus* in the structure of the mouthparts. The maxillae have similarly shaped setae on endites, which, at first, are evenly thin, but then sharply taper to a fine tip. They are brought together by the characteristic structure of one of the setae on the middle endite of *Heteropsyllus*, which, in the species of the genus *Mesopsyllus*, has an even more modified appearance. The maxilliped claw in *H. spongiophilus* and *M. glacialis* has four large, long spines, although a similar structure is not observed in other *Heteropsyllus* species.

Heteropsyllus differs from typical Hemimesochrinae in the absence of dimorphism in the structure of the P4 endopodite. However, for complete clarity, qualitative descriptions of the morphology of other genera of Hemimesochrinae, such as *Hemimesochra* Sars G.O., 1920 and especially *Hanikraia* Huys, 2009, are required.

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