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Revision of the genus *Canthocamptus* (Copepoda: Harpacticoida) with a description of a new species from the Lena River Delta (North-eastern Siberia)

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Abstract. The discovery of a new species of the genus *Canthocamptus*, *C. waldemarschneideri* sp. nov., in northern Siberia prompted a taxonomic analysis of this genus. In this work, on the basis of cladistic analysis, we show that the genus is not monophyletic. Based on differences in the structure of the endopods on the second pair of male swimming legs, fifth legs of males and females, and caudal rami, we conclude that the *Canthocamptus mirabilis* species group is a separate genus, *Kikuchicamptus* gen. nov. Additionally, two species are transferred to the genus *Attheyella*, and one species, *Canthocamptus gibba*, is synonymized. The subgenera *Canthocamptus* (*Baikalocamptus*) and *Canthocamptus* (*Canthocamptus*) are also synonymized. The new species, *Canthocamptus waldemarschneideri* sp. nov., is most closely related to the American *Canthocamptus assimilis* Kiefer, 1931 and differs from it in the ornamentation of the abdominal somites and the shape of the caudal setae.

Keywords. Lena River Delta, *Kikuchicamptus*, taxonomy, Canthocamptidae, Arctic invertebrates.

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Introduction

Canthocamptus Westwood, 1836 was one of the first described genera of canthocamptids and was greatly inflated due to the artificial inclusion of various species that only superficially resembled the type species, *C. staphilinus* (Jurine, 1820). Some of the species described as members of *Canthocamptus* do not even belong to the family Canthocamptidae Sars, 1906, e.g., *C. elegantulus* Fischer, 1860, *C. longisetosus* Daday, 1902, *C. mareoticus* Fischer, 1860, *C. megalops* Lilljeborg, 1902, *C. rostratus* Claus, 1863, *C. stroemii* Baird, 1850, *C. subsalus* Brady, 1895 and *C. virescens* Dana, 1849. As a result of various revisions, many species were transferred to other genera and families (Lang 1948). In this regard, it has not been entirely clear how many species are included in this genus. In his monograph, J. Wells provides an up-to-date list (2007). In this work, we have only supplemented it, considering taxonomic changes.

We discovered a new species of *Canthocamptus*, in Siberia in the Lena Delta region, which is closely related to the North American species *C. assimilis* Kiefer, 1931. This prompted us to conduct a revision of this genus with a complex history. Morphologically, *Canthocamptus* s. str. is a uniform genus and has only slight variations in the armature of the swimming legs; therefore, it is rather difficult to find good characteristics to distinguish between species. For the most part, new species were attributed to this genus precisely based on the armature of the swimming legs. However, these characteristics are the most plesiomorphic for the family as a whole and cannot be considered apomorphies of the genus. Because of this, there have been cases such as the description of *C. gibba* Okuneva, 1983, which by all features coincides with the species *Attheyella nordenskioldii* (Lilljeborg, 1902) and is obviously synonymous. We propose to use the characteristic of sexual dimorphism of swimming legs as an apomorphy of the genus. Based on this, we propose the genus *Kikuchicamptus* gen. nov. to include only the monophyletic group of species close to *C. mirabilis* Štěrba, 1968 (see Cladistic analysis), which is more closely related to *Attheyella* Brady, 1880 than to *Canthocamptus* s. str. We also present a number of microcharacteristics previously unreported in most descriptions, that may aid in the taxonomy of the genus: the structure of the maxillule, the shape of the base of caudal setae and pores on the abdominal somites.

Material and methods

The material was collected during the 'Lena-2019' expedition in the Lena River Delta (North-eastern Siberia). A small plankton net was used for collection. Samples were fixed in 4% formalin. Specimens were dissected under a stereo microscope, 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 ver. 1.0.

Heteropsyllus spongiophilus Novikov & Sharafutdinova, 2021 from the Laptev Sea and *Mesochra pontica* Marcus, 1965 from the Black Sea were used as outgroups. For comparison with other freshwater genera, we included the following species in the analysis: from Udmurtia (European part of Russia): *Attheyella* (*A.*) *crassa* (Sars G.O., 1863), *Elaphoidella gracilis* (Sars G.O., 1863); from Lena River Delta: *A.* (*Neomrazekiella*) *dentata* (Poggenpol, 1874), *A.* (*N.*) *nordenskioldii* (Lilljeborg, 1902), *Bryocamptus* (*B.*) *umiatensis* M.S. Wilson, 1958, *B.* (*B.*) sp. 1 (*B.* (*B.*) sp. 2 in Novikov *et al.* 2021); and *E. gradidieri* (Guerne & Richard, 1893) from Hamond (1987). One female *C. staphilinus* (Jurine, 1820) was collected in Lake Võrtsjärv (Estonia). Individuals of *C. glacialis* Lilljeborg, 1902 were collected in the Lena River Delta.

A cladistic analysis was performed using the PAUP ver. 4.0a program. To construct trees, the quartet puzzling method was used (Strimmer & Von Haeseler 1996). Using other methods showed slightly different tree topologies; however, the main branches were consistently present.

In the matrix, all morphometric characters and one morphological character are reversible; the rest of the characters are irreversible and polarized a priori, according to the basic principles in the evolution of copepods (Boxshall & Huys 1992). All characters are ordered, and the multistate characters are additive. The list of morphological characters is given in Table 1, the matrix in Supp. file 1 (construction based on Kiefer 1931; Coker 1934; Coker & Morgan 1940; Borutzky 1947, 1952; Lang 1948; Wilson 1956, 1958; Apostolov 1969; Miura 1969; Shen & Sung 1973; Okuneva 1983; Hamond 1987; Kikuchi & Ishida 1994; Chang 1998, 2001, 2002, 2010; Ishida & Kikuchi 1999; Chang & Ishida 2001). In this work, we consider *C. microstaphilinus* var. *rosei* Roy, 1927 as a junior synonym of *C. microstaphilinus monardi* Roy, 1927, according to Borutzky (1952).

All material is deposited in Zoological Museum of Kazan Federal University (KFU).

Table 1 (continued on two next pages). List of characters used in cladistic analysis. An asterisk marks irreversible characters; 0 is a plesiomorphic state, higher numbers are apomorphic states.

1*	Cephalothorax and genital somite not wider than other somites (0); wider (1)
2*	Rostrum without spinules (0); with spinules (1)
3*	Cephalothorax without dorsal window (0); with dorsal window (1)
4*	Dorsal window rhomboid or not dumbbell-shaped (0); dumbbell-shaped (1)
5*	Dorsal window rhomboid or not drop-shaped (0); sclerotized, drop-shaped (1)
6*	Dorsal window three lobed rhomboid or elongated (0); elongated, three lobed (1)
7*	Female A1 8-segmented (0); 7-segmented (1); 6-segmented (2); 5-segmented (3)
8*	A2 Exp 2-segmented (0); 1-segmented (1)
9*	A2 Exp with four setae (0); with three setae (1)
10*	A2 free endopodal segment with six apical setae (0); with five apical setae (without accessory seta) (1)
11*	A2 basal part of allobasis with seta (0); without seta (1)
12*	A2 endopodal part of allobasis with seta (0); without seta (1)
13*	Basis and endopod of mandible separated (0); fused (1)
14*	Mandible with exopod (0); without exopod (1)
15*	Basis of mandible with two setae (0); with one seta (1); without setae (2)
16*	Endopod of mandible with proximal seta (0); without proximal setae (1)
17*	Endopod of mandible with four apical setae (0); with three apical setae (1)
18*	Exopodal lobe of maxillule with two setae (0); with one seta (1); without setae (2)
19*	Endopodal lobe of maxillule with three setae (0); with two setae (1); with one seta (2); without setae (3)
20*	Arthrite of maxillule with two medial setae (0); with one medial seta (1); without medial setae (2)
21*	Maxilla with three endites (0); with two endites (1)
22*	Proximal endopodal segment of maxilla with two anterior setae (0); with one anterior seta (1); without anterior setae (2)
23*	Proximal endopodal segment of maxilla with posterior seta (0); without posterior seta (1)
24*	Distal endopodal segments with four setae (0); with three setae (1); with two setae (2); with one seta (3)
25*	Syncoxa of maxilliped with two setae (0); with one seta (1); without setae (2)
26*	Endopod of maxilliped with anterior seta (0); without anterior seta (1)
27*	Endopod of maxilliped with posterior seta (0); without posterior seta (1)
28*	P1 Exp3 with inner seta (0); without inner seta (1)
29*	P1 Exp3 with five setae (0); with four setae (1)
30	P1 Enp1 reaching middle of P1 Exp2 (0); reaching end of P1 Exp2 (1); reaching middle of P1 Exp3 (2); reaching end of P1 Exp3 (3)
31*	P1 Enp3 with three setae (0); with two setae (1)
32*	P2 Enp2 with inner seta (0); without inner seta (1)
33*	P2 Enp3 with two inner setae (0); with one inner seta (1)
34*	P2 Enp2 and Enp3 separated (0); fused (1)
35*	Male P2 Enp3 with outer seta (0); without outer seta (1)

Table 1 (continued). List of characters used in cladistic analysis. An asterisk marks irreversible characters; 0 is a plesiomorphic state, higher numbers are apomorphic states.

36*	Male P2 endopod not ‘Attheyella-like’ (0); ‘Attheyella-like’ (Fig. 11B) (1)
37*	Male P2 endopod not ‘Canthocamptus-like’ (0); ‘Canthocamptus-like’ (Fig. 10A–B) (1)
38*	P3 Enp3 with two inner setae (0); with one inner seta (1)
39*	P3 Enp2 and Enp3 separated (0); fused (1)
40*	Male P3 endopod 2-segmented (0); 3-segmented, divided into pseudo-segments (1)
41*	Male P3 Enp3 with normal inner setae (0); with small setae (1); with reduced small setae or without these setae (2)
42*	Male P3 Enp1 with inner seta (0); without inner seta (1)
43*	Male P3 distal segment with two normal apical setae (0); with one seta (1); with reduced small setae or without these setae (2)
44*	Male P3 endopod normal, elongate (0); robust (1)
45*	P4 Exp3 with three outer spines (0); with two outer spines (1)
46*	Female P4 Enp1 with inner seta (0); without inner seta (1)
47*	Female P4 Enp2 with two inner setae (0); with one inner seta (1)
48*	Male P4 Enp1 with inner seta (0); without inner seta (1)
49*	Male P4 Enp2 with two normal inner setae (0); with one inner seta (1); without inner setae (2)
50	Male P4 Enp2 with normal outer spine (0); with modified ‘finger-like’ outer spine (1)
51*	Female P5 with six endopodal setae (0); with five endopodal setae (1)
52*	Female P5 seta V normal, long (0); small (1)
53*	Female P5 exopod with five setae (0); with four setae (1)
54	Female P5 exopod short (l/w < 2) (0); long (l/w > 2) (1)
55*	Female P5 exopod with inner spinular row (0); without inner spinular row (1)
56*	Female P5 exopod with outer spinular row (0); without outer spinular row (1)
57*	Male P5 with three endopodal setae (0); with two endopodal setae (1)
58*	Male P5 exopod with inner pectinate seta (0); without inner seta (1)
59*	Male P5 exopod with three apical and two outer setae (0); with three apical and one outer seta (1)
60	Male P5 endopod: inner seta/outer seta length < 1.5 (0); 1.5–2.5 (1); 2.5–4 (2); > 4 (3)
61*	Male P6 medial seta setiform (0); spiniform (1)
62*	Male P6 with three setae (0); with two setae (1); with one seta (2); without setae (3)
63*	Female P6 with three setae (0); with two setae (1)
64*	Female genital field with labyrinthic ducts (0); without labyrinthic ducts (1)
65*	Penultimate somite without processes (0); with conical processes on posterior edge (1)
66*	Anal somite without ventral processes (0); with ventral processes (1)
67*	Anal somite without lateral processes (0); with lateral unguiform processes (1)
68*	Anal operculum with normal strong spinules (0); with dentate margin or with numerous small spinules (1)
69*	Anal operculum with spinules or dentate margin (0); with smooth margin (1)
70*	Anal operculum semilunar (0); with triangular hyaline frill (1)
71	Caudal rami short (l/w < 1.5) (0); long (1.5–3) (1); very long (> 3) (2)

Table 1 (continued). List of characters used in cladistic analysis. An asterisk marks irreversible characters; 0 is a plesiomorphic state, 1 is an apomorphic state.

72*	Caudal seta IV not sickle-shaped (0); sickle-shaped, with bulb at base (1)
73*	Caudal seta IV not curved (0); curved and thin (1)
74*	Caudal seta IV long (0); short (1)
75*	Caudal seta IV without bulb at base (0); straight, with bulb at base (1)
76*	Caudal seta IV not thin (0); thin, as seta VI (1)
77*	Caudal seta V without bulb (0); with bulb at base (1)
78*	Caudal seta V short and conical (1); long (0)
79*	Caudal seta V not curved (0); curved (1)
80*	Caudal seta IV with 'helle Stelle' (0); without 'helle Stelle' (1)
81*	Caudal seta V with 'helle Stelle' (0); without 'helle Stelle' (1)

Nomenclature and descriptive terminology follow Huys & Boxshall (1991), terminology in genital fields follows Moura & Pottek (1998), terminology in mandibular structure follows Mielke (1984), and terminology and homology of maxillary structures follow Ferrari & Ivanenko (2008). The armature formulae of swimming legs are given according to Lang (1934). By the term 'helle Stelle' we mean the inner cuticular disc at the base of the apical caudal setae (sensu Lang 1948).

Abbreviations used in the text

A1 = antennule
A2 = antenna
acr = acrothek
ae = aesthetasc
Enp1–Enp3 = first–third segments of endopod
Exp1–Exp3 = first–third segments of exopod
P1–P6 = legs 1–6

Results

New species

Subclass Copepoda H. Milne Edwards, 1840
Order Harpacticoida Sars, 1903
Family Canthocamptidae Sars, 1906
Genus *Canthocamptus* Westwood, 1836

Canthocamptus waldemarschneideri sp. nov.
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Figs 1–9; Table 2

Canthocamptus sp. 1 – Novikov *et al.* 2021: 268.

Etymology

The species is named after Mr Waldemar Schneider, who helped us during the expedition.

Material examined

Holotype
RUSSIA • ♀ (on 2 slides); Lena River Delta, small channel near Mount America-Haia; 72.467560° N, 126.285025° E; depth 1–1.5 m; 21 Aug. 2019; A. Novikov leg.; KFU BP 544/1-a, BP 544/1-b.

Allotype
RUSSIA • ♂ (on 2 slides); same collection data as for holotype; KFU BP 544/2-a, BP 544/2-b.

Paratypes
RUSSIA • 1 ♂, 1 ♀ (undissected; microtube); same collection data as for holotype; KFU BP 544/4 • 1 ♀; Lena River Delta, Krugloe Lake; 72.468859° N, 126.265658° E; depth 1–1.5 m; 21 Aug. 2019; A. Novikov leg.; KFU.

Other material
RUSSIA • 1 ♂; Lena River Delta, Samoylov Island, Yuzshnoe Lake; 72.369653° N, 126.509606° E; depth 1–1.5 m; 4 Aug. 2019; A. Novikov leg.; KFU • 2 ♂♂, 1 ♀; Lena River Delta, Samoylov Island, Ruiba Lake; 72.373173° N, 126.486302° E; depth 1–1.5 m; 4 Aug. 2019; A. Novikov leg.; KFU.

Description

Female (based on holotype)
Body. Subcylindrical (as in Fig. 1A). Total body length from anterior margin of rostrum to posterior margin of caudal rami: 904 µm. Cephalothorax (Fig. 2A–B) with blue naupliar eye, wider than remaining somites, largest width 204 µm. Rostrum small, fused with cephalothorax, with one pair of sensilla and one pore. Posterior margin of cephalothorax and all pedigerous somites slightly serrated.

Abdomen (Fig. 3). Consisting of genital double-somite, two free abdominal somites and anal somite with caudal rami. All somites except anal somite serrated on posterior margin, on surface with rows of small spinules. Genital double-somite wider than long; with seven pairs of sensilla, two pairs of lateral pores, paired ventral group of three pores, one unpaired ventral pore and two dorsal unpaired pores; on posterior margin with dorso-lateral row of spinules and small ventral row of spinules. P6 (Fig. 3B) fused with somite with one pinnate and one naked seta. Genital field (Fig. 3B) long, laterally with sieves; copulatory pore in middle of somite, copulatory duct strongly chitinised with two additional tubes, extending proximally to pair of labyrinthic rounded ducts. First free abdominal somite with three pairs of sensilla, one dorsal pore, one pair of lateral pores and five ventral pores; on posterior margin with dorso-lateral row of large spinules and ventral row of small spinules. Second free abdominal somite with one dorsal pore, pair of lateral pores and one ventral pore, on posterior margin with circumsomitic row of spinules. Anal somite with one pair of sensilla, three pairs of pores on ventral, dorsal and lateral sides, and ventral rows of spinules. Anal operculum semilunar, with four long spinules.

Caudal rami (Fig. 3). Length/width ratio 2, with two ventral pores; with rows of spinules on distal margin and rows of spinules at base of setae II and III. Seta I small, located near seta II. Apical seta IV (Fig. 1B) short, spinulose, with 'helle Stelle' (sensu Lang 1948). Apical seta V long, spinulose, with bulb at base. Length of apical setae IV and V 92 µm and 556 µm respectively. Seta VII triarticulated (Fig. 1A).

Antennule (Fig. 4A). 8-segmented. Segment 1 square, with one pinnate seta and two rows of spinules. Other segments with bare setae. Segment 4 with seta and aesthetasc fused basally. Distal segment with acrothek consisting of aesthetasc and two setae fused basally. Armature formula: 1-[1],2-[9],3-[5],4-[1+(1+ae)],5-[1],6-[3],7-[2],8-[5+acr].

Antenna (Fig. 4B). With allobasis. Coxa with three spinular rows. Allobasis with two pinnate setae and one spinular row. Free endopodal segment with two lateral rows of big spinules, with two spinulose spines and slender seta; distally with two rows of spinules; apically with three geniculate setae, two long spines and one small accessory seta; outermost geniculate seta fused basally with small seta. Exopod 2-segmented; first segment with one unipinnate seta; second segment with three bipinnate setae.

Labrum (**Fig**. 1C). Typical for Canthocamptidae. On outer side with row of thin setulles and a pore. On inner side with lateral rows of big spinules and rows of spinules fused into comb; with distal spinules and proximal groups of very thin setulles.

Mandible (**Fig**. 1D). Coxa with spinules proximally. Gnathobase with few multicuspidate teeth and spinulose seta; pars incisiva with one process; lacinia mobilis with two blunt teeth. Pars molaris sharply-

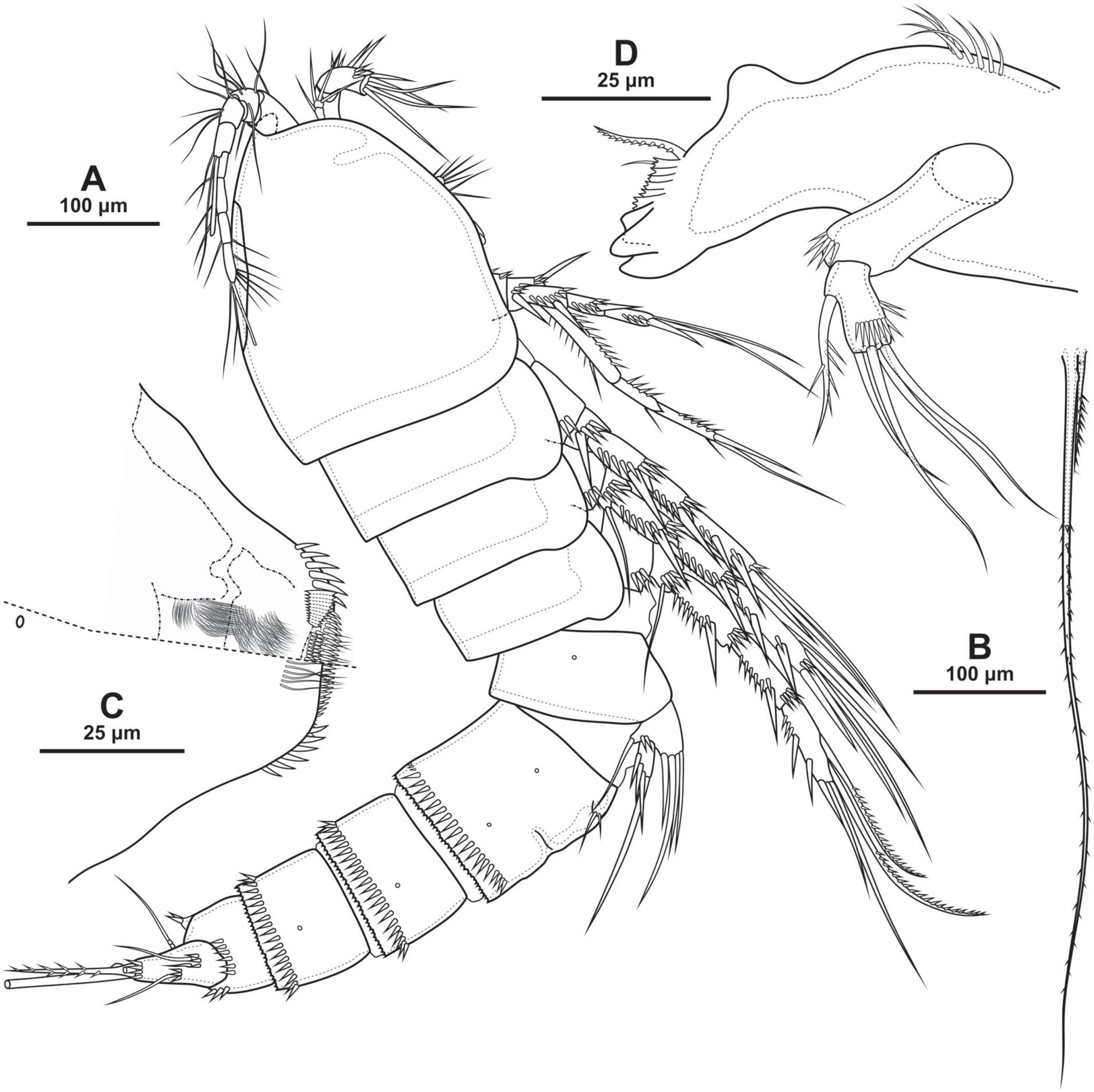

Fig. 1. *Canthocamptus waldemarschneideri* sp. nov. **A**. Paratype, ♀ (KFU BP 544/4); habitus, lateral view. **B–D**. Holotype, ♀ (KFU BP 544/1). **B**. Caudal setae IV and V. **C**. Labrum. **D**. Mandible.

edged. Palp consisting of free basis and 1-segmented endopod. Basis with row of spinules; endopod with two spinular rows, one pinnate proximal seta and four naked distal setae.

MAXILLULE (Fig. 4C–D). Praecoxa with two rows of slender spinules on outer edge and one row of spinules on posterior side. Praecoxal arthrite medially with row of spinules; with seven strong distal spines, distal seta with long spinules and two proximal setae. Coxa with row of slender spinules, coxal endite with one pinnate and spinulose setae. Basis with two groups of spinules, two subdistal setae and three distal setae. Endopod and exopod incorporated into basis, each represented by protuberance with two pinnate setae.

MAXILLA (Fig. 5A). Basis with several rows of spinules on outer and inner edge as figured, with two endites. Proximal endite with one strong bipinnate seta, two pinnate setae and spinular row, distal endite

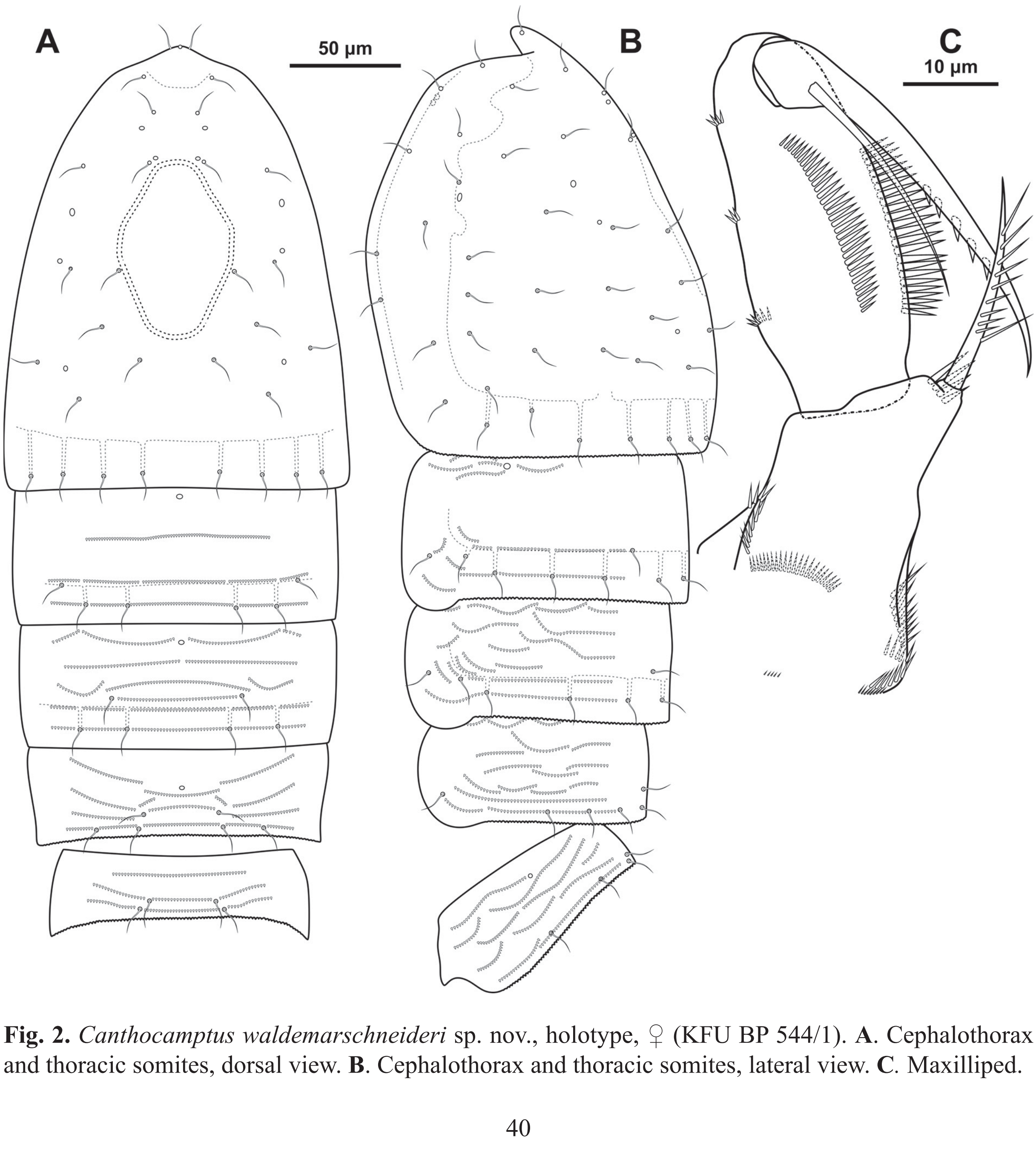

Fig. 2. *Canthocamptus waldemarschneideri* sp. nov., holotype, ♀ (KFU BP 544/1). **A**. Cephalothorax and thoracic somites, dorsal view. **B**. Cephalothorax and thoracic somites, lateral view. **C**. Maxilliped.

with three pinnate setae. Proximal endopodal segment with two setae, small process near one of setae and massive distal claw. Distal endopodal segment with three naked setae.

Maxilliped (Fig. 2C). Subchelate. Syncoxa elongated with several rows of spinules as figured, distally with one unipinnate seta. Basis with two rows of large spinules on anterior and posterior sides and three outer rows of small spinules. Endopod on posterior side with one seta. Endopodal claw elongated, with five small spinules.

P1 (Fig. 5B). With 3-segmented rami. Praecoxa with row of spinules. Coxa rectangular, with eight spinular rows. Intercoxal sclerite wide, with one pair of spinular rows. Basis with proximal pore, medial row of

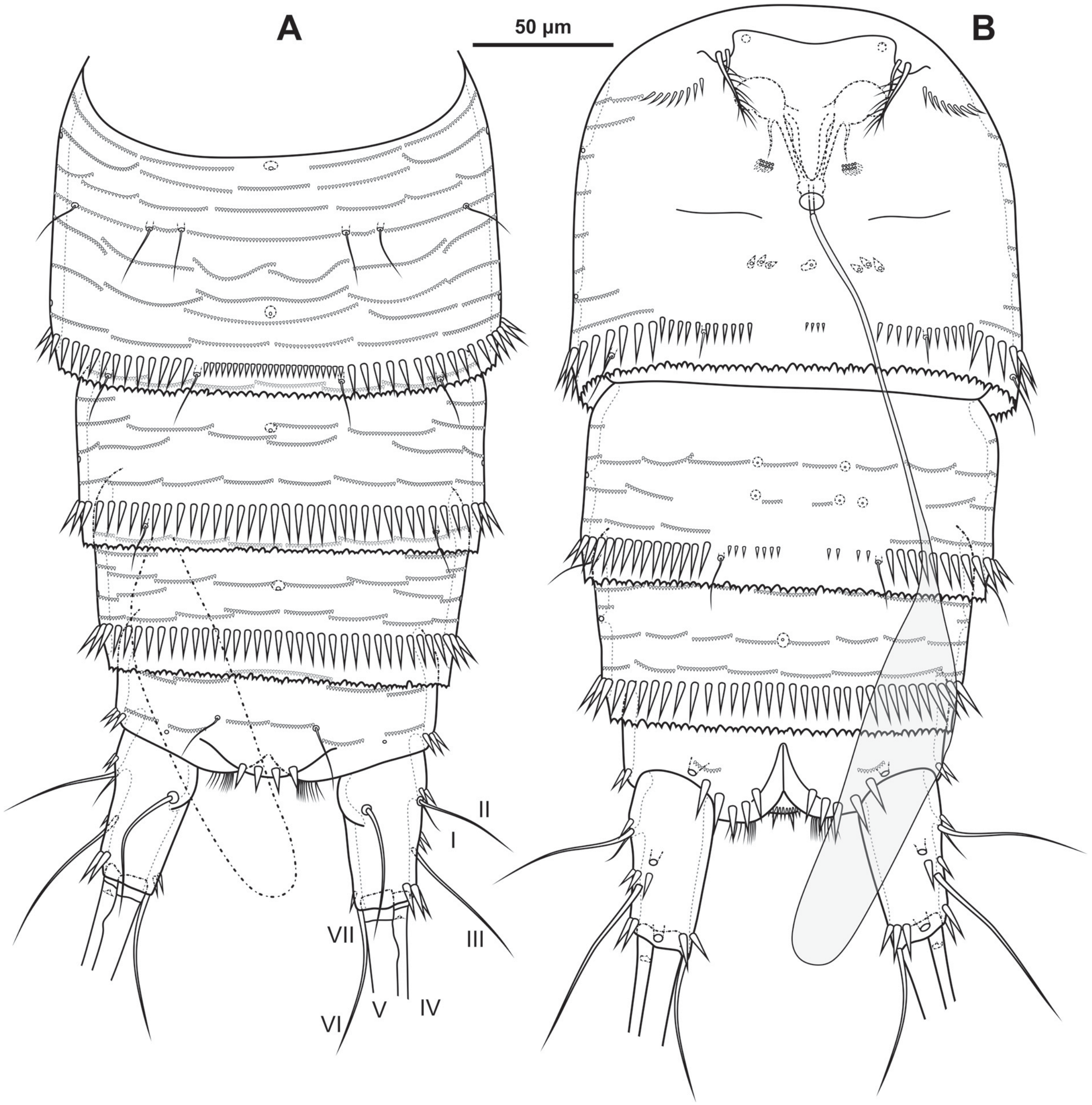

Fig. 3. *Canthocamptus waldemarschneideri* sp. nov., holotype, ♀ (KFU BP 544/1). **A**. Abdomen, dorsal view; setae of caudal ramus are labeled with Roman numerals. **B**. Abdomen, ventral view.

spinules, rows of spinules at base of endopod and exopod, row of spinules at base of inner seta and two inner rows of spinules; with strong inner and outer spines. All endopodal and exopodal segments with outer spinules. First exopodal segment with one outer spine; second segment with inner spinular row, inner seta and outer spine; third exopodal segment with two outer spines and two slender apical geniculate setae. Endopod longer than exopod. First endopodal segment reaching middle of third exopodal segment,

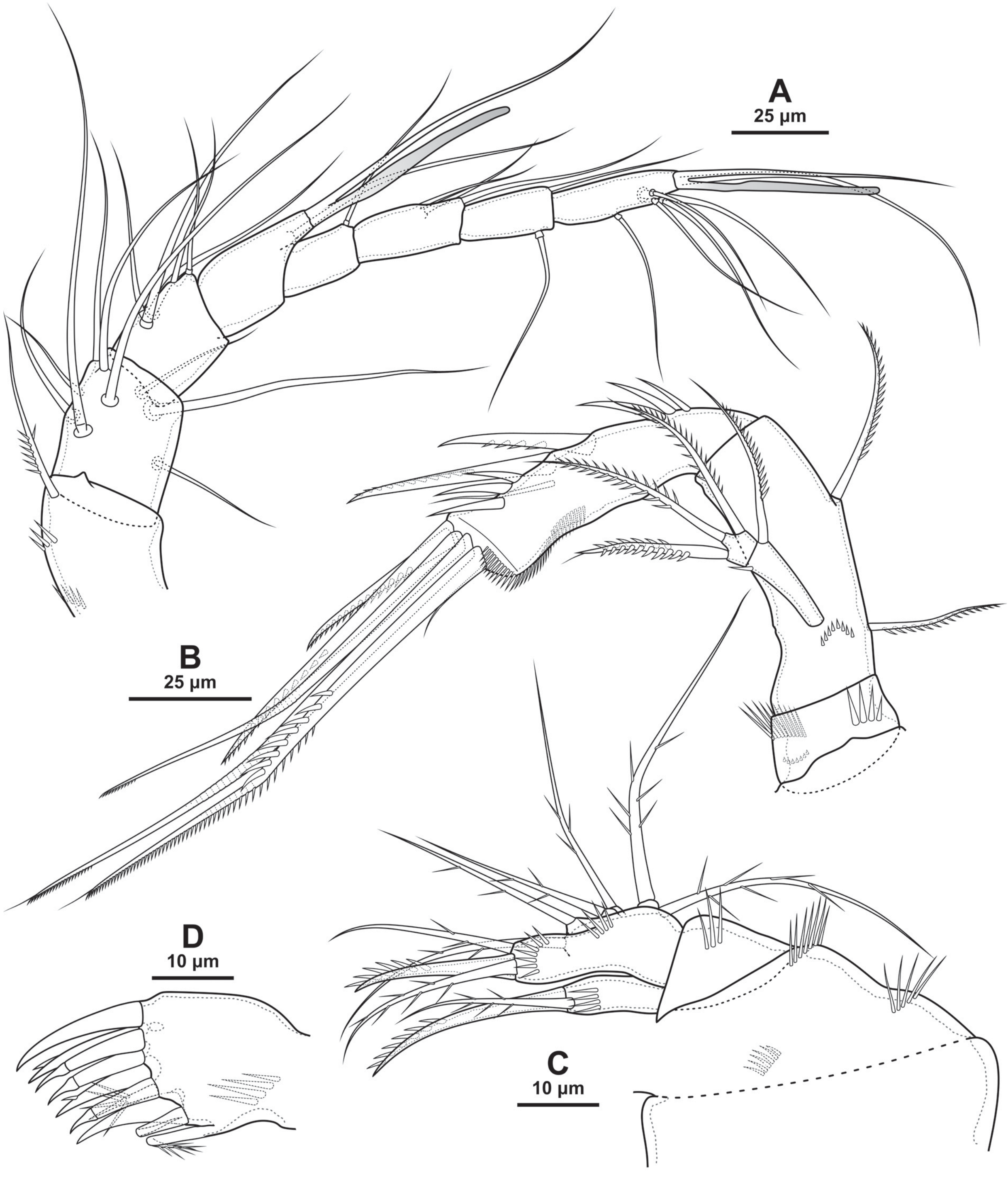

Fig. 4. *Canthocamptus waldemarschneideri* sp. nov., holotype, ♀ (KFU BP 544/1). **A**. Antennule. **B**. Antenna. **C**. Maxillule, without arthrite. **D**. Maxillule, arthrite.

with inner seta and inner spinular row; second endopodal segments with one inner seta, third segment with outer spine, long apical geniculate seta and small inner seta.

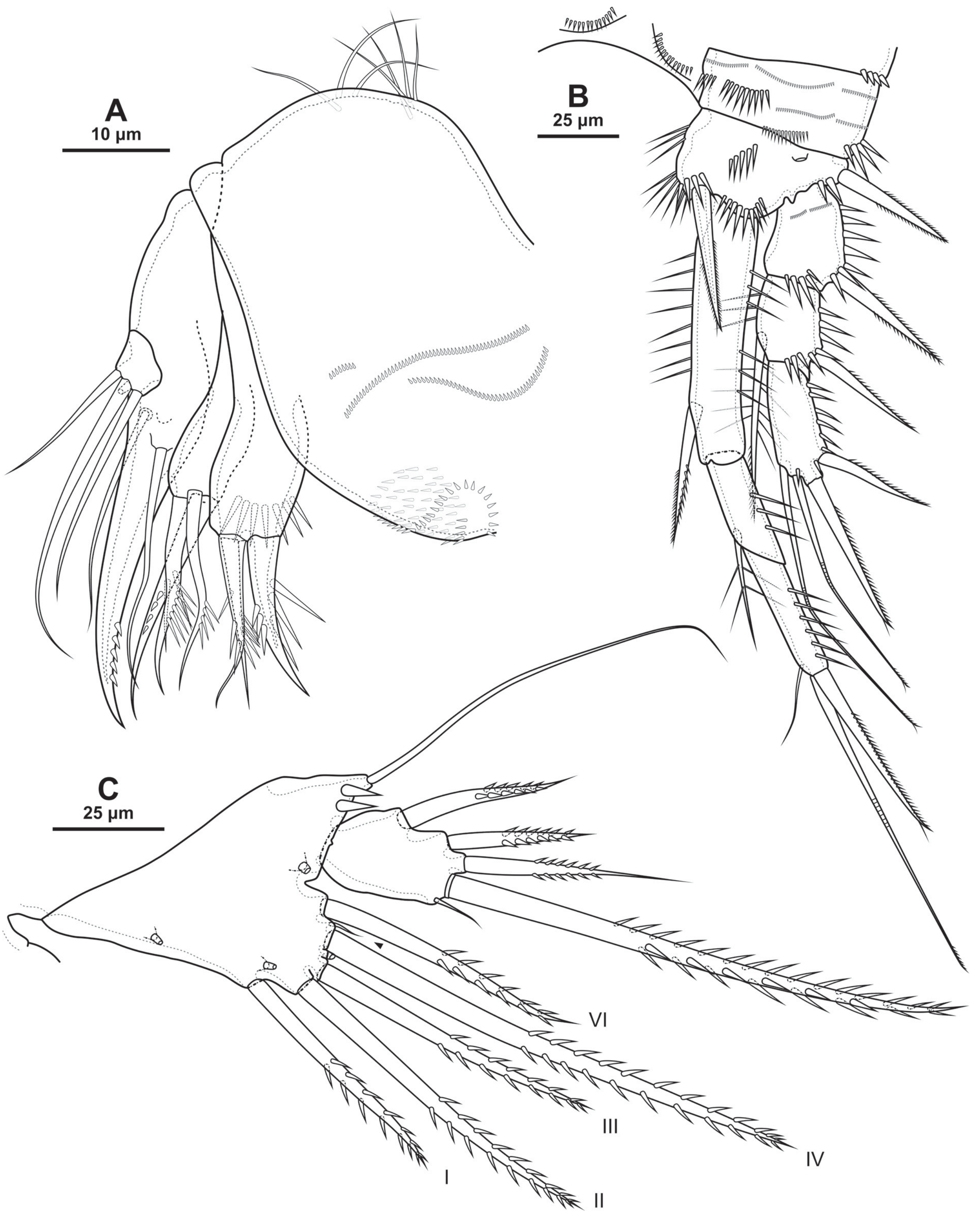

Fig. 5. *Canthocamptus waldemarschneideri* sp. nov., holotype, ♀ (KFU BP 544/1). **A**. Maxilla. **B**. P1. **C**. P5; setae of endopodal lobe are labeled with Roman numerals, seta V indicated by arrowhead.

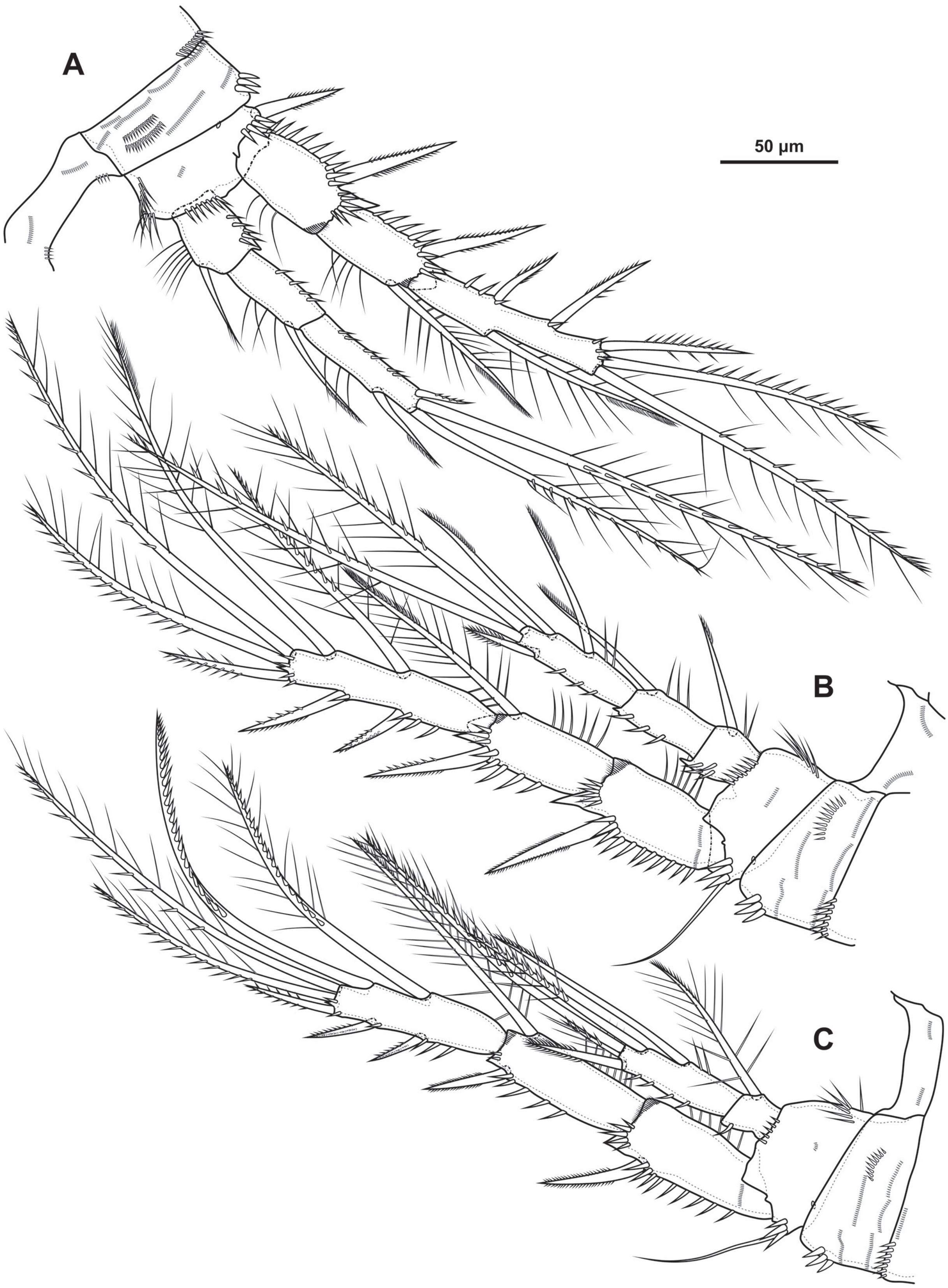

Fig. 6. *Canthocamptus waldemarschneideri* sp. nov., holotype, ♀ (KFU BP 544/1). **A**. P2. **B**. P3. **C**. P4.

Table 2. P1–P4 armature of *Canthocamptus waldemarschneideri* sp. nov.

	Female endopod	Male endopod	Exopod
P1	1; 1; 1,1,1	1; 1; 1,1,1	0; 1; 0,2,2
P2	1; 1; 1,2,1	1; 2,2,0	0; 1; 1,2,3
P3	1; 1; 2,2,1	1; 1 + apophysis; 2,2,0	0; 1; 2,2,3
P4	1; 2,2,1	1; 2,2,1 modified spine	0; 1; 2,2,3

P2 (Fig. 6A). Praecoxa with row of spinules. Coxa with one lateral row of spinules and six rows of spinules on anterior side. Intercoxal sclerite with two paired spinular rows. Basis with proximal pore, medial row of spinules, two rows of slender spinules on inner edge and rows of spinules at base of endopod and exopod; with outer spine. 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 setae and one inner seta. Endopod 3-segmented; first and second segments with inner setae and inner spinular rows; third segment with inner spinular row, small outer spine, two apical setae and one inner seta.

P3 (Fig. 6B). Similar to P2. Praecoxa, coxa, basis, first and second exopodal segments and first and second endopodal segments as in P2. Intercoxal sclerite with only one paired spinular row. Third exopodal segment with three outer spines, two apical setae and two inner setae. Third exopodal segment with outer spine, two long apical setae and two inner setae with pectinate tip.

P4 (Fig. 6C). Similar to P2. Praecoxa, coxa and basis as in P2. Intercoxal sclerite with only one paired spinular row. Exopod as in P2, but third exopodal segment with two inner setae with strong spinules. Endopod small; first segment with inner seta; second segment with outer spine, two apical setae and two inner pectinate setae; outer apical seta short, about as long as outer spine.

P5 (Fig. 5C). With separate right and left baseoendopods. Baseoendopod reaching about proximal third of exopodal segment; with three pores, spinular row at base of outer seta; outer seta of basis naked. Endopodal lobe with five long bipinnate setae and one minute seta between fourth and sixth normal setae. Exopod with three equal outer setae, one long apical seta and minute inner seta.

Male

Total body length from tip of rostrum to posterior margin of caudal rami: 765 µm. Sexual dimorphism expressed in the antennule, P2–P6, genital segmentation and ornamentation. Cephalothorax and thoracic somites as in female. P6 (Fig. 7B) two asymmetric flaps fused to somite, with two slender setae and pinnate inner spine. Anal somite and caudal rami as in female, but seta V without bulb at base. Anal operculum with five spinules.

Antennule (Fig. 8A–B). 10-segmented, haplocer with geniculation between segments 7 and 8. Segment 5 with large aestetasc fused at base with long seta. Segment 7 with articular plate, with one filiform seta, one pinnate seta and with two modified laminar setae. Segment 8 with 3 similar modified laminar setae. Segment 10 with acrothek consisting of slender aesthetasc and two setae. Armature formula: 1-[1],2-[9],3-[8],4-[2],5-[7+(1+ae)],6-[2],7-[2+2 modified],8-[3 modified],9-[1],10-[7+acr].

P2 (Figs 9A, 10A–B). Praecoxa, coxa, intercoxal sclerite and basis as in female. Exopod as in female, but segments broader and shorter. Endopod 2-segmented. First segment as in female. Second segment long, with well-defined border between original segments evidenced by proximal inner seta and outer cuticular process; with two apical setae and two inner setae.

P3 (Figs 9B, 10C–D). Praecoxa, coxa, intercoxal sclerite and basis as in female. Exopod as in female, but segments broader and shorter. Endopod 3-segmented. First endopodal segment with slender seta and cuticular process on posterior side. Second endopodal segment with one small posterior seta and long apophysis with tip. Third segment with two small inner setae and one apical pinnate seta and one apical naked seta.

P4 (Fig. 9C). Praecoxa, coxa, intercoxal sclerite and basis as in female. Exopod as in female, but segments broader and shorter, and outer spines of third exopodal segment curved. Endopod 2-segmented; first

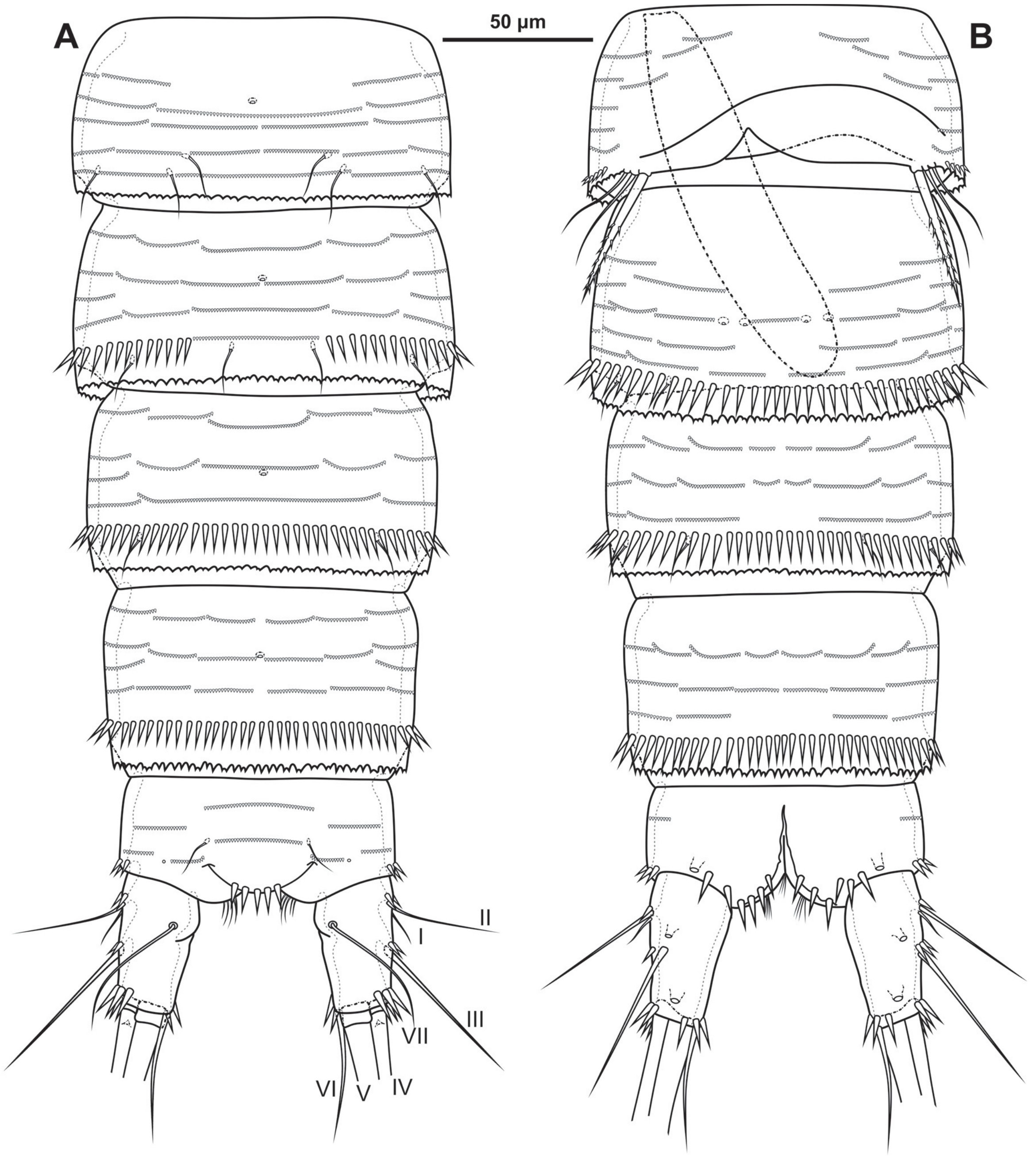

Fig. 7. *Canthocamptus waldemarschneideri* sp. nov., allotype, ♂ (KFU BP 544/2). **A**. Abdomen, dorsal view. **B**. Abdomen, ventral view.

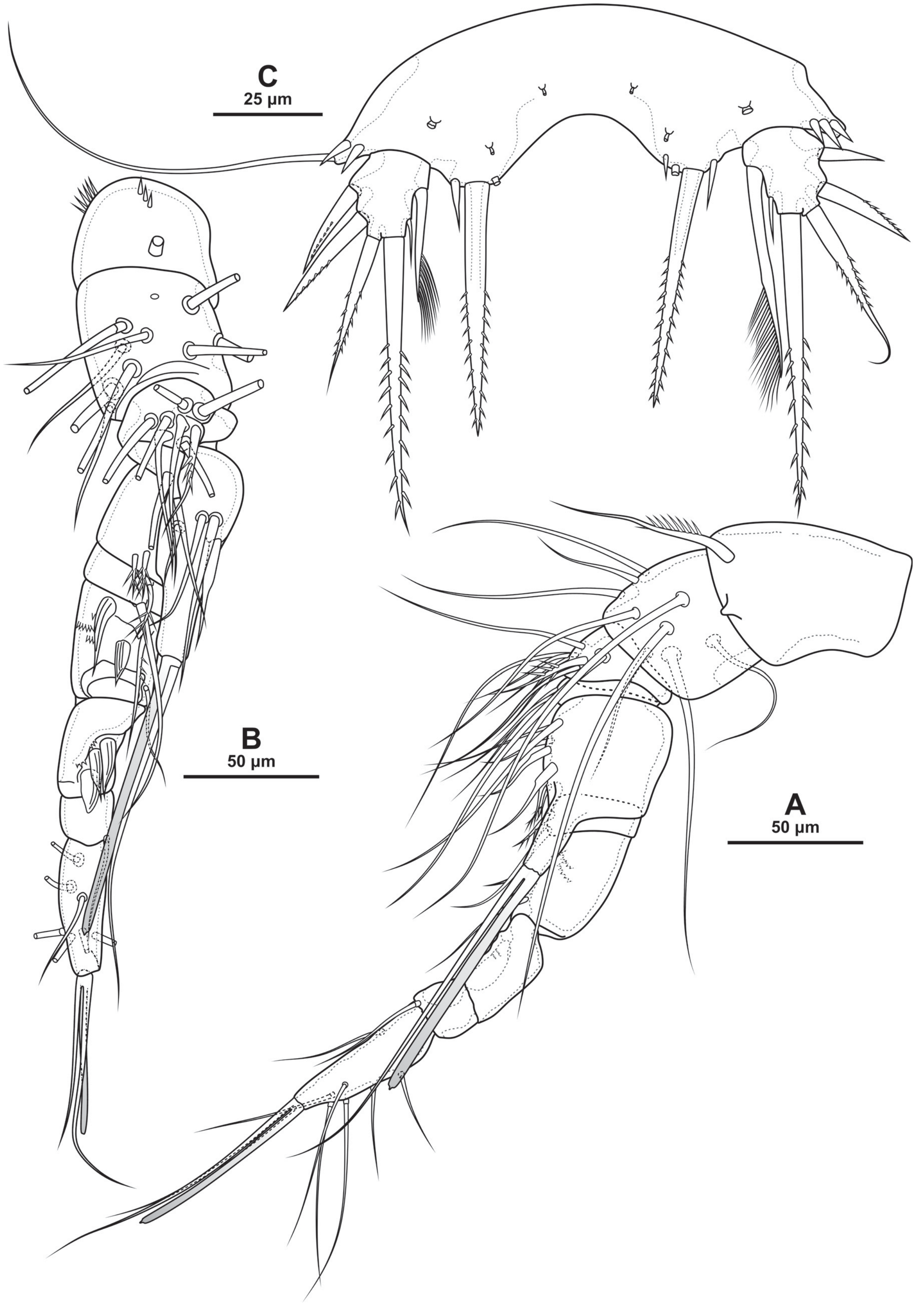

Fig. 8. *Canthocamptus waldemarschneideri* sp. nov., allotype, ♂ (KFU BP 544/2). **A**. Antennule, dorsal view. **B**. Antennule, anterior view. **C**. P5.

segment with inner seta; second segment with outer spinules, outer seta modified into finger-like process, two long apical setae and two pectinate inner setae.

P5 (Fig. 8C). Asymmetric; right and left P5 fused medially. Baseoendopod with four pairs of pores, outer spinular row and long outer naked seta; endopodal lobe with strong apical spine and small inner seta; left lobe with spinule near distal margin. Exopod with three equal in length outer setae, long apical seta, one

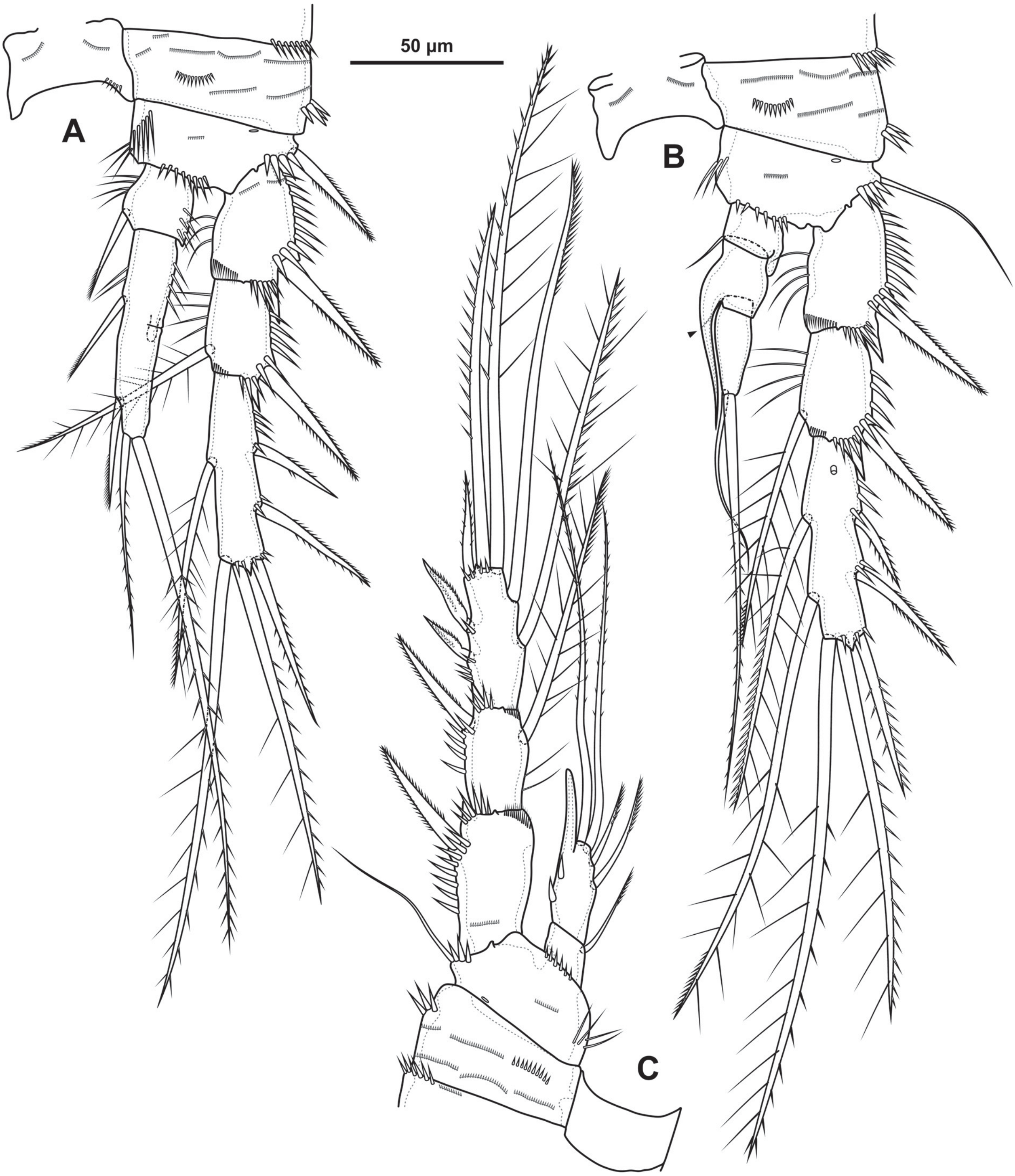

Fig. 9. *Canthocamptus waldemarschneideri* sp. nov., allotype, ♂ (KFU BP 544/2). **A**. P2. **B**. P3; small seta indicated by arrowhead. **C**. P4.

minute inner seta and one long inner pectinate seta. Difference between left and right exopods is that left one has much longer inner seta and shorter proximal outer spine.

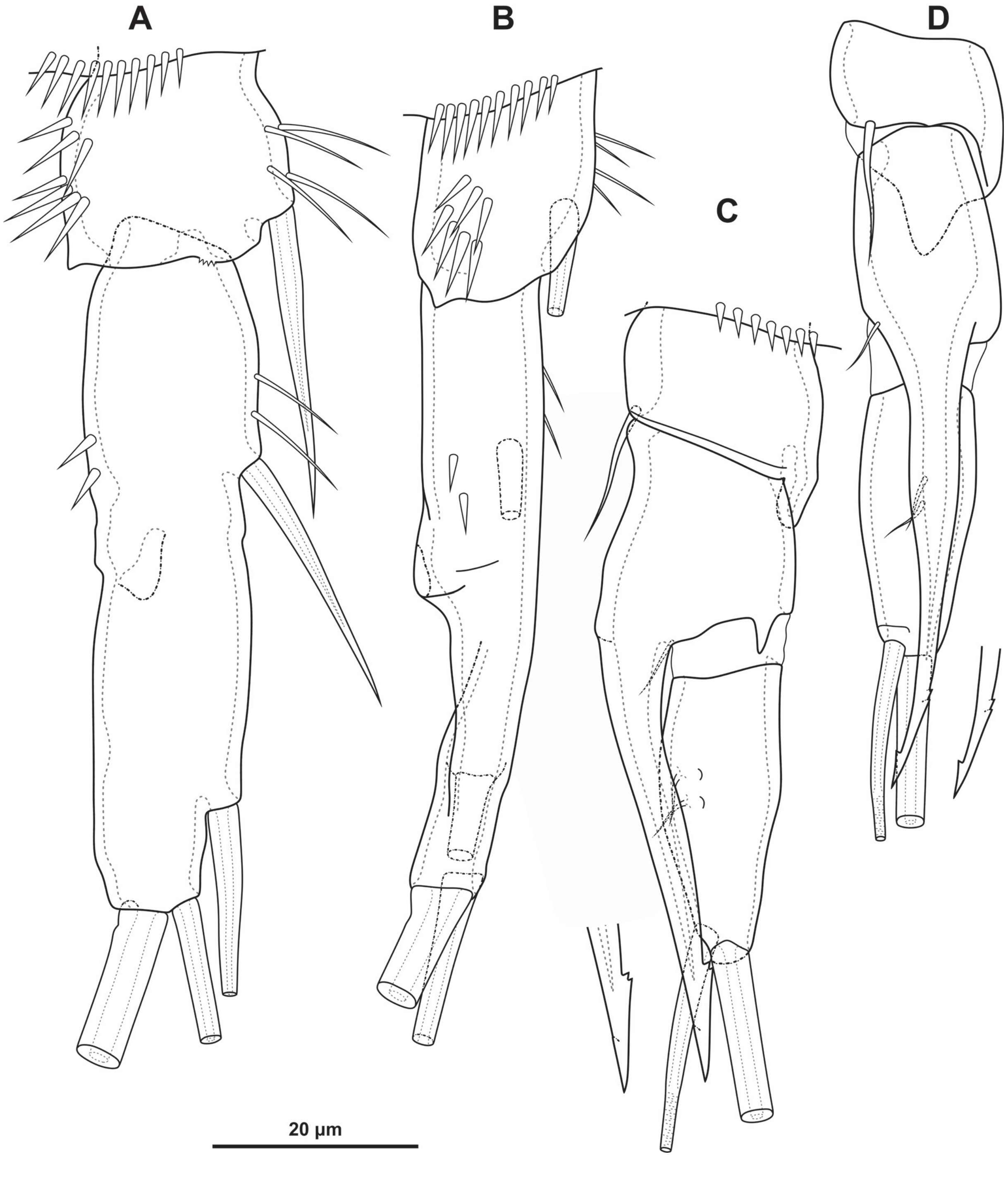

Fig. 10. *Canthocamptus waldemarschneideri* sp. nov., ♂, Yuzshnoe Lake (KFU). **A**. P2 endopod, anterior view. **B**. P2 endopod, outer side. **C**. P3 endopod, anterior view. **D**. P3 endopod, inner side.

Ecology

The species was found in four water-bodies of the Lena River Delta. The type locality at the collection site is a small channel without macrophytes with a silty bottom. The other three reservoirs are typical old thermokarst lakes with a large number of macrophytes and a silty bottom. At the type locality, the species was found with the following Copepoda species: *Attheyella nordenskioldii* (Lilljeborg, 1902), *Bryocamptus nivalis* (Willey, 1925), *Moraria duthiei* (Scott T. & Scott A., 1896), *Cyclops kikuchi* Smirnov, 1932, *Diacyclops bicuspidatus* (Claus, 1857), *Eucyclops serrulatus* (Fischer, 1851), *Macrocyclops albidus* (Jurine, 1820), *Megacyclops gigas* (Claus, 1857), *Megacyclops viridis* (Jurine, 1820), *Metacyclops planus* (Gurney, 1909), *Paracyclops fimbriatus* (Fischer, 1853) and *Eurytemora gracilicauda* Akatova, 1949.

Remarks

C. waldemarschneideri sp. nov. is closely related to the North American species with four setae on P2 endopod. This is an apparent synapomorphy of this group of species, which also includes *C. assimilis* Kiefer, 1931, *C. robertcockeri* M.S. Wilson, 1958 and *C. vagus* Coker & Morgan, 1940. The new species is closely related to *C. assimilis* based on similar caudal rami and the shape and length of the setae of P5. The differences between these two species are as follows: 1) the new species has a closed row of spinules on the posterior edge of the third abdominal somite, whereas *C. assimilis* has a gap on the dorsal side; 2) the caudal seta V of *C. waldemarschneideri* sp. nov. has a clearly visible thickening at the base, directed upwards; 3) the setal lengths of the male P5 vary more markedly in *C. waldemarschneideri* sp. nov., especially in the basoendopod, where inner seta/outer seta length = 4.8, whereas in *C. assimilis* inner seta/outer seta length = 3.1 (Kiefer 1931).

Cladistic analysis

The result of the cladistic analysis is the puzzled tree shown in Fig. 11A. The length of the tree is 216, and the consistency index (CI) and retention index (RI) are 0.468 and 0.703, respectively.

The most interesting feature was the division of the genus into two groups, one of which (*C. mirabilis* species group) is closely related to the genera *Attheyella* and *Bryocamptus* Chappuis, 1929. Such a division was previously assumed, and this group of species was considered intermediate between the genera *Canthocamptus* and *Attheyella* (Ito & Takashio 1980). The most significant characteristic connecting the *C. mirabilis* species group and the genus *Attheyella* is the form of the male P2 endopod, with the third segment without an outer seta and with a notch on the distal outer margin ('Attheyella-like' endopod, Fig. 11B, character 36). Other synapomorphies of this group include dumbbell-shaped dorsal window (character 4), basis of mandible without setae (character 15), long first endopodal segment of P1 (character 30) and anal operculum with smooth margin (character 69). Based on this and some other differences (Table 7), we propose a new genus, *Kikuchicamptus* gen. nov., for this monophyletic group.

One species, *C. gibba*, is most closely related to *A. nordenskioldii*. According to the characteristics described and depicted by Okuneva (1983), this species is completely identical to the studied individuals of the species *A. nordenskioldii* from the Lena River Delta; therefore, it should be its junior synonym.

The *Canthocamptus* clade is supported by two reliable characters in the structure of the male P2 and P4 endopods: the endopod P2 with fused second and third segment, the third ancestral segment without outer seta, and with a posterio-lateral cuticular process on the border between the second and the third segment ('Canthocamptus-like' endopod, character 37); the P4 endopod with modified 'finger-like' outer spine (character 50). The division within *Canthocamptus* s. str. is rather controversial. The entire genus is divided into three large but poorly supported clades.

One of the clades includes *C. staphilinus* and all Baikal species. They were brought together by the similarity in the structure of the male P3 endopod, with a powerful second segment (character 44) and

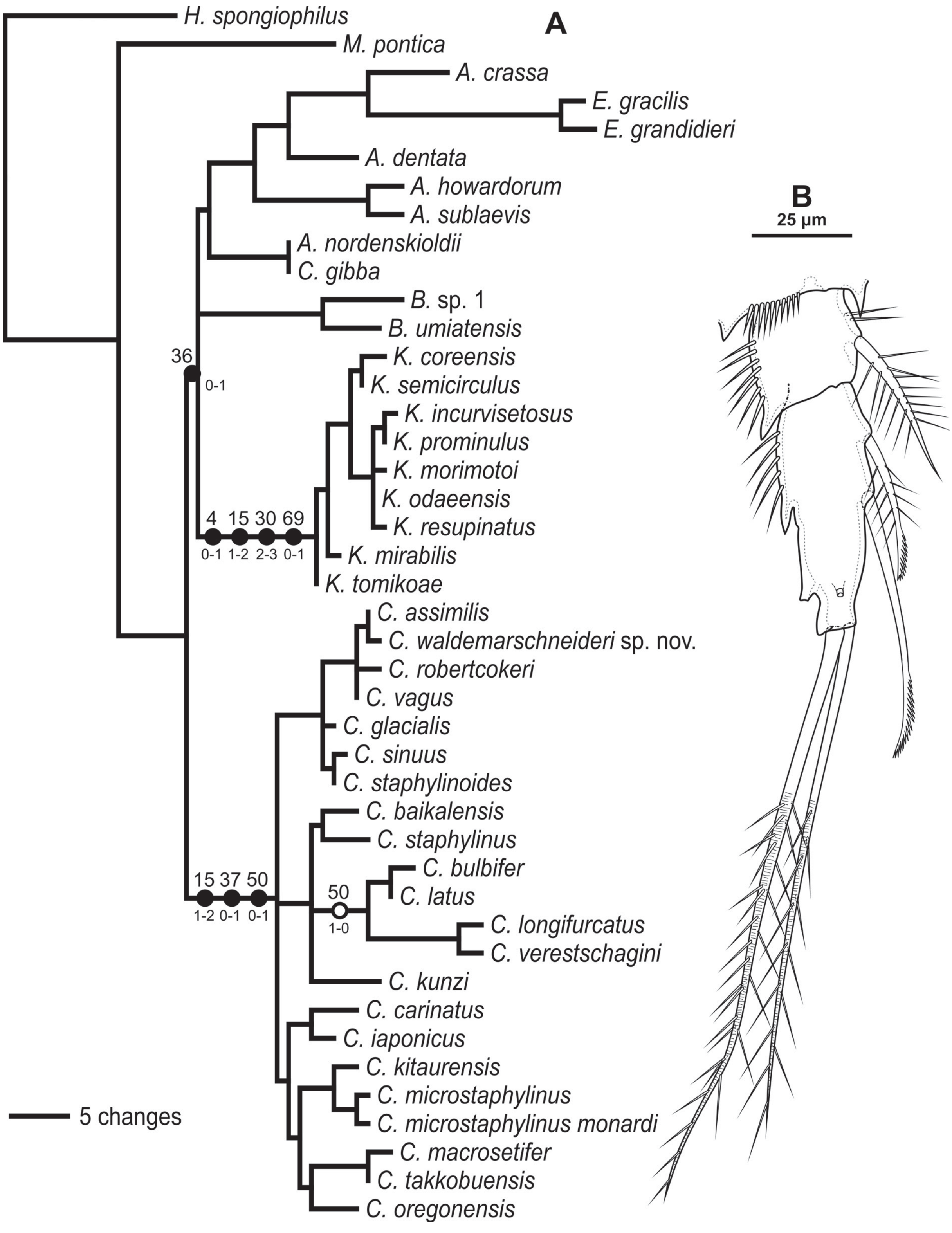

Fig. 11. A. Quartet puzzling tree of the genus *Canthocamptus* Westwood, 1836, constructed by the parsimony method based on the matrix from Supp. file 1. Dots mark the main changes in character states in studied branches. Changes in the characters are marked under the dot. **B**. *Attheyella nordenskioldii* (Lilljeborg, 1902), ♂, P2 endopod. Generic abbreviations: *A.* = *Attheyella*; *B.* = *Bryocamptus*; *C.* = *Camptocamptus*; *E.* = *Elaphoidella*; *H.* = *Heteropsyllus*; *K.* = *Kikuchicamptus* gen. nov.; *M.* = *Mesochra*.

different degrees of reduction in the apical setae (character 43). If this hypothesis is correct, then the simple spine on the male P4 endopod (character 50) of the Baikal species is an apomorphy, not a plesiomorphy. In addition, the placement of the Baikal species *C. verestschagini* (Borutzky, 1931) and *C. longifurcatus* Borutzky, 1947 into a separate subgenus, *C.* (*Baikalocamptus*) Borutzky, 1931, is also incorrect in this case, since the subgenus *Canthocamptus* (*Canthocamptus*), in which Borutzky (1952) proposed to include all other species of the genus, becomes non-monophyletic. Moreover, our own material from Baikal shows that the spine on the male P4 endopod is modified in all the studied males of *Canthocamptus* sp. However, further research is needed here.

Another interesting clade is the *C. glacialis* species group, which includes *C. glacialis*, *C. sinuus* Coker, 1934, *C. staphylinoides* Pearse, 1905, *C. assimilis*, *C. robertcokeri* M.S. Wilson, 1958, *C. vagus* and *C. waldemarschneideri* sp. nov. Most species of this group live in North America. The relationship of *C. glacialis* to the American species was pointed out by M.S. Wilson (1956), though without naming specific common characters. Representatives of the group as a whole are characterized by the primitive structure of the male P2, P3 and P4 endopods (all endopods are slender, with unmodified, normally developed setae). They also lack the characteristic unguiform processes on the anal somite. However, the synapomorphies that combine these species are not sufficiently reliable. These are the loss of outer spinules on the P5 exopod (character 56) and a large difference between the length of the spines on the P5 baseoendopod of males (character 60). Thus, the monophyly of the clade remains in question.

Based on the results of the cladistic analysis, we carry out the following taxonomic changes.

Systematics

Genus ***Attheyella*** Brady, 1880

New combinations

A. howardorum (Hamond, 1987) comb. nov.; *Attheyella sublaevis* (Hamond, 1987) comb. nov.

Remarks

Two Australian species, *A. howardorum* and *A. sublaevis* (Hamond 1987), must belong to the genus *Attheyella* on the basis of the following characteristics: 1-segmented exopod of the antenna (character 8), the male P3 endopod ‘Attheyella-like’ (character 36), normal setae on the female P5 baseoendopod (character 52), and reduced number of setae on the male P5 exopod (four instead of six in the primitive structure, like *Bryocamptus*, characters 58–59). Placing them in any subgenus is difficult. By morphological characters, these species are close to *Attheyella* (*Neomrazekiella*) Özdikmen & Pesce, 2006; however, its representatives have not yet been found in the Australian region. In general, the genus *Attheyella* is in great need of revision, and the boundaries of the subgenera are not precisely defined.

Attheyella (Neomrazekiella) nordenskioldii (Lilljeborg, 1902)

Canthocamptus nordenskioldii Lilljeborg, 1902: 1, pl. 3, figs 1–6 (original description).
Canthocamptus gibba Okuneva, 1983: 1343, fig. 1, syn. nov.

Remarks

The synonymy of *C. gibba* and *A. nordenskioldii* described from Baikal is confirmed by a comparison of Okuneva’s drawings (1983) with specimens of *A. nordenskioldii* from the Lena Delta and the original description. In particular, the shape of the caudal rami and their setae are completely identical (characters 73, 77). *Canthocamptus gibba*, like other species of the genus *Attheyella*, has a 1-segmented exopod of antenna (character 8) and only five setae on the male P5 exopod (character 58).

Genus ***Canthocamptus*** Westwood, 1836
Table 3

Canthocamptus Westwood, 1836: 227.
Baikalocamptus Borutzky, 1931: 281.
Canthocamptus (*Canthocamptus*) Westwood, 1836, syn. nov.
Canthocamptus (*Baikalocamptus*) Borutzky, 1931, syn. nov.

Type species

Canthocamptus staphylinus (Jurine, 1820).

Other species and subspecies

C. assimilis Kiefer, 1931; *C. baikalensis* Borutzky, 1931; *C. bulbifer* Borutzky, 1947; *C. carinatus* Shen & Sung, 1973; *C. glacialis* Lilljeborg, 1902; *C. iaponicus* Brehm, 1927; *C. kitaurensis* Kikuchi in Ishida & Kikuchi, 1999; *C. kunzi* Apostolov, 1969; *C. latus* Borutzky, 1947; *C. longifurcatus* Borutzky, 1947; *C. macrosetifer* Ishida in Ishida & Kikuchi, 1999; *C. microstaphylinus* s. str. Wolf, 1905; *C. microstaphylinus monardi* Roy, 1927; *C. oregonensis* M.S. Wilson, 1956; *C. robertcokeri* M.S. Wilson, 1958; *C. sinuus* Coker, 1934; *C. staphylinoides* Pearse, 1905; *C. takkobuensis* Ishida in Ishida & Kikuchi, 1999; *C. vagus* Coker & Morgan, 1940; *C. verestschagini* (Borutzky, 1931); *C. waldemarschneideri* sp. nov.

Species nomen nudum (according to Lang 1948)

C. aloisianus Brehm, 1908; *C. brunnthaleri* Brehm, 1913; *C. cavernarum* Packard, 1879; *C. elegantulus* Fischer, 1860; *C. linearis* Dana, 1852; *C. maoricus* Brehm, 1928; *C. mareoticus* Fischer, 1860; *C. mobilensis* Herrick, 1887; *C. tatricus* Daday, 1897.

Species inquirendae

C. aequipes Krichagin, 1877; *C. bicolor* Wilson C.B., 1932; *C. borcherdingii* Poppe, 1889; *C. cingalensis* (Brady, 1886); *C. crenulatus* Mrázek, 1901; *C. dentatus* Poggenpol, 1874; *C. elaphoides* Chappuis, 1924; *C. finni* Bourne, 1893; *C. fontinalis* Rehberg, 1880; *C. hyperboreus* Willey, 1925; *C. laciniatus* Douwe, 1911; *C. longicaudatus* Krichagin, 1877; *C. longisetosus* Daday, 1902; *C. megalops* Lilljeborg, 1902; *C. northumbricoides* Willey, 1925; *C. rostratus* Claus, 1863; *C. stroemii* Baird, 1850; *C. subsalus* Brady, 1895; *C. tenuicaudis* Herrick, 1884; *C. virescens* Dana, 1849; *C. wiegoldi* Brehm, 1923; *C. willeyi* Kiefer, 1925.

Amended diagnosis

Canthocamptidae. Body semi-cylindrical. Rostrum short. Caudal rami cylindrical; setae IV and V usually long and pinnate. Female antennule 8-segmented; male antennule 10-segmented, haplocer with geniculation between segments 7 and 8. Antenna with allobasis, exopod 1- to 2-segmented, with 4 setae. Mandible with well-developed gnathobase; palp 1- to 2-segmented. Maxilla with two endites; endopod 1-segmented. P1 with 3-segmented rami; first endopodal segment long, reaching about midlength of third exopodal segment. P2–P3 with 3-segmented rami; P4 exopod 3-segmented, endopod 2-segmented. Female P5 endopod with 6 setae, typically seta V small (except in *C. iaponicus*); exopod short ($l/w < 2$), with 5 setae, typically seta I small, equal to or shorter than outer setae (except in *C. iaponicus*). Male P2 endopod sexually dimorphic, 'Canthocamptus-like' (Fig. 9A), second and third segments fused, third segment without outer seta, on border between ancestral second and third segments with posterio-lateral cuticular process. Male P3 endopod typical for Canthocamptidae, with long apophysis with tip; third segment with 0, 1 or 2 setae. Male P4 endopod usually with modified finger-like outer seta (simple spine in *C. latus*, *C. bulbifer*, *C. longifurcatus* and *C. verestschagini*.) Male P5 endopod with 2 setae, outer seta much smaller than inner one, inner seta/outer seta length from 1.5 to 10, typically 3; exopod with 5 or 6 setae; inner seta, if present, long, pectinate (absent in *C. latus*, *C. bulbifer*, *C. longifurcatus* and *C. robertcokeri*).

Table 3. Armature formula of P1–P4 of *Canthocamptus* Westwood, 1836.

	Female endopod	Male endopod	Exopod
P1	1; 1; 1,1,1	1; 1; 1,1,1	0; 1; 0,2,2
P2	1; 1; 1–2,2,1	1; 2–3,2,0	0; 1; 1,2,3
P3	1; 1; 1–2,2,1	1; 1? + apophysis; 2?,0?-2,0	0; 1; 2,2,3
P4	1; 2,2,1	1; 0–2,2,1	0; 1; 2,2,3

Distribution

Species of this genus are widespread in the Holarctic, with special diversity in Asia, where 12 species occur along with the new species. Five of them are endemics of Lake Baikal. The findings of *C. staphilinus* in Borneo (Spandl 1924) are most likely due to a misidentification. Thus, the range of all *Canthocamptus* covers the entire Holarctic, not going beyond its limits.

Remarks

Despite the up-to-date lists of K. Lang (1948) and J.B.J. Wells (2008), still has about 77 valid names occur in the genus *Canthocamptus* in the WoRMS database (Walter & Boxshall 2021). Here we consider as *Canthocamptus* only those 22 species closely related to the type species, also establishing a new genus, *Kikuchicamptus* gen. nov., for the species closely related to *Kikuchicamptus mirabilis* (Sterba, 1968) comb. nov. This leaves 43 species out of the new definition of *Canthocamptus*, which is based on clear synapomorphies. These species belong to different lineages, some related to other freshwater genera such as *Bryocamptus*, *Elaphoidella* Chappuis, 1929, *Attheyella*, etc. Therefore, the WoRMS database must be updated to include in *Canthocamptus* only the species listed in this publication, and the species included in Tables 4 and 5 must be treated as nomina nuda, junior synonyms or species inquirendae.

Table 4. List of species of *Canthocamptus* Westwood, 1836, valid according to WoRMS (Walter & Boxshall 2021), that should be treated as junior synonyms or belong to a different genus, according to K. Lang (1948).

	Species	Status	Senior synonym or valid name
1	*C. gauthieri* Roy, 1924	another genus	*Bryocamptus* (*B.*) *gauthieri* (Roy, 1924)
2	*C. kamerunensis* Kiefer, 1928	another genus	*Pilocamptus kamerunensis* (Kiefer, 1928)
3	*C. australis* Coker, 1934	junior synonym	*B.* (*B.*) *hiatus* (Willey, 1925)
4	*C. catalanus* Monard, 1925	junior synonym	*B.* (*Rheocamptus*) *zschokkei* (Schmeil, 1893)
5	*C. cuspidatoides* Kiefer, 1924	junior synonym	*B.* (*Arcticocamptus*) *laccophilus* (Kessler 1914)
6	*C. inornatus* T. Scott, 1897	junior synonym	*Elaphoidella gracilis* (Sars, GO, 1863)
7	*C. mirus* Minkiewicz, 1916	junior synonym	*B.* (*A.*) *alpestris* (Vogt, 1845)
8	*C. niloticus* Chappuis, 1922	junior synonym	*E. grandidieri* (Guerne & Richard, 1893)
9	*C. papuanus* Daday, 1901	junior synonym	*Epactophanes richardi* Mrázek, 1893
10	*C. parvus* T. Scott & A. Scott, 1896	junior synonym	*Mesochra pygmaea* (Claus, 1863)
11	*C. setosus* Claus, 1866	junior synonym	*M. pygmaea* (Claus, 1863)
12	*C. signatus* Daday, 1901	junior synonym	*E. grandidieri* (Guerne & Richard, 1893)

Table 5. List of species of *Canthocamptus* Westwood, 1836, valid according to WoRMS (Walter & Boxshall 2021), that should be treated as species nomina nuda (according to Lang, 1948) or species inquirendae.

	Species	Status	Probable genus or family
1	*C. aloisianus* Brehm, 1908	nomen nudum	*Bryocamptus*
2	*C. brunnthaleri* Brehm, 1913	nomen nudum	?
3	*C. cavernarum* Packard, 1879	nomen nudum	*Attheyella*
4	*C. elegantulus* Fischer, 1860	nomen nudum	not Canthocamptidae
5	*C. linearis* Dana, 1852	nomen nudum	?
6	*C. maoricus* Brehm, 1928	nomen nudum	?
7	*C. mareoticus* Fischer, 1860	nomen nudum	not Canthocamptidae
8	*C. mobilensis* Herrick, 1887	nomen nudum	?
9	*C. tatricus* Daday, 1897	nomen nudum	?
10	*C. aequipes* Krichagin, 1877	species inquirenda	?
11	*C. bicolor* C.B. Wilson, 1932	species inquirenda	*Cletocamptus* Schmankevitsch, 1875
12	*C. borcherdingii* Poppe, 1889	species inquirenda	*Bryocamptus*
13	*C. cingalensis* (Brady, 1886)	species inquirenda	*Elaphoidella* or *Attheyella*
14	*C. crenulatus* Mrázek, 1901	species inquirenda	*Attheyella*
15	*C. dentatus* Poggenpol, 1874	species inquirenda	*Attheyella*
16	*C. elaphoides* Chappuis, 1924	species inquirenda	*Elaphoidella*
17	*C. finni* Bourne, 1893	species inquirenda	*Elaphoidella*
18	*C. fontinalis* Rehberg, 1880	species inquirenda	*Attheyella*
19	*C. hyperboreus* Willey, 1925	species inquirenda	*Attheyella*
20	*C. laciniatus* Douwe, 1911	species inquirenda	*Elaphoidella*
21	*C. longicaudatus* Krichagin, 1877	species inquirenda	Ameiridae Boeck, 1865
22	*C. longisetosus* Daday, 1902	species inquirenda	Ectinosomatidae Sars G.O., 1903
23	*C. megalops* Lilljeborg, 1902	species inquirenda	not Canthocamptidae
24	*C. northumbricoides* Willey, 1925	species inquirenda	*Attheyella*
25	*C. rostratus* Claus, 1863	species inquirenda	not Canthocamptidae
26	*C. stroemii* Baird, 1850	species inquirenda	?
27	*C. subsalus* Brady, 1895	species inquirenda	?
28	*C. tenuicaudis* Herrick, 1884	species inquirenda	*Elaphoidella*
29	*C. virescens* Dana, 1849	species inquirenda	?
30	*C. wiegoldi* Brehm, 1923	species inquirenda	*Attheyella*
31	*C. willeyi* Kiefer, 1925	species inquirenda	*Attheyella*

Kikuchicamptus gen. nov.
urn:lsid:zoobank.org:act:BF57749D-DB49-4790-B64D-8B0069B4CA3A
Table 6

Type species

Kikuchicamptus mirabilis (Sterba, 1968) comb. nov., designated here.

Other species

Kikuchicamptus coreensis (Chang, 2002) comb. nov., *K. incurvisetosus* (Chang & Ishida, 2001) comb. nov., *K. morimotoi* (Miura, 1969) comb. nov., *K. odaeensis* (Chang & Ishida, 2001) comb. nov., *K. prominulus* (Kikuchi in Kikuchi & Ishida, 1994) comb. nov., *K. resupinatus* (Ishida in Kikuchi & Ishida, 1994) comb. nov., *K. semicirculus* (Kikuchi in Kikuchi & Ishida, 1994) comb. nov. and *K. tomikoae* (Ishida in Kikuchi & Ishida, 1994) comb. nov.

Diagnosis

Canthocamptidae. Body semi-cylindrical. Rostrum short. Caudal rami cylindrical; setae IV and V usually long and pinnate. Female antennule 8-segmented; male antennule 10-segmented, haplocer with geniculation between segments 7 and 8. Antenna with allobasis, exopod 2-segmented, with 4 setae. Mandible with well-developed gnathobase; palp 2-segmented. Maxilla with two endites; endopod 1-segmented. P1 with 3-segmented rami; first endopodal segment long, reaching about end of third exopodal segment. P2–P3 with 3-segmented rami; P4 exopod 3-segmented, endopod 2-segmented. Female P5 endopod with 6 setae, seta V approximately equal in length to adjacent setae; exopod long (l/w > 1.7, typically 2.5–3), with 5 setae. Male P2 endopod sexually dimorphic, 'Attheyella-like' (Fig. 11B), second and third segment fused, third segment without outer seta and with notch on distal outer margin. Male P3 endopod typical for Canthocamptidae, with long apophysis with tip; third segment with 2 setae. Male P4 as in female. P5 endopod with 2 setae, inner seta/outer seta length from 1.3 to 1.5; exopod with 6 setae; inner seta minute, pinnate, usually not reaching end of exopod.

Etymology

This genus is named after Dr Yoshiaki Kikuchi, who contributed greatly to the study of Copepoda in Asia.

Remarks

Differences from similar genera, *Canthocamptus* and *Attheyella*, are presented in Table 7. The new genus differs well from *Canthocamptus* in a number of characters: the shape of the male P2 endopod; longer first segment of the P1 endopod; the absence of dimorphism in the structure of the P4 endopod; the setae on the female P5 exopod and endopod of normal length; the small inner seta on the male P5 exopod. It differs from *Attheyella* in the 2-segmented exopod of the antenna, in the presence of six setae on the male P5 exopod and in the absence of setae on the arthrite of the maxillule.

Distribution

The species of the genus are distributed only in East Asia. They are recorded in Far-East Russia, China, Japan and Korea (Chang 2001, 2010).

Table 6. Armature formula of P1–P4 of *Kikuchicamptus* gen. nov.

	Female endopod	Male endopod	Exopod
P1	1; 1; 1,1,1	1; 1; 1,1,1	0; 1; 0,2,2
P2	1; 1; 2,2,1	1; 3,2,1	0; 1; 1,2,3
P3	1; 1; 2,2,1	1; 1 + apophysis; ?,2,0	0; 1; 2,2,3
P4	1; 2,2,1	1; 2,2,1	0; 1; 2,2,3

Table 7. Differences between *Attheyella* Brady, 1880, *Canthocamptus* Westwood, 1836 and *Kikuchicamptus* gen. nov.

	Attheyella	***Canthocamptus***	***Kikuchicamptus* gen. nov.**
A2 exopod	1-segmented	1- or 2-segmented	2-segmented
♀ P2 Enp3 setation	5 setae or less	4–5 setae	5 setae
♂ P2 endopod	‘*Attheyella*-like’ or not dimorphic	‘*Canthocamptus*-like’	‘*Attheyella*-like’
♂ P4 Enp2 outer seta	spine	finger-like process or spine [1]	spine
♀ P5 baseoendopod seta V	normal	typically minute [2]	normal
♂ P5 baseoendopod setation	2–3	2	2
♂ P5 exopod setation	5 [3]	5–6	6
Anal operculum	varied	semilunar, spinulose [4]	semilunar or triangle, naked

[1] Unmodified only in the Baikalian species *C. verestschagini*, *C. latus*, *C. longifurcatus* and *C. bulbifer* (Borutzky 1952).
[2] Only one species, *C. iaponicus*, has a normal seta V (Ishida & Kikuchi 1999).
[3] Only one species, *Attheyella* (*Attheyella*) *tahoensis* Bang, Baguley & Moon, 2015, has 6 setae (Bang *et al.* 2015).
[4] *C. glacialis* has anal operculum without spinules.

Key to the species of Canthocamptus *for males* (female characters indicated by asterisk)

1. Mandibular palp with 3 setae .... ***C. kunzi*** Apostolov, 1969
– Mandibular palp with 5 setae..................... 2

2. P4 Enp2 with normal outer spine 3
– P4 Enp2 with modified finger-like outer spine 6

3. Habitus wide; P1 Enp1 reaching end of Exp2; anal somite with ventral processes 4
– Habitus sub-cylindrical; P1 Enp1 reaching middle of Exp3; anal somite without ventral processes 5

4. P5 exopod with 6 setae; *caudal rami seta V of female conical .... ***C. verestschagini*** (Borutzky, 1931)
– P5 exopod with 5 setae; *caudal rami seta V of female long, normal .... ***C. longifurcatus*** Borutzky, 1947

5. *Caudal rami seta IV of female normal .... ***C. latus*** Borutzky, 1947
– *Caudal rami seta IV of female sickle-like, with bulb .... ***C. bulbifer*** Borutzky, 1947

6. Anal somite with unguiform processes 7
– Anal somite without processes 12

7. P3 Enp3 with 2 normal setae 8
– P3 Enp3 with vestigial or without setae 9

8. Caudal rami setae IV and V with 'helle Stelle' .... ***C. oregonensis*** M.S. Wilson, 1956
– Caudal rami setae IV and V without 'helle Stelle' .... ***C. staphylinus*** (Jurine, 1820)

9. P4 Enp2 with 2 normal inner setae 10
– P4 Enp2 with 2 vestigial or without inner setae 11

10. Caudal rami without inner spinules; *P5 exopod of female without inner spinules ....
.... ***C. microstaphylinus*** s. str. Wolf, 1905
– Caudal rami with inner spinules; *P5 exopod of female with inner spinules ....
.... ***C. microstaphylinus monardi*** Roy, 1927

11. Distal edge of caudal rami with spinules .... ***C. macrosetifer*** Ishida in Ishida & Kikuchi, 1999
– Distal edge of caudal rami without spinules ....***C. takkobuensis*** Ishida in Ishida & Kikuchi, 1999

12. P2 Enp2 with 5 setae 13
– P2 Enp2 with 4 setae 19

13. P3 Enp3 with vestigial seta 14
– P3 Enp3 with 2 normal setae 15

14. Caudal rami with inner spinules; *P3 Enp3 of females with 5 setae ....
.... ***C. kitaurensis*** Kikuchi in Ishida & Kikuchi, 1999
– Caudal rami without inner spinules; *P3 Enp3 of females with 4 setae ....
.... ***C. carinatus*** Shen & Sung, 1973

15. P5 endopod inner seta/outer seta length > 5 .... ***C. sinuus*** Coker, 1934
– P5 endopod inner seta/outer seta length < 5 16

16. Anal operculum naked .... ***C. glacialis*** Lilljeborg, 1902
– Anal operculum spinulose 17

17. Caudal rami short (length to width ratio = 2) ....***C. baikalensis*** Borutzky, 1931
– Caudal rami long (length to width ratio = 2.5) 18

18. Caudal rami seta V with 'helle Stelle' ....***C. iaponicus*** Brehm, 1927
– Caudal rami seta V without 'helle Stelle' ....***C. staphylinoides*** Pearse, 1905

19. Caudal rami very long (length to width ratio > 3.5) .... ***C. robertcokeri*** M.S. Wilson, 1958
– Caudal rami of normal length (length to width ratio < 3) 20

20. Caudal rami with inner spinules; *P5 exopod of females with inner spinules ....
.... ***C. sinuus*** Coker, 1934
– Caudal rami without inner spinules; *P5 exopod of females without inner spinules 21

21. Spinular row of penultimate somite with gap; *caudal rami seta V of female without bulb ....
....***C. assimilis*** Kiefer, 1931
– Penultimate somite with circumsomitic spinular row; *caudal rami seta V of female with bulb ....
.... ***C. waldemarschneideri*** sp. nov.

Discussion

The genus *Canthocamptus* is a typical example of when diagnoses are based on plesiomorphies rather than apomorphies. Such plesiomorphic states of characteristics of the genus *Canthocamptus* are: the armature of the swimming legs, the 2-segmented exopod of the antenna, and the armature of P5. After revision, *Canthocamptus* spp. were assigned to 3 different genera: *Canthocamptus*, *Kikuchicamptus* gen. nov. and *Attheyella*.

Kikuchicamptus gen. nov. contains 9 species, distributed exclusively in East Asia, demonstrating an example of high species diversity in a small area. According to the results of this revision, the genus *Canthocamptus* now has 21 species and 1 subspecies.

The *Canthocamptus* of Lake Baikal are an example of extreme morphological radiation within a single body of water. According to the current data, the number of species is probably underestimated, as there are a number of species that have not yet been described (E.B. Fefilova, pers. com.), which is associated with the complexity of selecting characteristics for describing new species. The position of the so-called '*Baicalocamptus*' is unclear. Initially, Borutzky (1931) separated the species *C. verestschagini* into a separate family, Baicalocamptidae Borutzky, 1931, but Chapuis (1935) proved the closeness between *C. verestschagini* and other species of the genus and included this species in the genus *Canthocamptus*. At the same time, the subgenus *C.* (*Baicalocamptus*) has survived. According to our data, the *C. verestschagini* species group (with *C. longifurcatus*, *C. latus* and *C. bulbifer*) descended from a Palearctic species similar to *C. staphilinus* on the basis of the structure on the male endopod P3, which is strongly thickened and bears reduced setae. However, the species of the *C. verestschagini* species group have an uncharacteristic structure of the outer spine on the male endopod P4, which is not modified into a finger-like process. We associate this with a transition back to a plesiomorphic state, that is, as an apomorphy, not a plesiomorphic state. Therefore, isolation of the subgenus *Canthocamptus* (*Baikalocamptus*) will lead to the paraphyly of *Canthocamptus* (*Canthocamptus*); thus, we believe that it should be reduced to the type subgenus. Isolation of any subgenera is possible only with a thorough revision of all species with the involvement of a larger number of morphological characters and with the use of molecular data.

One European species, *C. kunzi*, also appeared to be close to the Baikal species in the cladogram (Fig. 11A). It demonstrates similar features in the structure of P1 and P5; however, this species is known only from the female, so its position in the *Canthocamptus* system remains questionable. The described holotype is likely the fifth copepodid stage, as indicated by the structure of P5, which resembles the P5 of the fifth copepodids of other species of the genus, and a strongly elongated anal somite (Apostolov 1969). There are no drawings of the genital somite and P6 in the description, which would allow more accurate conclusions. Nevertheless, the fifth copepodids already have a characteristic composition of segments and setae on the oral limbs. In *C. kunzi*, the palp of the mandible is very uncharacteristic, 1-segmented, with 3 setae. This makes any conclusion regarding the validity of this species or its placement in *Canthocamptus* difficult; it is even possible that it could belong to a different genus.

Based on the results of this work, we propose several characters to consider when working with species of the genus *Canthocamptus*:

1. The structure of the maxillule. Within the genus, the following elements can be distinguished: setae on the posterior surface of the arthrite and the number of setae on the endopod fused with the basis.

2. The shape of the bases of the caudal setae and 'helle Stelle'. The presence of small thickenings on the caudal setae may have been overlooked by previous authors, especially if they are directed upward, as in *C. waldemarschneideri* sp. nov. By 'helle Stelle', we mean the cuticular septum at the base of the apical setae of the caudal rami (Lang 1948). The presence or absence of a 'helle Stelle' seems to be rather stable within species and can be considered a diagnostic, albeit unreliable, feature.

Table 8. Pore composition of the abdominal somites of three species of *Canthocamptus* Westwood, 1836. Decoding of the entries in the cells: paired pores + unpaired pores. The lateral group is always paired.

Species		**1 abd. somite**			**2 abd. somite**			**3 abd. somite**		
		dorsal	lateral	ventral	dorsal	lateral	ventral	dorsal	lateral	ventral
C. waldemarschneideri sp. nov.	♀	0+1	1	3+1	0+1	1	0+5	0+1	1	0+1
	♂	0+1	1	2+0	0+1	1	0+0	0+1	1	0+0
C. glacialis	♀1	0+3	3	4+0	0+2	2	0+7	0+2	1	1+0
	♀2	0+2	2	4+0	0+2	1	0+6	0+2	1	1+0
	♀3	0+2	4	3+1	0+4	3	0+7	0+2	1	1+0
	♀4	0+3	3	3+0	0+4	3	0+7	0+2	1	1+0
	♂	0+3	1	2+0	0+2	1	2+0	0+1	1	1+0
C. staphilinus	♀	0+6	12	5+7	0+6	8	0+20	0+2	4	1+0

3. Pores on the abdominal somites. In contrast to other genera of cantocamptids, the genus *Canthocamptus* is characterised by a very unusual pore structure. In general, the marine species of canthocamptids have a typical structure (Novikov & Sharafutdinova 2021); in this case, each somite carries one unpaired dorsal pore, one pair of lateral pores and one pair of ventral pores. However, *Canthocamptus* spp. usually have a multiple number of pores. We had only three species at our disposal, but they all had completely different combinations of the number of paired and unpaired pores (Table 8). Although some variability has been found, it is possible that this could also be used for species diagnoses in the future.

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References

Apostolov A. 1969. Copepoda Harpacticoida von Bulgarien. *Crustaceana.*16 (3): 311–320. https://doi.org/10.1163/156854069X00349

Bang H.W., Baguley J.G. & Moon H. 2015. First record of harpacticoid copepods from Lake Tahoe, United States: two new species of *Attheyella* (Harpacticoida, Canthocamptidae). *ZooKeys* 479: 1–24. https://doi.org/10.3897/zookeys.479.8673

Borutzky E.V. 1931. Materialen zur Harpacticidenfauna des Baikalsees II. *Zoologischer Anzeiger* 93: 263–273.

Borutzky E.V. 1947. Materials on the fauna of Copepoda, Harpacticoida of Lake Baikal. Genus *Canthocamptus* Westwood. *Doklady Akademii Nauk SSSR* 58 (8): 1825–1828.

Borutzky E.V. 1952. *Crustacea: Freshwater Harpacticoida. Fauna SSSR 3 (4)*. Izdaniya Akademia Nauk SSSR, Moscow-Leningrad.

Boxshall G.A. & Huys R. 1992. A homage to homology: patterns of copepod evolution. *Acta Zoologica* 73 (5): 327–334. https://doi.org/10.1111/j.1463-6395.1992.tb01102.x

Chang C.Y. 1998. Redescription of *Canthocamptus morimotoi* Miura, a stygobiontic harpacticoid species from Korea, with a brief review on *C. mirabilis* group. *Korean Journal of Biological Sciences* 2 (4): 427–434. https://doi.org/10.1080/12265071.1998.9647441

Chang C.Y. 2001. Redescription of *Canthocamptus mirabilis* Štěrba (Copepoda, Harpacticoida), based on the topotypic material from China. *Animal Systematics, Evolution and Diversity* 17 (1): 1–11.

Chang C.Y. 2002. Taxonomy on *Canthocamptus semicirculus* and *C. coreensis* n. sp. (Harpacticoida, Canthocamptidae), with a key to the *C. mirabilis* species group from South Korea. *Animal Systematics, Evolution and Diversity* 18 (2): 233–244.

Chang C.Y. 2010. *Continental Harpacticoida. Invertebrate Fauna of Korea 21 (4)*. National Institute of Biological Resources, Ministry of Environment, Seoul.

Chang C.Y. & Ishida Y. 2001. Two new species of *Canthocamptus mirabilis* group (Copepoda, Harpacticoida, Canthocamptidae) from South Korea. *Proceedings of the Biological Society of Washington* 114 (3): 667–679.

Chappuis P.A. 1935. Notes sur les Copépodes. 8. Sur la systematique de Canthocamptinae. 9. Sur le Canthocamptinae de Canada. 10. *Baikalocamptus Verestschagini* Borutzky = *Canthocamptus verestschagini* (Bor.). *Buletinul Societăţii de ştiinţe din Cluj* 7: 279–285.

Coker R.E. 1934. Contribution to knowledge of North American freshwater harpacticoid copepod Crustacea. *Journal of the Elisha Mitchell Scientific Society* 50 (1/2): 75–141.

Coker R.E. & Morgan J. 1940. A new harpacticoid copepod from North Carolina. *Journal of the Washington Academy of Sciences* 30 (9): 395–398.

Ferrari F.D. & Ivanenko V.N. 2008. The identity of protopodal segments and the ramus of maxilla 2 of copepods (Copepoda). *Crustaceana* 81: 823–835. https://doi.org/10.1163/156854008784771702

Hamond R. 1987. Non-marine harpacticoid copepods of Australia. I. Canthocamptidae of the genus *Canthocamptus* Westwood s. lat. and *Fibulacamptus*, gen. nov., and including the description of a related new species of *Canthocamptus* from New Caledonia. *Invertebrate Systematics* 1 (8): 1023–1247. https://doi.org/10.1071/IT9871023

Huys R. & Boxshall G.A. 1991. *Copepod Evolution*. The Ray Society (Publications), London.

Ishida T. & Kikuchi Y. 1999. *Canthocamptus iaponicus* (Crustacea: Copepoda: Harpacticoida), and three new species of the genus from Japan. *Species Diversity* 4 (2): 339–352. https://doi.org/10.12782/specdiv.4.339

Ito T. & Takashio T. 1980. *Canthocamptus mirabilis* Štěrba (Copepoda, Harpacticoida) from Hokkaido, northern Japan. *Annotationes Zoologicae Japonenses* 53: 210–219.

Kiefer F. 1931. Kurze Diagnosen neuer Süsswasser-Copepoden. *Zoologischer Anzeiger* 94 (5/8): 219–224.

Kikuchi Y. & Ishida T. 1994. A species group of genus *Canthocamptus* (Copepoda: Harpacticoida) in Japan, including descriptions of four new species. *Bulletin of the Biogeographical Society of Japan* 49: 37–46.

Lang K. 1934. Marine Harpacticiden von der Campbell-Insel und einigen anderen südlichen Inseln. *Acta Universitatis Lundensis, New Series* 2 (30):1–56.

Lang K. 1948. *Monographie der Harpacticiden*. Otto Koeltz Science Publishers, Königstein, Germany.

Lilljeborg W. 1902. Tres species novae generis Canthocampti e Novaja Semlja et Sibiria Boreali, sive Trenne nya Arter af Skäktet *Canthocamptus* från Novaja Semlja och Norra Sibirien. *Bihang till Kongliga Svenska Vetenskaps-akademiens Handlingar* 28 (4): 9.

Mielke W. 1984. Some remarks on the mandible of the Harpacticoida (Copepoda). *Crustaceana* 46 (3): 257–260. https://doi.org/10.1163/156854084X00162

Miura Y. 1969. A new harpacticoid copepod from a sandy beach of Lake Biwa. *Annotationes Zoologicae Japonenses* 42 (1): 40–44.

Moura G. & Pottek M. 1998. *Selenopsyllus*, a new genus of Cylindropsyllinae (Copepoda, Harpacticoida) from Atlantic and Antarctic deep waters. *Senckenbergiana Maritima* 28 (4): 185–209. https://doi.org/10.1007/BF03043149

Novikov A. & Sharafutdinova D. 2021. Two new Canthocamptidae (Copepoda, Harpacticoida) from sponges of the Kara and Laptev Seas. *Zootaxa* 4948 (3): 336–362. https://doi.org/10.11646/zootaxa.4948.3.2

Novikov A.A., Abramova E.N. & Sabirov R.M. 2021. Fauna of freshwater Harpacticoida (Copepoda) in the Lena River Delta. *Zoologichesky Zhurnal* 100 (3): 264–274. https://doi.org/10.31857/S0044513421010049 [In Russian.]

Okuneva G.L. 1983. New species of Copepoda (Harpacticoida) in the Baikal Lake fauna. *Zoologichesky Zhurnal* 62 (9): 1343–1352.

Shen C. & Sung T. 1973. The freshwater copepods from three provinces in northeastern China. *Acta Zoologica Sinica* 19: 35–42.

Spandl H. 1924. Entomostraken von Borneo. *Annalen des naturhistorischen Museums in Wien* 38: 89–95.

Strimmer K. & von Haeseler A. 1996. Quartet puzzling: a quartet maximum-likelihood method for reconstructing tree topologies. *Molecular Biology and Evolution* 13 (7): 964–969. https://doi.org/10.1093/oxfordjournals.molbev.a025664

Walter T.C. & Boxshall G. 2021. World of Copepods database. *Canthocamptus* Westwood, 1836. Available from https://www.marinespecies.org/copepoda/index.php [accessed 5 May 2022].

Wells J.B.J. 2007. An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa* 1568 (1): 1–872. https://doi.org/10.11646/zootaxa.1568.1.1

Westwood J.O. 1836. *Canthocamptus*. *In*: Partington C.F. (ed.) The *British Cyclopaedia of Natural History 2*: 227. Orr & Smith, London.

Wilson M.S. 1956. North American harpacticoid copepods: 1. Comments on the known fresh-water species of the Canthocamptidae. 2. *Canthocamptus oregonensis*, n. sp. from Oregon and California. *Transactions of the American Microscopical Societ*y 75 (3): 290–307. https://doi.org/10.2307/3223958

Wilson M.S. 1958. North American harpacticoid copepods 4. Diagnosis of new species of freshwater Canthocamptidae and Cletodidae (genus *Huntemannia*). *Proceedings of the Biological Society of Washington* 71 (1): 43–48.

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Supplementary file

Supp. file 1. Data matrix used for the cladistic analysis.
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