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Новый вид *Bryocamptus* Chappuis, 1929 (Copepoda: Harpacticoida: Canthocamptidae) из гидротермального сипа озера Байкал

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KEY WORDS: Baikalian endemic, biodiversity, *Bryocamptus* (*Rheocamptus*), caudal rami, deep-water fauna, sexual arms race.

КЛЮЧЕВЫЕ СЛОВА: байкальские эндемики, биоразнообразие, *Bryocamptus* (*Rheocamptus*), каудальные ветви, глубоководная фауна, половая гонка вооружений.

ABSTRACT. *Bryocamptus* (*Rheocamptus*) *sitnikovae* sp.n. was described from a hydrothermal seep at a depth of 409 metres as a result of studying samples of deep-water Harpacticoida from Lake Baikal. The new species differs from other representatives of the subgenus in the modified outer apical caudal seta with a circle dorso-ventral extension at the base in females, as well as in the absence of lateral spinules of the anal somite in females and males. A high variability in the spinular ornamentation of the caudal rami and the anal operculum of the new species is described. Descriptions of other endemic Baikalian *Bryocamptus* (*Rheocamptus*) are considered; the characters most suitable for species identification are given.

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РЕЗЮМЕ. *Bryocamptus* (*Rheocamptus*) *sitnikovae* sp.n. описан из гидротермального сипа на глубине 409 метров в результате изучения проб глубоководных Harpacticoida озера Байкал. Новый вид отличается от других представителей подрода модифицированной внешней апикальной каудальной щетинкой с дисковидным дорсо-вентральным расширением у самок, а также отсутствием латеральных шипиков на анальном сомите самок и самцов. Описана высокая изменчивость вооружения шипиками каудальных ветвей и анального оперкулюма. Рассмотрены описания других эндемичных байкальских *Bryocamptus* (*Rheocamptus*); приведены признаки, наиболее подходящие для идентификации видов.

Introduction

The fauna of Lake Baikal is characterised by extremely high diversity. According to the number of endemic forms among crustaceans, amphipods occupy the first place, and ostracods the second. In third place are Harpacticoida with 62 endemic species. At the same time, until recently, the deep-water fauna of Harpacticoida was rarely studied. Fragmentary data are mentioned in several works [Boxshall, Evstigneeva, 1994; Evstigneeva, Okuneva, 2001], but comprehensive studies have not been conducted. A recent work provided a summary that mentions 19 species of Canthocamptidae from depths of 270 to 1632 [Fefilova *et al*., 2023]. Only 8 species of them have been identified. At the same time, 8 unidentified species belonged to the genus *Bryocamptus* Chappuis, 1929.

In Lake Baikal, *Bryocamptus* is one of the most abundant genera of Harpacticoida both in terms of number of species and abundance. There are endemic representatives in three subgenera: *B*. (*Bryocamptus*) — 13 species, *B*. (*Rheocamptus*) Borutzky, 1952 — 10 species including the new one, and *B*. (*Echinocamptus*) Chappuis, 1929 — 4 species. Representatives of the last two subgenera are generally similar to each other and do not have a strong morphological radiation, in contrast to *B*. (*B*.), whose

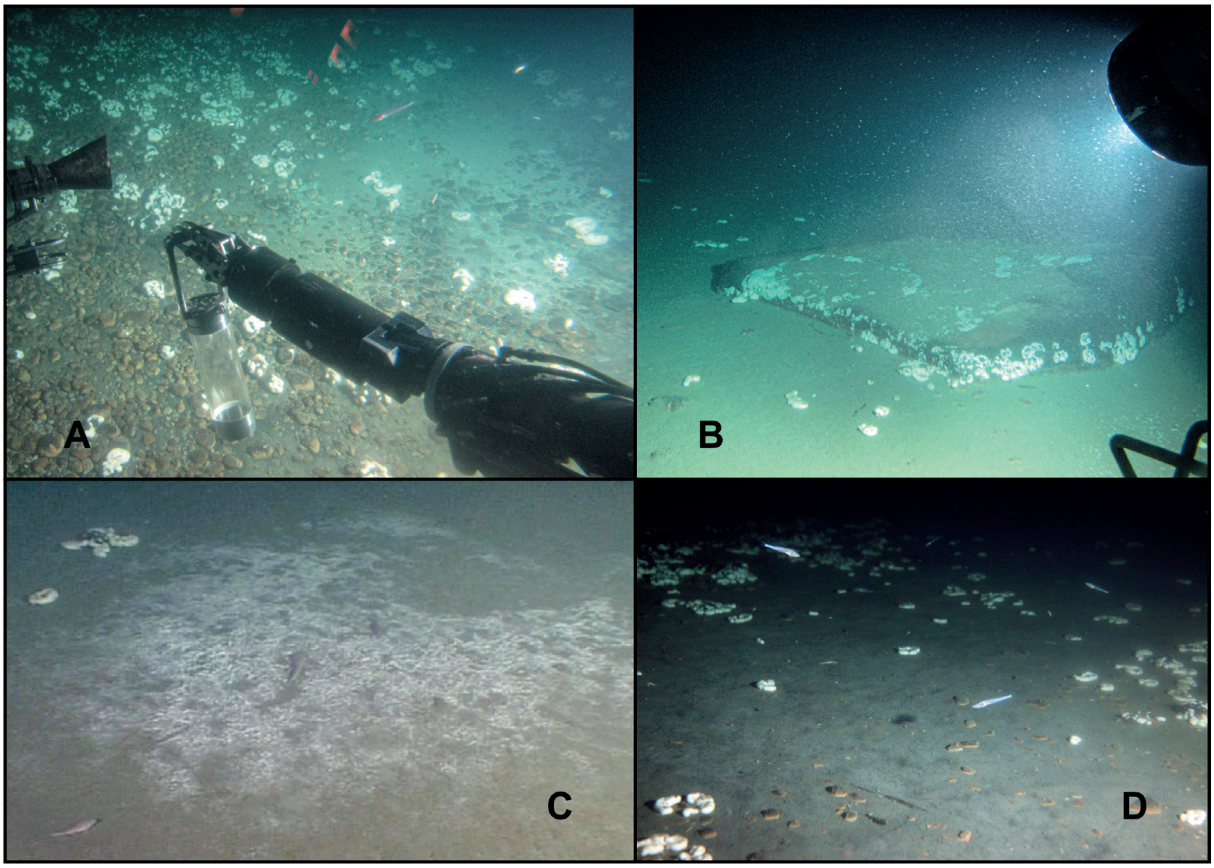

Fig. 1. Photographs of the Frolikha hydrothermal seep bottom taken by underwater submersibles 'Mir', habitats of *Bryocamptus sitnikovae* sp.n.: A — gravel, boulders and exposed mudstone, benthic core – equipment of the 'Mir'; B — flagstone and sponges; C — bacterial mat and sponges; D — boulders and sponges.

Рис. 1. Фотографии дна гидротермального сипа Фролиха сделанные подводным аппаратом «Мир», местообитание *Bryocamptus sitnikovae* sp.n.: А — гравий, валуны и обнаженные аргиллиты, трубчатый пробоотборник — оборудование «Мира»; Б — плитняк и губки; В — бактериальный мат и губки; D — валуны и губки.

morphological diversity is much higher [Borutzky, 1952; Borutzky, Okuneva, 1971].

A large number of species, their high variability and the low quality of the original descriptions pose a challenge to modern researchers of the Baikalian fauna, where even the seemingly trivial task of identifying species can turn out to be difficult. Therefore, the purpose of our work was a detailed description of the first species of Baikalian true deep-water Harpacticoida from the hydrothermal seep and a taxonomic analysis of endemic *B*. (*Rheocamptus*).

Materials and methods

Samples of bottom sediments (near Frolikha Bay, Northern Baikal) at the depths 409 m were collected by means of a deepwater manned submersibles Mir-1 equipped with a benthic corer. This habitat displays a diverse range of bottom substrates, including smooth, rounded pebbles and boulders encrusted with sponges, as well as soft, oxic aleurite silts that may be accompanied by sand or bacterial mats (Fig. 1).

Samples were fixed in 4% formalin. 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.

Nomenclature and descriptive terminology follows Huys & Boxshall [1991], terminology in genital fields follows Moura & Pottek [1998], terminology in mandibular structure follows Mielke [1984], terminology and homology of maxillary structures follow Ferrari & Ivanenko [2008]. The armature formulae of swimming legs are given according to Lang [Lang, 1934]. The numbering of setae of the exopod and endopodal lobe of P5 follows from inner to outer (I–VI).

Abbreviations used in the text: A1 — antennule, A2 — antenna, ae — aesthetasc, acr — acrothek, ap — apophysis, P1–P6 — legs 1–6, Exp1–Exp3 — first–third segments of exopod.

Material was deposited in Zoological Museum of Kazan Federal University (KFU) and in Zoological Museum of the Institute of Biology, Komi Scientific Centre, Ural Branch of the Russian Academy of Sciences (IBKSC).

Results

Subclass Copepoda H. Milne Edwards, 1840
Order Harpacticoida Sars, 1903
Family Canthocamptidae Sars, 1906
Genus *Bryocamptus* Chappuis, 1929
Subgenus *Rheocamptus* Borutzky, 1952

Bryocamptus (*Rheocamptus*) *sitnikovae* **sp.n.**
Figs 2–10.

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Bryocamptus (*Rheocamptus*) sp. 6 — Fefilova *et al*., 2022: 10–11, Fig. 4e–g.

ETYMOLOGY. The species is named after Tatyana Ya. Sitnikova, a collector of this material and a well-known specialist in the deep-water fauna of Lake Baikal.

MATERIAL. **Holotype** ♀ dissected on two slides, RUSSIA, Baikal Lake, Frolikha hydrothermal seep; 55.517° N, 109.767° E; depth 409 m; 23 July 2010; T.Ya. Sitnikova leg; KFU ZM&G SC-68/1, SC-68/2. **Allotype** ♂ dissected on one slide; collection data as for holotype; KFU ZM&G SC-69. **Paratypes:** 1 ♀ dissected on two slides; collection data as for holotype; KFU ZM&G SC-70/1, SC-70/2; 28 ♀ and 1 ♂ undissected, preserved in 4% formalin; collection data as for holotype; KFU ZM&G SC-N/V-1; 3 ♀ and 1 ♂ dissected on four slides; RUSSIA, Baikal Lake, Frolikha hydrothermal seep; 55.517° N, 109.767° E; depth 432 m; 24 July 2010; T.Ya. Sitnikova leg; IBKSC HRP-29, HRP-30, HRP-31, HRP-32.

DESCRIPTION. **Female.** Body subcylindrical (Fig. 2A). Total body length of holotype from anterior margin of rostrum to posterior margin of caudal rami: 748 μm. Cephalothorax (Fig. 2B–C), wider than remaining somites, length with rostrum 182 μm, largest width 153 μm. Naupliar eye not discovered. Rostrum (Fig. 2D–E) small, fused with cephalothorax, with rounded end, with one pair of sensillae and ventral pore. Posterior margin of cephalothorax and all pedigerous somites smooth.

Cephalothorax (Fig. 2B–C) with dumbbell-shaped dorsal window; with 34 pairs of sensillae and 15 pairs of pores, two of which located on lateral margin of cephalothorax. Second and third pedigerous somites with lateral windows, dorsal unpaired pore, lateral pair of pores and eight pairs of sensillae. Fourth pedigerous somite with dorsal unpaired pore, lateral pair of pores and seven pairs of sensillae. Fifth pedigerous somite with lateral pair of pores and four pairs of sensillae.

Abdomen (Fig. 3) consisting of fused genital-double somite, two free abdominal somites and anal somite with caudal rami. All somites except anal somite on posterior margin serrated, on surface with rows of small spinules. Genital-double somite consists of last thoracic somite and first abdominal somite; longer than wide; anterior part with three pairs of sensillae, dorsal unpaired pore, lateral paired pores, ventro-lateral rows of spinules; posterior part with four pairs of sensillae, dorsal unpaired pore, pairs of ventral and lateral pores and lateral rows of spinules.

P6 (Fig. 3A) fused with somite with one pinnate and one naked setae. Genital field (Fig. 3A) long, laterally with sieves; copulatory pore displaced to posterior part of somite, copulatory duct chitinised, extending proximally to pair of labyrinthic rounded ducts and one chitinised unpaired duct. Egg sac absent in holotype. Paratypes with 10 to 13 eggs in their egg sacs (n = 4: 10, 11, 13, 13).

Second abdominal somite (Fig. 3A–C) with three pairs of sensillae, unpaired dorsal pore, pairs of lateral and ventral pores; on posterior margin with lateral row of large spinules. Third abdominal somite (Fig. 3A–C) with pair of lateral pores, on posterior margin with lateral row of large spinules and ventral row of thin spinules. Anal somite (Fig. 3A–C) with one pair of sensillae, ventral and lateral pairs of pores. Anal operculum (Fig. 3C) semilunar, with five small spinules.

Caudal rami (Fig. 3). Length/width ratio 1.3, with dorsal carina; with one large and one-two small ventral pores; with two large spinules on ventral side at base of seta V, two large spinules on inner side and rows spinules at base of setae II and III. Seta I small, located near seta II. Setae II and III normal, located on outer side of ramus. Apical seta IV (Fig. 3) modified, with thick proximal part and thin distal part; proximal part with fracture plane and with large hyaline dorsal and ventral protrusions forming circle. Apical seta V (Fig. 3D) long, bipinnate, with fracture plane. Base of seta VI located slightly under base of seta V. Seta VII triarticulated, located near dorsal crest (Fig. 3C).

Antennule (Fig. 4A) eight-segmented. Segment 1 short, with one pinnate seta and two rows of spinules. Other segments with bare setae. Segment 4 with fused basally seta and aesthetasc. 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 rows of spinules. Allobasis with spinulose basal seta and bare endopodal seta; with spinular rows at base of endopodal setae. Free endopodal segment with two lateral rows of large spinules, 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 to small seta. Exopod 2-segmented; first segment with one pinnate seta and row of spinules; second segment with three pinnate setae.

Labrum (Fig. 4C). On outer side with row of thin setules and large proximal pore. Distal margin with lateral rows of robust spinules, rows of fused spinules into comb and three rows of small spinules. On inner side medially with three unpaired pores, two pared pores, with lateral spinular row, groups of thin setules and spinules.

Mandible (Fig. 4D). Coxa with proximal rows of spinules. Gnathobase with pars incisiva, lacinia mobilis, complex dental battery and spinulose seta; pars incisiva two-pointed; lacinia mobilis three-pointed. Dental battery (Fig. 4E) consisting of five fused blocks of small short teeth, innermost one fused at base with seta. Pars molaris sharply-edged. Palp two-segmented; first segment with row of long spinules; second segment with one medial and four apical bare setae.

Paragnaths (Fig. 4F) with paired lateral lobes and unpaired posterior rounded lobe. Lateral lobes extended in distal part; proximally with lateral pore (probably); with three groups of long spinules on outer side; distally with round group of spinules; with three-four rows of spinules on inner side; anterior side with three medial rows of strong spinules and proximal row of spinules.

Maxillule (Fig. 5A). Praecoxa with two rows of slender spinules on outer edge and one row of spinules on posterior side. Praecoxal arthrite medially with two rows of spinules and one bare seta; distally with four strong spines with pectinate end, three biarticulate spines, one proximal thick pinnate seta and one thin seta with long spinules. Coxa with row of spinules, coxal endite with one geniculate and one pinnate setae. Basis with two subdistal setae and three distal setae, one of which geniculate. Endopod and exopod incorporated into basis; exopod represented by long pinnate and short bare setae; endopod represented by three bare setae.

Maxilla (Fig. 5B). Basis with several rows of spinules on outer and inner edge as figured, with two endites. Proximal endite with spinular row, one spinulose spine and two pinnate setae, distal endite with one strong pinnate spine and two thin pinnate setae. Proximal endopodal segment with two setae, outer tube pore and massive distal claw. Distal endopodal segment with three naked setae.

Maxilliped (Fig. 5C) subchelate. Syncoxa elongated with several rows of spinules as figured, distally with one pinnate seta. Basis with two longitudinal rows of large spinules on anterior and posterior sides and three transversal outer rows of small spinules. Endopod on posterior side with one seta, on anterior

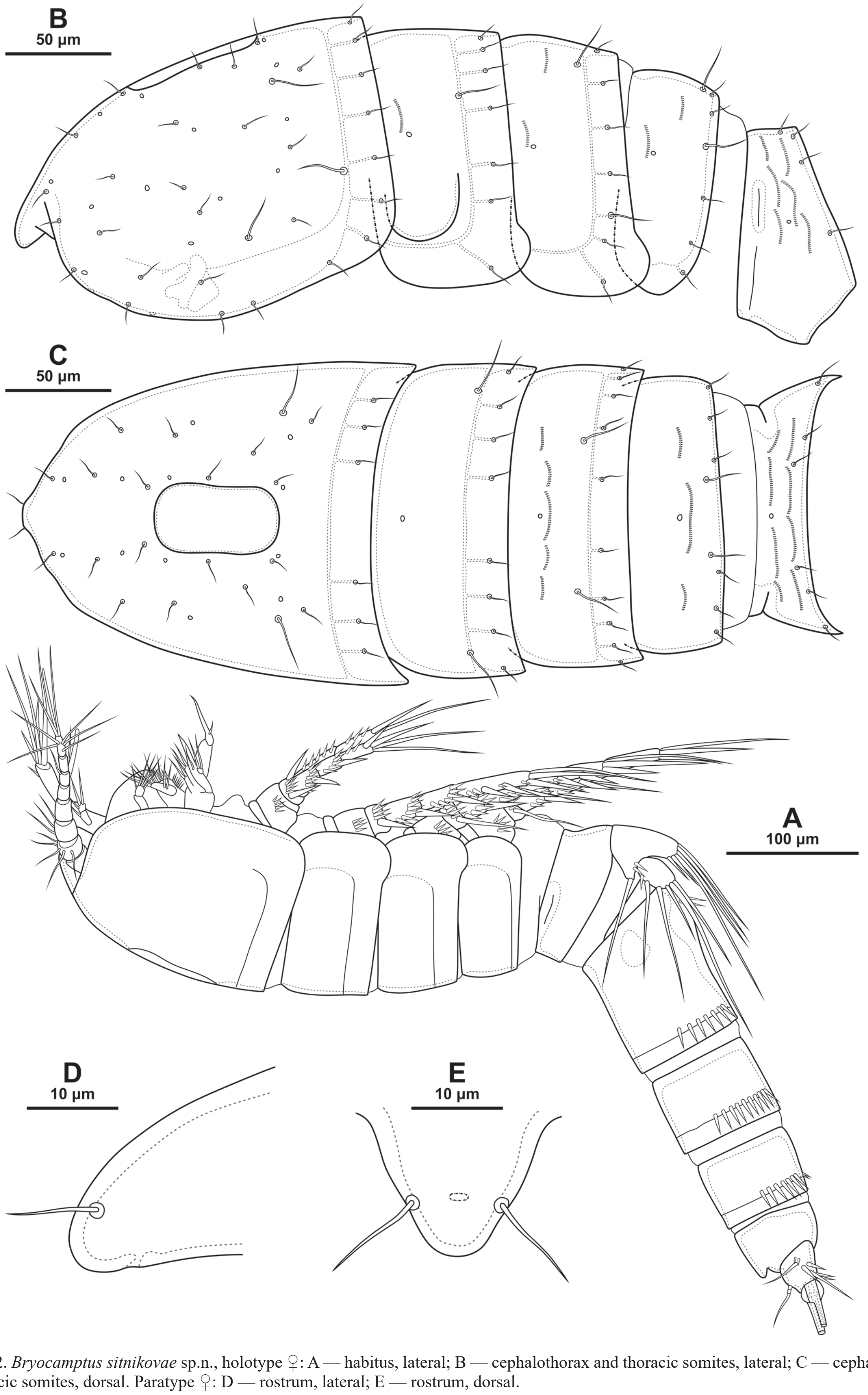

Fig. 2. *Bryocamptus sitnikovae* sp.n., holotype ♀: A — habitus, lateral; B — cephalothorax and thoracic somites, lateral; C — cephalothorax and thoracic somites, dorsal. Paratype ♀: D — rostrum, lateral; E — rostrum, dorsal.

Рис. 2. *Bryocamptus sitnikovae* sp.n., голотип ♀: A — габитус, латерально; B — цефалоторакс и торакальные сомиты, латерально; C — цефалоторакс и торакальные сомиты, дорсально. Паратип ♀. D — рострум, латерально. E — рострум, дорсально.

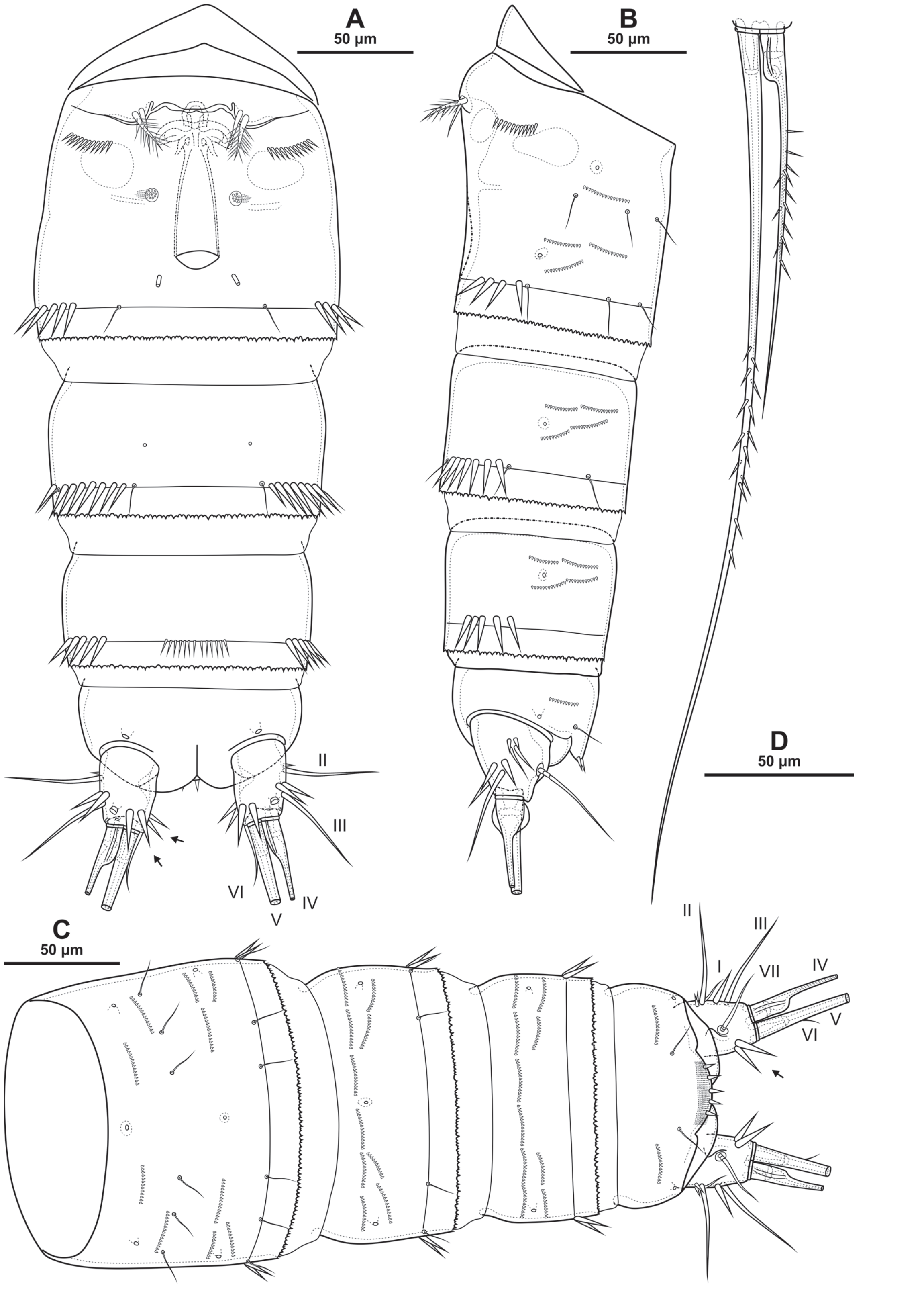

Fig. 3. *Bryocamptus sitnikovae* sp.n., holotype ♀: A — abdomen, ventral; B — abdomen, lateral; C — abdomen, dorsal; D — caudal setae, dorsal.

Рис. 3. *Bryocamptus sitnikovae* sp.n., голотип ♀: A — абдомен, вентрально; B — абдомен, латерально; C — абдомен, дорсально; D — каудальные щетинки, дорсально.

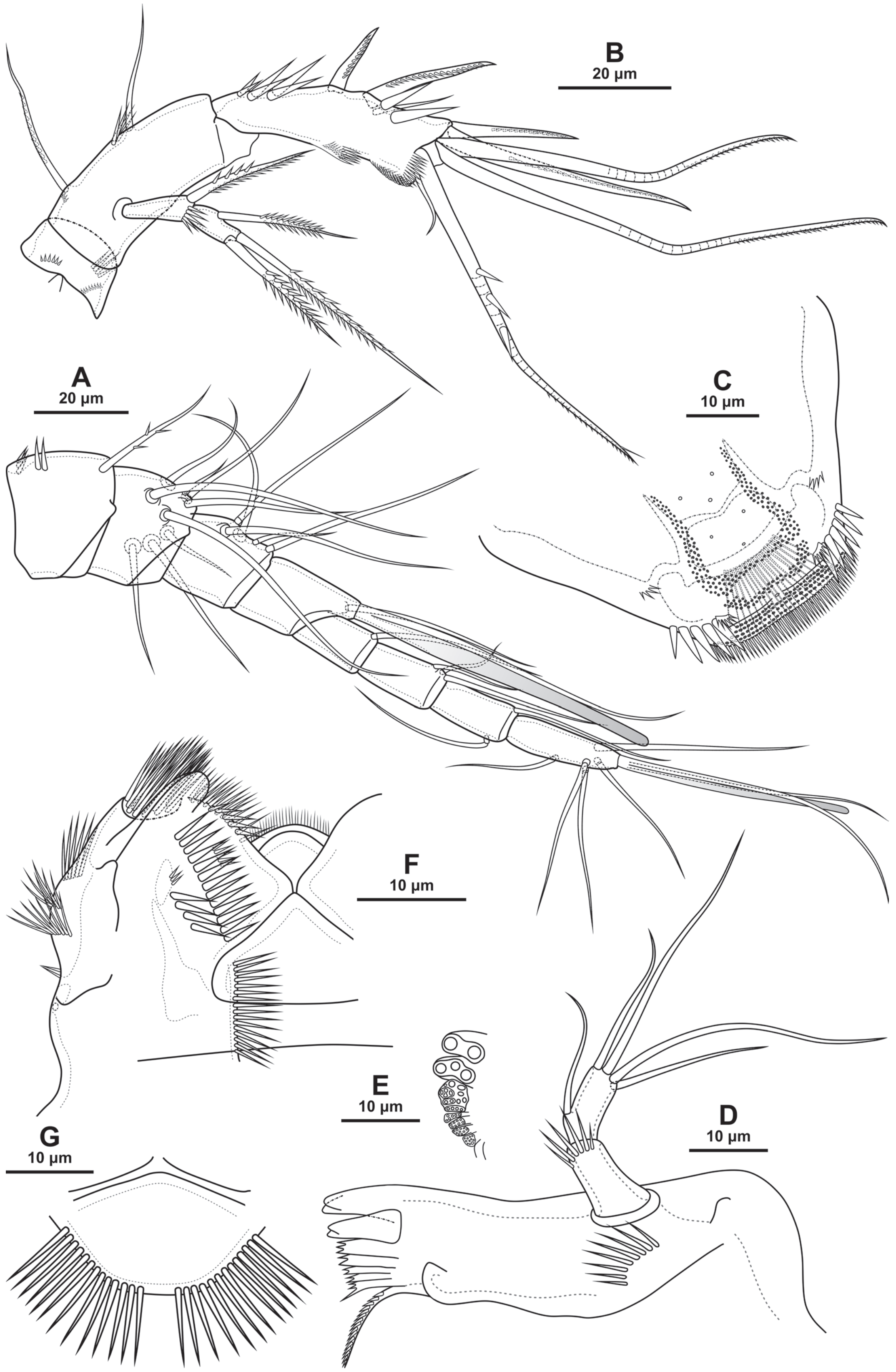

Fig. 4. *Bryocamptus sitnikovae* sp.n., holotype ♀: A — antennule; B — antenna; D — mandible; E — scheme of teeth of mandibular gnathobase. Paratype ♀: C — labrum, posterior side; F — paragnaths, anterior; G — cuticular process between maxillipeds and P1.

Рис. 4. *Bryocamptus sitnikovae* sp.n., голотип ♀: A — антеннула; B — антенна; D — мандибула; E — схема зубов гнатобазы мандибулы. Паратип ♀: C — лабрум, задняя сторона; F — парагнаты, спереди; G — кутикулярный вырост между максиллипедами и P1.

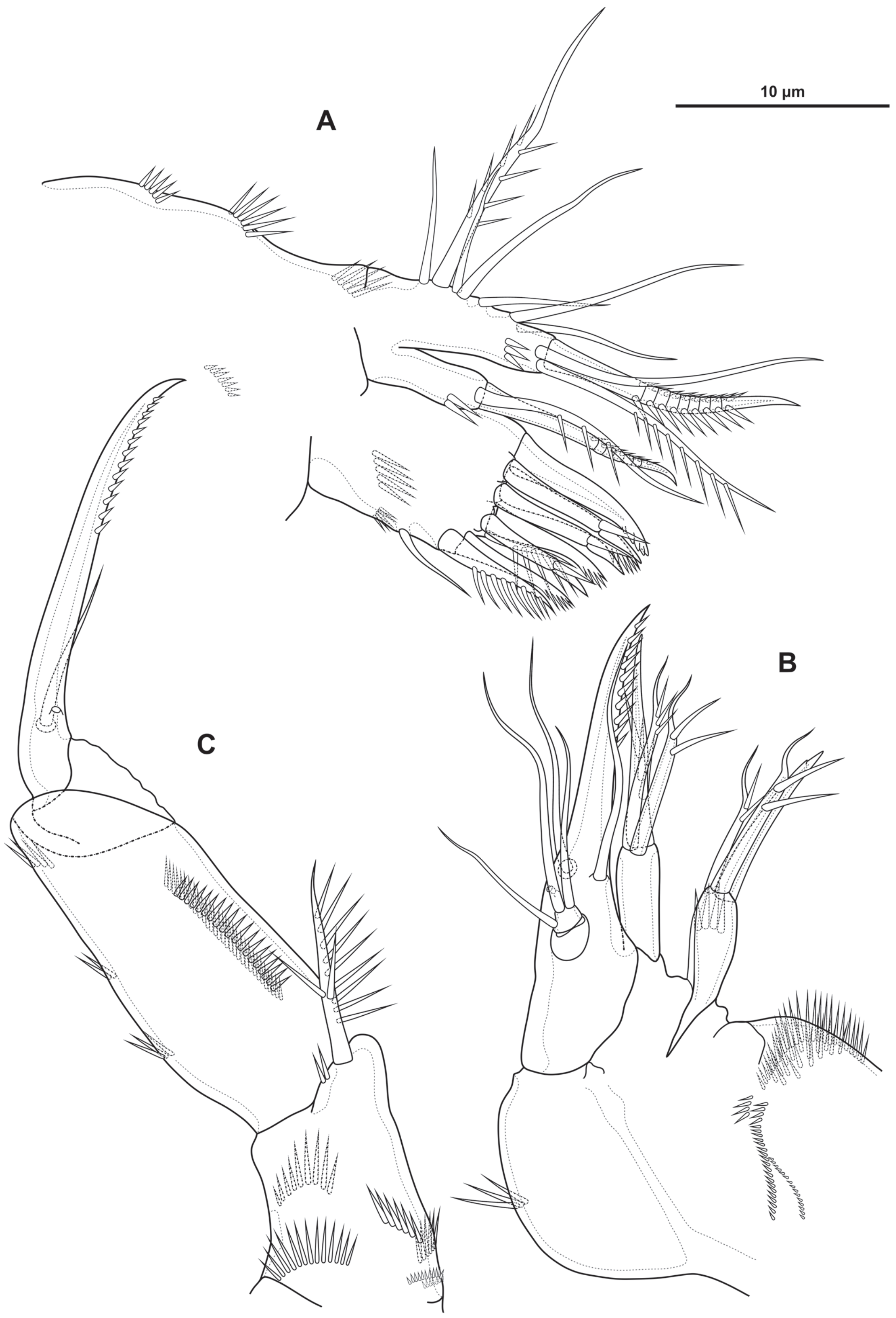

Fig. 5. *Bryocamptus sitnikovae* sp.n., holotype ♀: A — maxillule; B — maxilla; C — maxilliped.
Рис. 5. *Bryocamptus sitnikovae* sp.n., голотип ♀: A — максиллула; B — максилла; C — максиллипеда.

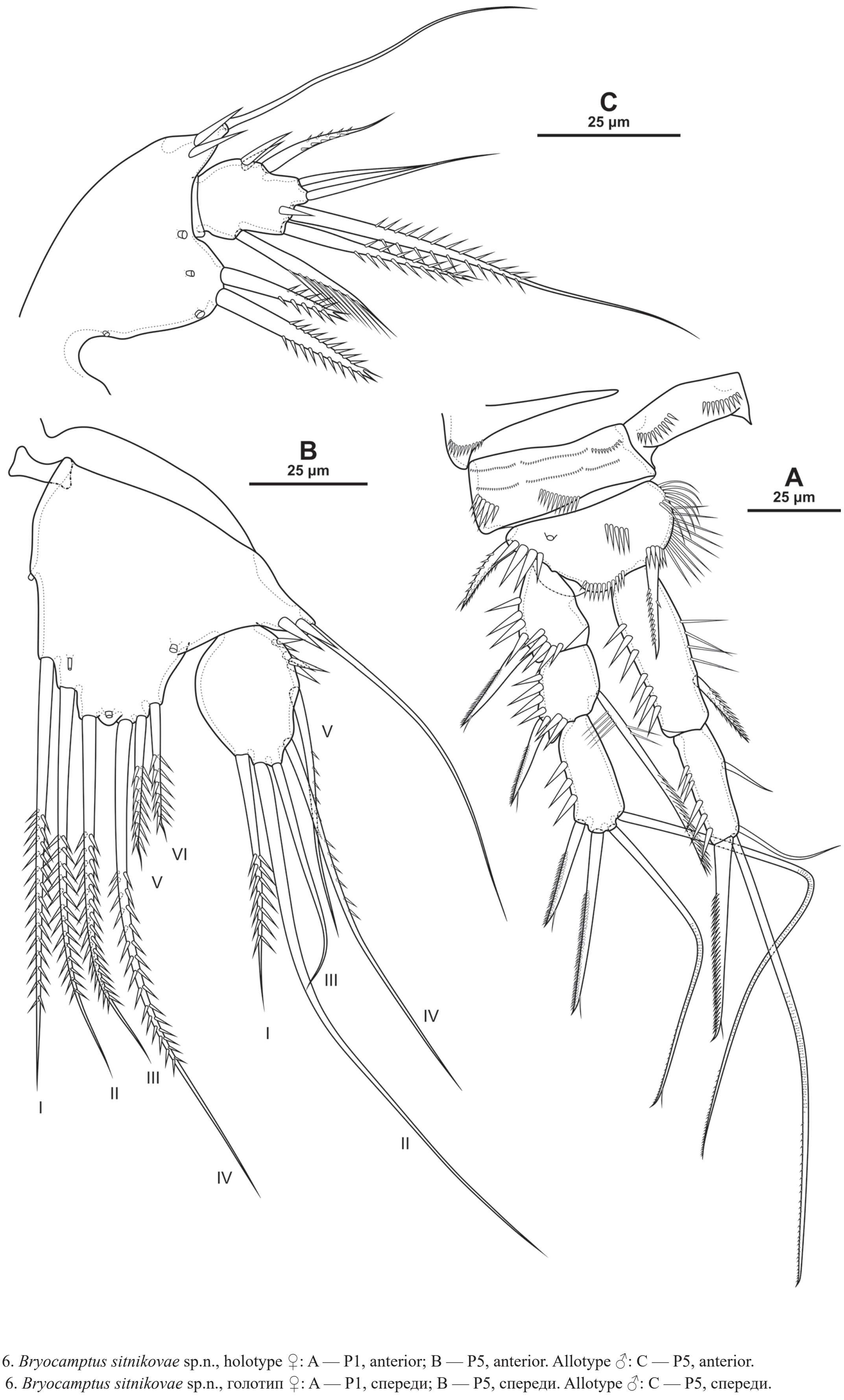

Fig. 6. *Bryocamptus sitnikovae* sp.n., holotype ♀: A — P1, anterior; B — P5, anterior. Allotype ♂: C — P5, anterior.
Рис. 6. *Bryocamptus sitnikovae* sp.n., голотип ♀: A — P1, спереди; B — P5, спереди. Allotype ♂: C — P5, спереди.

Fig. 7. *Bryocamptus sitnikovae* sp.n., holotype ♀: A — P2, anterior; B — P3, anterior; C — P4, anterior.
Рис 7. *Bryocamptus sitnikovae* sp.n., голотип ♀: A — P2, спереди; B — P3, спереди; C — P4, спереди.

Table 1. P1–P4 armature of *Bryocamptus sitnikovae* sp.n.
Таблица 1. Вооружение P1–P4 *Bryocamptus sitnikovae* sp.n.

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

side with small protuberance, probably tube pore. Endopodal claw elongated, with row of small spinules.

Cuticular process between maxillipeds and P1 (Fig. 4G) larger than tall, with long spinules, 10–13 long setules on each side.

P1–P4 well developed, setae/spine armature formula listed in Table 1.

P1 (Fig. 6A). Praecoxa with outer spinular row. Coxa rectangular, with eight spinular rows, five of which consisting of little spinules. Intercoxal sclerite wide, with one paired spinular rows. Basis with proximal pore, medial row of small spinules, rows of spinules at base of endopod and exopod, row of spinules at base of inner seta, two inner rows of setules; with inner and outer strong spinulose spines. All endopodal and exopodal segments with longitudinal row of spinules on outer margin. Exopod three-segmented; first segment with one outer spinulose spine; second segment with inner pectinate seta and outer spinulose spine; third exopodal segment with two outer spinulose spines and two apical slender geniculate setae. Endopod two-segmented, longer than exopod; first endopodal segment reaching third of distal exopodal segment, with inner pectinate seta and inner spinular row; second endopodal segments proximally with one inner bare seta; distally with outer spinulose spine, apical long geniculate seta and inner bare seta.

P2 (Fig. 7A). Praecoxa with row of small spinules. Coxa with one lateral row of large spinules and five rows of spinules on anterior side. Intercoxal sclerite with paired spinular rows. Basis with proximal pore, rows of spinules at base of endopod and exopod and row of inner spinules; with outer spine. All endopodal and exopodal segments with longitudinal row of spinules on outer margin. Exopod three-segmented; first exopodal segment with outer spinulose spine, with apical frill; second segment with outer spinulose spine, inner pectinate seta, inner setules and apical frill; third segment with three outer spinulose spines, two apical setae and one inner pectinate seta. Endopod two-segmented; first segment with inner seta; second segment on inner side with prominent border between ancestral segments, with outer spinulose spine, two apical pinnate setae and two inner pectinate setae.

P3 (Fig. 7B). Praecoxa, coxa and basis similar to that in P2, but basis with outer seta instead of spine. Intercoxal sclerite without spinules. Exopod three-segmented; all segments with longitudinal row of spinules on outer margin; first exopodal segment with outer spinulose spine, apically with frill; second segment with outer spinulose spine, inner pectinate seta, inner setules and apical frill; third segment with three outer spinulose spines, two apical setae and two inner pectinate setae. Endopod two-segmented; first segment with inner seta; second segment on medial and posterior side with prominent border between ancestral segments, with outer spinules, outer spinulose spine, two apical pinnate setae and three inner pectinate setae.

P4 (Fig. 7C). Praecoxa with spinular row. Coxa with one lateral row of large spinules and four rows of spinules on anterior side. Intercoxal sclerite without spinules. Basis with outer seta, proximal pore, rows of spinules at base of endopod and exopod. Exopod 3-segmented; first exopodal segment with outer naked spine, outer spinules, apically with frill; second segment with outer naked spine, outer spinules, inner pectinate seta, inner slender spinules and apical frill; third segment with three outer spinulose spines, two apical setae and two inner pectinate setae. Endopod two-segmented; first segment with inner seta; second segment with outer spinules, outer spinulose spine, two apical pinnate setae and two inner pectinate setae.

P5 (Fig. 6B) with separate right and left baseoendopods. Baseoendopod reaching about half of exopodal segment; with four pores, two spinules at base of outer seta; outer seta of basis slender. Endopodal lobe with four long bipinnate setae and two short bipinnate setae V and VI on outer side; with small process between setae III and IV. Exopod with outer spinules; with inner pinnate seta, two apical bare setae, and two unipinnate outer setae.

Male. Sexual dimorphism expressed in the antennule, P2–P6, genital segmentation and ornamentation, shape of caudal rami. Cephalothorax and thoracic somites as in female.

P6 (Fig. 8B) two asymmetric flaps fused to the somite, with three long naked setae. Differences from female in abdomen structure as follows (Fig. 8): first abdominal somite free; first and second abdominal somites with spinular row encircling somite ventrally and laterally; anal somite with ventral spinules; caudal rami with seta IV not transformed.

Antennule (Fig. 9) ten-segmented, haplocer with geniculation between segments 7 and 8. Segment 5 with large aestetasc fused at base with long seta, with one strong "caudate" seta. Segment 7 with articular plate, with one filiform seta, one small "caudate" seta and with two modified laminar setae. Segment 8 with proximal dentate plate and three strong modified laminar setae. Segment 10 with acrothek consisting of slender aestetasc and two setae. Armature formula: 1-[1],2-[9],3-[8],4-[2],5-[6+(1+ae)],6-[2],7-[2+2 modified],8-[3 modified],9-[1],10-[7+acr].

P2 as in female, except basis and endopod. Basis similar to that in female, but with small inner process. Endopod (Fig. 10A) two-segmented, reaching third of distal exopodal segment. First segment with outer spinules and inner pectinate seta. Second segment with notch on distal outer margin, outer spinules, two apical pinnate slender setae and two inner pectinate setae.

Praecoxa, coxa, intercoxal sclerite of P3 as in female. Basis as in female, but with small inner process (Fig. 10B–C). Exopod as in female, but third segment with subapical tube pore (Fig. 10D). Endopod (Fig. 10B–C) three-segmented, reaching third of distal exopodal segment. First endopodal segment with strong bare seta. Second endopodal segment with small posterior seta and long apophysis with bifid tip; length of apophysis 98 μm, ratio between apophysis and third endopodal segment 2.28. Third segment with inner round protrusion; with two small in-

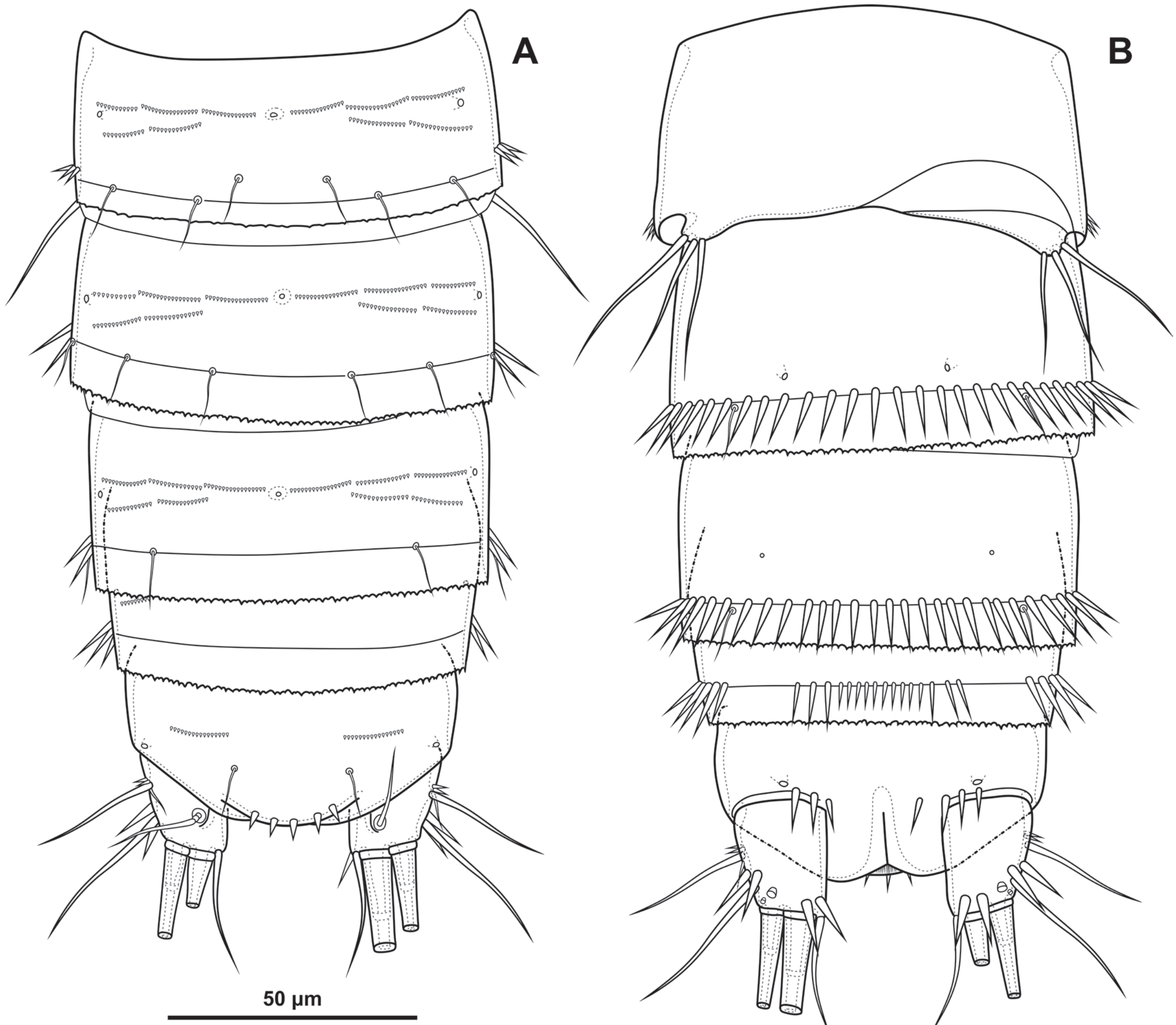

Fig. 8. *Bryocamptus sitnikovae* sp.n., allotype ♂: A — abdomen, dorsal; B — abdomen, ventral.
Рис. 8. *Bryocamptus sitnikovae* sp.n., аллотип ♂: A — абдомен, дорсально; B — абдомен, вентрально.

ner setae, posterior pore and two apical setae. Inner apical seta displaced to posterior side, bipinnate, short, with wide base. Outer apical seta modified brush-like: evenly thick, with two rows of spinules distally and thin apex.

P4 (Fig. 10E): praecoxa, coxa, intercoxal sclerite, basis, exopod as in female. Endopod two-segmented; reaching two thirds of second segment of exopod; first segment short unarmed; second segment with outer spinules, spinulose spine, outer apical spiniform spinulose seta, inner apical bipinnate seta and inner naked seta.

P5 (Fig. 6C) right and left fused medially. Baseoendopod with four pairs of pores, outer spinular row and outer long slender seta; endopodal lobe with two strong spinulose apical spines, ratio between inner and outer spines 1.37. Exopod with one spinule on distal edge and spinules on outer side; with long inner pectinate seta with long setules, two subapical inner spinulose setae, two apical naked setae and outer spinulose seta.

VARIABILITY. The left P4 Exp3 of one of the females has only one inner seta. The right exopod P5 of the holotype has seven setae instead of five, the right endopodal lobe P5 of one of the females has only four setae instead of six. All these characters were found only once on one side of the body, and therefore can be considered as morphological abnormalities.

The ornamentation of the anal operculum is variable. In total, out of 12 individuals studied (10 females and 2 males), 4 individuals completely lack spinules; if spines are present, then their number ranges from three to seven (n = 8: 3, 5, 5, 5, 5, 6, 6, 7).

Variability in the ornamentation of the caudal rami. The holotype has both ventral and inner groups of spines on the rami (arrowed in Fig. 3A, C). However, all possible combinations occur: with both groups, with either one of them, and generally without ventral and inner spinules. Including one female may have different options on right and left rami. Of the examined 10 females, two caudal rami each (total 20 rami) showed the following variants: there are both groups present: 6 (30%); only the ventral group present: 8 (40%); only the inner group present: 2 (10%), both groups absent: 4 (20%).

ECOLOGY. The species has been found so far in the one locality, on the Frolikha hydrothermal seep at a depth of 409–432 m. *Bryocamptus* (*Rheocamptus*) *sitnikovae* sp.n. is a dominant species of this habitat, since in four marked samples

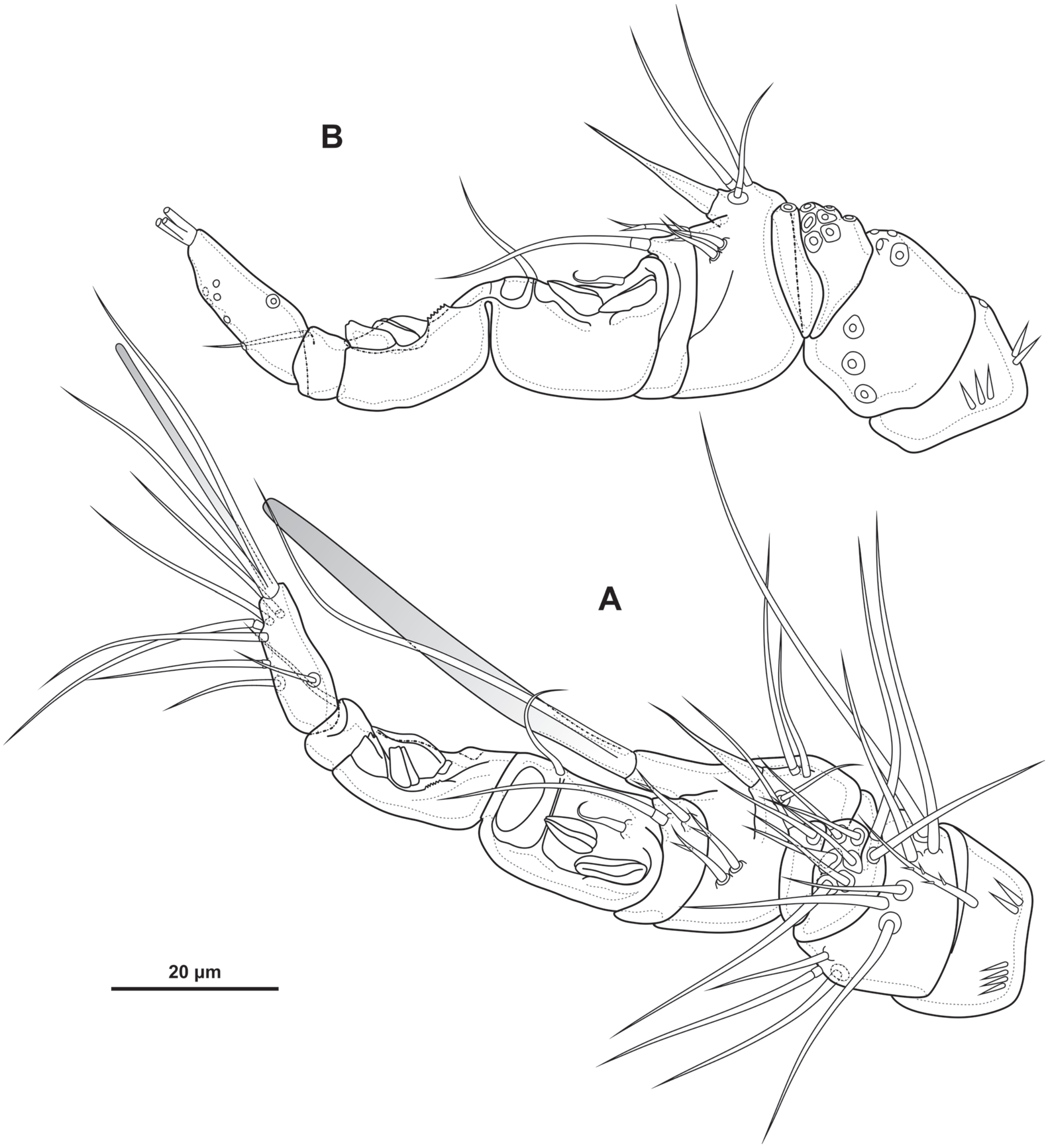

Fig. 9. *Bryocamptus sitnikovae* sp.n., allotype ♂: A — antennule, anterior; B — antennule, dorsal.
Рис. 9. *Bryocamptus sitnikovae* sp.n., аллотип ♂: A — антеннула, спереди; B — антеннула, дорсально.

from this seep it was 94% of the abundance of Copepoda [Fefilova *et al*., 2023].

Discussion

***Bryocamptus zschokkei* (Schmeil, 1893) species group**

The new species is included in the group *B. zschokkei* (Schmeil, 1893) (sensu Lang [1948]). Lang [1948] and Wells [2007] included this group in subgenus *B.* (*Bryocamptus*). Borutzky [1948b, 1952] separated this group, along with the *B. pygmaeus* (Sars, 1863) group, into a new subgenus *B.* (*Rheocamptus*) with the type species *B. zschokkei*. The same scheme is followed by most subsequent authors [Dussart, Defaye, 1990]. In general, the entire genus *Bryocamptus* requires revision. In our opinion, the subgenus *B.* (*Rheocamptus*) is hardly monophyletic, however, at the moment, it is impossible to revise the genus. The main difficulty lies in collecting a sufficient number of species from different groups.

All the ten species of endemic Baikalian *B.* (*Rheocamptus*) [Evstigneeva, Okuneva, 2001] belong to the

Fig. 10. *Bryocamptus sitnikovae* sp.n., allotype ♂: A — P2 endopod, anterior; B — P3 endopod, anterior; C — P3 endopod, inner side; D — P3 Exp3, anterior; E — P4 endopod, anterior.

Рис. 10. *Bryocamptus sitnikovae* sp.n., аллотип ♂: A — P2 эндоподит, спереди; B — P3 эндоподит, спереди; C — P3 эндоподит, внутренняя сторона; D — P3 Exp3, спереди; E — P4 эндоподит, спереди.

B. zschokkei group: *B. albidus* Okuneva, 1983; *B. baikalensis* Borutzky, 1931; *B. brevipes* Borutzky, 1948; *B. crassipes* Borutzky et Okuneva, 1972; *B. cristatus* Borutzky et Okuneva, 1972; *B. denticulatus* Borutzky et Okuneva, 1972; *B. littoralis* Borutzky et Okuneva, 1972; *B. rylovi* Borutzky, 1931; *B. saxicola* Borutzky et Okuneva, 1972; and *B. sitnikovae* sp.n. Together with the non-Baikalian *B. zschokkei, B. spinulosus* Borutzky, 1934, *B. alosensis* Apostolov, 1998 and *B. madarensis* Apostolov, 1969, the group is characterised by a set of characters which are primitive for the entire genus: a two-segment mandible palp, two exopodal and three endopodal setae of the maxillule and a complete composition of setae and spines on P1–P5. There are few reliable synapomorphies of the species of the group; they include two-segment endopods P1–P2, the ratio of the lengths of setae on the baseoendopod P5 of the female (from the longest to the shortest: IV-II-I-III-V-VI or IV-II-III-I-V-VI), as well as the ratio between the apical setae of the P3 endopod of the male, where one of the setae is much longer and more massive than the other. The Baikalian species of the *B. zschokkei* group most likely represent a monophyletic lineage. They are similar in basic characters, such as leg armature, abdominal somite and anal operculum ornamentation, but almost all of these characters are plesiomorphic for the *B. zschokkei* group. Unfortunately, we were unable to detect significant synapomorphies for Baikalian species.

Several species such as *B. balcanicus* (Kiefer, 1933), *B. pyrenaicus* (Chappuis, 1923) and *B. zschokkei kalinae* Petkovski, 1956 can probably also be classified as a group of *B. zschokkei*, however, they all differ in the reduction in the number of setae on the female P5 (3–5 setae on baseoendopod) [Chappuis, 1923; Petkovski, 1956]. *Bryocamptus mirus* Petkovski et Karanovic, 1997 also has similar characters, as two-segmented P1 endopod, but differs from the group of species under consideration in the ratio of P5 setae, in the male P3 endopod with two unmodified apical setae, and in the presence of an exopodal mandible seta [Petkovski, Karanovic, 1997].

In the *B. zschokkei* group endopods P2–P3 of females are often incompletely fused. In *B. zschokkei* and *B. spinulosus*, endopods have sometimes been described as three-segmented [Kiefer, 1960; Sterba, 1967; Caramujo, Boavida, 2009], which may also reflect a lack of fusion or incomplete fusion of the segments. In *B. sitnikovae* sp.n., the boundary between the ancestral segments of the P3 endopod is clearly visible. So, it can be described as both 3-segmented and 2-segmented. Such an incomplete fusion of segments can also be seen in other species of *Bryocamptus*, such as *B. putoranus* Novikov, Sharafutdinova et Chertoprud, 2023 [Novikov *et al*., 2023], or in species of other genera, for example in *Attheyella nordenskioldii* (Lilljeborg, 1902) [Novikov *et al*., unpublished].

The structure of the P3 male endopod is rather unusual in this group of species. In the new species, the outer seta is massive, evenly thickened, and has two rows of spinules in the distal part. Such an interesting structure could be attributed to the peculiarity of the species, given that the structure of the P3 male endopod can often be species-specific both in *Bryocamptus* [Novikov *et al*., 2023] and in other genera of Canthocamptidae and genera from families, close related to Canthocamptidae, for example, *Lourinia* C.B. Wilson, 1924 [Karaytuğ *et al*., 2021], *Mesochra* Boeck, 1865 [Soyer, 1977] or *Cletocamptus* Schmankevitsch, 1875 [Gómez *et al*., 2017]. However, an almost identical structure is found in both the Baikalian endemic species [Borutzky, Okuneva, 1972], *B. zschokkei* from Korea [Lee, Chang, 2006] and *B. spinulosus* [Borutzky, 1934]. Taking into account the low quality of the description of the last century, such a modification of the seta may also be found in other species of the *B. zschokkei* group. Among the Baikalian species, *B. rylovi* [Okuneva, 1989] and *B. denticulatus* [Borutzky, Okuneva, 1972] have the same seta, something similar can be seen in *B. brevipes* [Borutzky, 1948b], *B. crassipes*, *B. cristatus*, *B. saxicola* and *B. littoralis* [Borutzky, Okuneva, 1972]. Only in one species, *B. albidus*, is this seta depicted without features [Okuneva, 1983]; however, given the low quality of the figures and the existing taxonomic errors in this work (the description of *A. nordenskioldii* as a new species of *Canthocamptus gibba* Okuneva, 1983) [Novikov, Sharafutdinova, 2022], most likely, all Baikalian species have this brush-like seta.

The structure of the caudal rami of females and the antennules of males

Bryocamptus sitnikovae sp.n. has an interesting modification of caudal rami with an expanded base of seta IV. At the same time, there are also modifications of the male antennules. On segment 8, the laminar setae are considerably enlarged, one of them is elongated and its apical end extends beyond the base of segment 9. Previously, Novikov *et al*. [2023] suggested that the coevolution of male antennules and female caudal rami is associated with a sexual arms race. Since it is more difficult for males to grasp a female with modified caudal rami, males with the most successful form of antennules leave more offspring. Boxshall & Evstigneeva [1994] suggested as well that the main evolutionary vector in the Baikalian Canthocamptidae is reproductive isolation through the transformation of female caudal rami. However, they consider specific mate recognition systems to be the reason for this (mainly studied in the genus *Moraria* Scott et Scott, 1893). These two hypotheses have in common that the main factor of speciation in both is reproductive isolation; however, the role of the males differs. In the second hypothesis, the male recognises a female of a different species and does not continue mating. On the contrary, in the first hypothesis, the male can and would begin to fertilise a female not of his own species; however, due to the structural features of the antennules, he would not be able to complete the process of fertilisation. At the moment, it is impossible to say which hypothesis is more correct. Moreover, both of them can be true to one degree or another for different groups of species. So, for further conclusions, it is necessary to conduct experiments with living individuals.

Differences from other Baikalian *Bryocamptus* (*Rheocamptus*) species

First of all, when studying the Baikalian Canthocamptidae, it is necessary to pay attention to several main problems. First, the descriptions are of poor quality for most species. It should be taken into account that most of the species of *Bryocamptus* and *Moraria* are included in species flocks [Boxshall, Evstigneeva, 1994], the species of which differ little from each other. Given the high variability of Baikalian species, any characters may be important for identification. The authors, however, often cited only drawings of diagnostic characters in the descriptions [Borutzky, 1947]. Also, despite the indication that species are represented by a large number of individuals, the authors rarely mentioned the variability of species [Borutzky, 1952; Borutzky, Okuneva, 1972].

The second problem is the difficulty of matching males and females of the same species in a sample. Most samples may contain several species from the same species flock. According to the available descriptions, only females can be distinguished (for example, genus *Moraria*: [Borutzky 1952]); it is almost impossible to correlate males purely morphologically. Therefore, it is often necessary to rely on samples where representatives of only one species from any species flock are numerous, as is the case with the description of *B. sitnikovae* sp.n.

Be sure to keep in mind the problems described above as we consider the group of species. The 10 species of Baikalian *B.* (*Rheocamptus*) listed earlier can be distinguished by several features, including:

1. Segmentation of the female antennule. Only one species, *B. crassipes*, has a 7-segmented antennule [Borutzky, Okuneva, 1972].

2. Number of inner setae on the P3 female endopod. All species have three, except for *B. crassipes* which does not have any inner seta and *B. saxicola* which has two inner setae [Borutzky, Okuneva, 1972].

3. Shape of the outer spine of the P4 male endopod. In most species, this spine is not modified, as in *B. sitnikovae* sp.n. However, a modified spine is present in *B. cristatus* (curve spine) and *B. littoralis* (bifurcate blunt spine) [Borutzky, Okuneva, 1972].

4. Spinular ornamentation of the P5 female exopod. The exopod may have spinules on the outer, inner and apical margins; one species, *B. denticulatus*, has a group of spinules on the anterior surface of the exopod [Borutzky, Okuneva, 1972].

5. Length of setae on the P5 female exopod. Setae I and V are the most variable. The first seta is shorter than the exopodal segment in *B. albidus*, *B. baikalensis*, *B. cristatus* and *B. rylovi*. In other species, this seta is longer than the exopod [Borutzky, 1952; Borutzky, Okuneva, 1972; Okuneva, 1983].

6. Presence of ventral and lateral spinules on the anal somite of females and males. All studied females of *B. sitnikovae* sp.n. did not have both groups of spinules, which may indicate the diagnostic nature of this character. However, in the earlier descriptions, unfortunately, this feature was not given attention. It can only be assumed from the figures that *B. rylovi* females do not have lateral spinules, and *B. littoralis* females do not have ventral spinules [Borutzky, 1952; Borutzky, Okuneva, 1972].

7. Length of caudal rami. In species of the group, the ratio of length to width of the caudal rami ranges on average from 1 to 1.5. Only one *B. cristatus* has an elongated caudal rami; their ratio is almost 2 [Borutzky, Okuneva, 1972].

8. Ornamentation of the caudal rami is a traditional diagnostic feature widely used in keys [Borutzky, Okuneva, 1972; Okuneva, 1989]. However, in the taxonomy and identification of the Baikalian species of *B.* (*Rheocamptus*), one should be very careful about the groups of spinules of the caudal rami. For instance, in *B. sitnikovae* sp.n., these characters are highly variable; *B. baikalensis* and *B. cristatus*, judging by the descriptions, have no spinules, except for the spinules at the base of setae I–III; in *B. denticulatus* and *B. saxicola*, dorsal spinules are also observed to the ventral and inner groups of spinules [Borutzky, 1952; Borutzky, Okuneva, 1972].

9. Shape of caudal setae in female. In our opinion, this is one of the most useful characters since it is associated with reproductive isolation and is unlikely to be subject to significant intra-species variability. Seta IV is modified in *B. crassipes*, *B. denticulatus*, *B. littoralis* and *B. sitnikovae* sp.n. [Borutzky, Okuneva, 1972]. A study of new material shows that, for example, in *B. littoralis* the modification of the seta is exactly as shown in the description and is not similar to that in *B. sitnikovae* sp.n. However, the descriptions of other species are not detailed enough to understand what kind of modifications these species exhibit and whether they are similar to the modification in *B. sitnikovae* sp.n.

It is also worth noting some of the features mentioned in the descriptions and keys are most likely deformities or errors:

1. Three setae on the distal segment of the P1 endopod in *B. albidus* [Okuneva, 1983]. Most likely, the small apical seta was ovelooked.

2. Three inner setae on the P2 female endopod in *B. rylovi* [Borutzky, 1952; Okuneva, 1989]. In the genus *Bryocamptus*, as a whole, one of the inner setae of the P2 endopod is always reduced. This character is present in different species groups, for example, *B. minutus* species group [Novikov, Sharafutdinova, 2022], *B. jejuensis* Lee et Chang, 2016 [Lee, Chang, 2016], species of the subgenus *B.* (*Echinocamptus*) [Lee, Lee, 2010]. So, this is most likely either an abnormality, or an error in the interpretation of setule/seta, or the P2 and P3 were confused.

3. Seven setae on the P5 male exopod in *B. brevipes* [Borutzky, 1948b]. In the entire family, exopods of males have a maximum of six setae. Additional setae are not uncommon in females and males, but in all cases, they are individual deviations.

Finally, the spinular ornamentation of the abdominal somites can certainly be taxonomically important, but it is currently unclear how variable it is, and it is also rather poorly described in most species. Most do not have drawings, and in *B. saxicola*, the description and drawing do not match [Borutzky, Okuneva, 1972], which further adds to the doubts about the use of this character.

Table 2. Comparison of morphological characters distinguishing the females of endemic species of *Bryocamptus* (*Rheocamptus*) of the Baikal Lake.
Таблица 2. Сравнение морфологических признаков, различающих самок эндемичных видов *Bryocamptus* (*Rheocamptus*) озера Байкал.

Species	A1, segments	P3Enp3, inner setae	P5Exp, spinules	P5Exp, seta I / exopod length	Anal somites, spinules	Caudal ramus length / width	Caudal rami, spinules	Caudal seta IV, shape of base
Bryocamptus albidus Okuneva, 1983	8	3	O+A+I	0.8	L+V	1.1	V	normal
Bryocamptus baikalensis Borutzky, 1931	8	3	?	0.85	L+V	1.35	–	normal
Bryocamptus brevipes Borutzky, 1948	8	3	?	1.7	L+?	1.2	V+I	normal
Bryocamptus crassipes Borutzky et Okuneva, 1972	7	0	O+I	1.8	L+V	1.35	V+I	bulb
Bryocamptus cristatus Borutzky et Okuneva, 1972	8	3	O	0.65	L	1.8	–	normal
Bryocamptus denticulatus Borutzky et Okuneva, 1972	8	3	O+A+F	1.8	L+V	1.25	V+I+D	modified
Bryocamptus littoralis Borutzky et Okuneva, 1972	8	3	–	1.1	L	1.1	V+I	modified
Bryocamptus rylovi Borutzky, 1931	8	3	O+A	0.85	V	1.2	V	normal
Bryocamptus saxicola Borutzky et Okuneva, 1972	8	2	O+A+I	1.13	L+V	1.15	V+I+D	normal
Bryocamptus sitnikovae sp.n.	8	3	O	1.8	absent	1.3	variable	bulb

Abbreviations for groups of spinules: O — outer; A — apical, near setae II–IV of P5Exp; I — inner; F — frontal; L — lateral; V — ventral.

In conclusion, it can be noted that the taxonomy of Baikalian representatives of the genus *Bryocamptus* is quite confusing. It requires the study of new material and a redescription of described species. The new species is one of the exceptions; it is quite stable morphologically and has good distinctive characters. And given that other species often exhibit significant variability, a full revision is probably impossible without the use of molecular genetic methods to determine species boundaries.

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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