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Anton Brancelj^{ab} & Tomislav Karanovic^{cd}

^a National Institute of Biology, Ljubljana, Slovenia

^b School of Environmental Sciences, University of Nova Gorica, Nova Gorica, Slovenia

^c Department of Life Sciences, Hanyang University, Seoul, Korea

^d IMAS, University of Tasmania, Hobart, Tasmania, Australia

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A new subterranean *Maraenobiotus* (Crustacea: Copepoda) from Slovenia challenges the concept of polymorphic and widely distributed harpacticoids

Anton Brancelj^{a,b} and Tomislav Karanovic^{c,d,*}

^aNational Institute of Biology, Ljubljana, Slovenia; ^bSchool of Environmental Sciences, University of Nova Gorica, Nova Gorica, Slovenia; ^cDepartment of Life Sciences, Hanyang University, Seoul, Korea; ^dIMAS, University of Tasmania, Hobart, Tasmania, Australia

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Maraenobiotus slovenicus sp. nov. is described from subterranean waters of a very cold, temporary karstic spring in the vicinity of Velika Pasica cave, central Slovenia. A detailed examination of numerous specimens reveals a low level of morphological variability in this population. Morphological characters traditionally used in the genus *Maraenobiotus* Mrázek, 1893 would identify our population as a subspecies of the polymorphic and widely distributed *M. vej dovskyi* Mrázek, 1893. This species was reported from the Palearctic, with at least six accepted subspecies, some of which have been reported in sympatry or parapatry, sometimes even without any apparent niche partitioning. One of these subspecies, *M. vej dovskyi truncatus* Gurney, 1932, originally described from the UK and later on also reported from Italy and Japan, shares with our population the extremely reduced female principal caudal setae. However, a closer examination of the caudal armature and other characters reveals significant differences between these disjunct populations. We propose a hypothesis of distinct species within the *M. vej dovskyi*-complex, and critically review all recognized and some unrecognized morphotypes and subspecies. As a result, three new species names are proposed for previously reported populations from Italy and Japan: *Maraenobiotus galassiae* sp. nov.; *M. isidai* sp. nov.; and *M. pescei* sp. nov. Four subspecies of *M. vej dovskyi* are now elevated to the full specific rank: *M. anglicus* Gurney, 1932; *M. arctica* Löffler; *M. tenuispina* Roy; and *M. truncatus* Gurney, 1932. This hypothesis remains to be tested using molecular (and other) tools, but can serve as a viable alternative to the concept of polymorphic and widely distributed freshwater harpacticoids.

<http://zoobank.org/urn:lsid:zoobank.org:pub:92302CF9-21BA-4454-A3DD-337BB7152DCE>

Keywords: Canthocamptidae; cave; copepod; stygofauna; taxonomy; temporary spring

Introduction

The genus *Maraenobiotus* was established by Mrázek (1893) for the newly described subterranean species from the Czech Republic, *M. vej dovskyi* Mrázek, 1893 (see Huys 2009). This species was afterwards found in Scotland

*Corresponding author. Email: Tomislav.Karanovic@utas.edu.au

(Scott T. 1895, 1896, 1898, 1899, 1903, 1906; Scott T. and Scott A. 1896; Gurney 1932), Germany (Kiefer 1923, 1925; Donner 1928), and Switzerland (Chappuis 1916; Haberbosch 1916), mostly from mossy habitats (for a complete list of localities before 1940 see Lang 1948). In addition to the nominotypical morphotype, several researchers reported various forms of variability, sometimes recognizing them taxonomically as separate subspecies, forms or varieties (today they are all considered subspecies): *M. vej dovskyi anglicus* Gurney, 1932; *M. vej dovskyi arctica* Löffler; *M. vej dovskyi tenuispina* Roy and *M. vej dovskyi truncatus* Gurney, 1932 (Walter and Boxshall 2014). Another variety, described by Keilhack (1909) from the French Alps, was considered as uncertain by Lang (1948) and was not mentioned subsequently. *Maraenobiotus zschokkei* Kreis, 1920a, originally described from Switzerland (Kreis 1920, 1921, 1923), was also for a while considered as a subspecies of *M. vej dovskyi* by Chappuis (1935), Lang (1948), and Borutzky (1952) among others.

Today there are 39 accepted species and subspecies considered valid in this nearly cosmopolitan genus (Walter and Boxshall 2014), but almost half of them are subspecies of several widely distributed and very variable species, with relationships among them admittedly problematic (Borutzky 1952). Gurney (1932) reported the two above-mentioned subspecies of *M. vej dovskyi* with parapatric ranges (*M. vej dovskyi anglicus* and *M. vej dovskyi truncatus*), while Löffler (1968) described two new subspecies of *M. insignipes* (Lilljeborg) living sympatrically in at least four localities in Nepal (*M. insignipes altissimus* Löffler, 1968 and *M. insignipes nepalensis* Löffler, 1968). Obviously, the genus is in urgent need of revision, and so far there has been no challenge to the concept of polymorphic and widely distributed members.

Ishida (1987) reported great phenotypic variability of *M. vej dovskyi* in Japan, with three different types of female caudal rami, one with truncated principal caudal setae (as in *M. vej dovskyi truncatus*), claiming that these characters even 'vary by individuals within a same place'. He, however, did not provide a list of localities studied nor those where he found more than one morphotype, and his illustrated specimens came from at least two very different localities. Pesce et al. (1994) studied variability of this species in Italy and also found three different morphotypes, two of them with truncated principal caudal setae. All morphotypes came from different localities (i.e. no sympatry), from different altitudes, were collected in different months, and also had different physical environmental conditions (Table 1). The authors concluded that they are dealing with one very variable species and argued for abandoning subspecific divisions. It should be mentioned that Gurney (1932) also never found *M. vej dovskyi* s. str., *M. vej dovskyi truncatus* or *M. vej dovskyi anglicus* in the same locality, and he noticed that the second taxon could only be found in peat bogs, while the latter inhabits lakes.

Schminke (1991) summarized our knowledge of sexual dimorphism in caudal ramus shape in harpacticoids, while working on another freshwater family (Parastenocarididae Chappuis), but he also argued for a widespread polymorphism in the same structure. The only case where this has been tested so far, using molecular tools, was in the genus *Schizopera* Sars (family Miraciidae Dana), when Karanovic and Cooper (2012) showed that two parapatric morphotypes with

Table 1. Locality data for three distinct morphotypes of *Maraenobiotus vej dovskyi* Mrázek, 1893 from Italy, reported by Pesce et al. (1994).

Population	Altitude (m)	Temperature (°C)	pH	Conductivity ($\mu\Omega$)	Date	Substrate
Fosso Perrone	1330	5.5	8	185	20 May 1992	Organic detritus
Sorgenti del Sangro	1370	18	7.7	475	26 June 1992	Sandy clay
Seenlein	2886	13	?	10	16 August 1993	Coarse gravel

different caudal rami shape are in fact two distinct (but closely related) species. Kim et al. (2014) provided molecular evidence for the variability in the caudal rami shape between disjunct (Korean and Russian) populations of the marine littoral *Enhydrosoma intermedia* Chislenko, but these are only minor in nature and congruent with their geographic variation in body size.

In this paper we describe a new subterranean harpacticoid from Slovenia (Europe) that has female caudal rami with truncated principal caudal setae, like those of *M. vej dovskyi truncatus* from Great Britain and some specimens of *M. vej dovskyi* from Japan and Italy reported by Ishida (1987) and Pesce et al. (1994) respectively. We also critically review recognized and unrecognized morphotypes and subspecies within the *M. vej dovskyi*-complex, and propose a hypothesis of distinct species for at least some of them.

Material and methods

The type locality for our new species is a temporary spring Močilo, 45.551464° N, 14.293337° E, 647 m above sea level. It is on the western side of the village Gornji Ig (c.20 km south of Ljubljana, capitol of Slovenia) and about 200 m north-west from the entrance of Velika Pasica cave (Brancelj 2000, 2002, 2009). Part of the water in the spring originates from the cave and part from an undefined catchment area (c.0.5 km²). The spring is at the base of c.10 m steep cliff and about 25 m below the Velika Pasica cave entrance. The mouth of the spring Močilo is triangular in shape, about 20 cm wide at the base and about 30 cm high, descending at an angle of 45° into the rock. The geology is thinly bended Norian–Retian dolomite from the Upper Triassic period (Pleničar 1970). The spring is usually active between 48 and 72 h, and only after heavy rain or snow melt, with a maximum discharge of about 10 l s⁻¹. It is surrounded by a forest of the *Abieti fagetum dinaricum*-type and small patches of meadows.

Basic physical parameters of water quality (cave water mixed with melted snow water) during our sampling period were: water temperature, average 4.4°C, (range:

4.0–4.8°C); conductivity: average 460 $\mu\text{S cm}^{-1}$ (range: 445–478 $\mu\text{S cm}^{-1}$); pH: average 7.2 (range: 7.0–7.4).

Basic chemical parameters of water quality (cave water mixed with melted snow water) during sampling period were: nitrate (NO_3^-): average 4.66 mg l^{-1} (range: 4.10–5.04 mg l^{-1}); sulphate (SO_4^{2-}): average 1.98 mg l^{-1} (range: 1.87–2.13 mg l^{-1}); potassium (K^+): average 0.76 mg l^{-1} (range: 0.25–1.84 mg l^{-1}); sodium (Na^+): average 0.69 mg l^{-1} (range: 0.61–0.84 mg l^{-1}); calcium (Ca^{2+}): average 69.03 mg l^{-1} (range: 64.33–70.85 mg l^{-1}); chloride (Cl^-): average 1.16 mg l^{-1} (range: 0.90–1.42 mg l^{-1}); magnesium (Mg^{2+}): average 35.66 mg l^{-1} (range: 32.61–37.13 mg l^{-1}).

Sampling of the spring Močilo took place three times in the beginning of 2014 (20 January, and 8 and 22 February). A drift-net (mouth diameter 30 cm, length of the filtering cone 1.5 m, mesh size 60 μm , fitted at the end with a special filtering bottle; Brancelj 2004) was inserted at the mouth of the spring for 24 h on each sampling occasion. The majority of filtered water was collected from the mouth of the spring, but part of it originated from slopes surrounding the spring (area of about 10 m^2). Slopes at the mouth of the spring were covered with litter; the main source was beech leaves (*Fagus sylvatica* L.). Collected material from the drift net was transferred into 750 ml plastic bottle and fixed in c.60% ethanol. Water temperature, electric conductivity and oxygen concentration were measured on-the-spot with a Multi 340i instrument (WTW Company, Oberbayern, Germany). Samples for water chemistry analyses (major ions: Ca^{2+} , Mg^{2+} , K^+ , Na^+ , SO_4^{2-} , Cl^- and NO_3^-) were collected into 50 ml plastic bottles. They were transferred in the laboratory, into a cold box, stored in a refrigerator at +4°C, and analysed within 48 h using an ion chromatograph (761 Compact IC, Methrom, Herisau, Switzerland).

Biological samples were checked several hours after sampling and specimens of different animal groups were picked out and stored in 70% ethanol in plastic vials (details of the accompanying fauna are listed in the Discussion).

Before dissection, specimens were placed in a mixture of glycerol and 70% alcohol (ratio ~1:10 v/v), which was replaced within half an hour by pure glycerol. They were dissected at 100 \times magnification under an Olympus SZH 2 stereomicroscope (Olympus, Tokyo, Japan). Examination of all appendages and body ornamentation was done under a magnification of 1000 \times . Drawings were made at a magnification of 1000 \times with a drawing tube mounted on an Olympus microscope (BHS 40), except for the female/male habitus (400 \times magnification). The final version of the drawings was made using the CorelDRAW[®]12 graphic program (www.corel.com). For permanent slides all body parts were placed in a drop of glycerol on a microscope slide, covered by a cover glass, and sealed with nail polish.

Specimens for scanning electron micrography (SEM) were dehydrated in progressive ethanol concentrations, transferred into pure isoamyl-acetate, critical-point dried, mounted on stubs, coated in gold, and observed under a Hitachi S-4700 scanning microscope (Hitachi, Japan) on the in-lens detector, with an accelerating voltage of 10 kV and working distances between 12.3 and 13.4 mm; micrographs were taken with a digital camera.

Taxonomic account

Order **HARPACTICOIDA** Sars
 Family **CANTHOCAMPTIDAE** Sars
 Genus *Maraenobiotus* Mrázek, 1893

Maraenobiotus slovenicus sp. nov.
 (Figures 1–8)

Material examined

Holotype. adult female (length 658 μm), completely dissected and mounted on a slide in glycerol and sealed with nail polish; collected on 20 January 2014 in the temporary spring Močilo near village Gornji Ig (Ljubljana, Slovenia); deposited in the Slovenian Museum of Natural History (Ljubljana), registration no. PMS 2014.1352.

Allotype. adult male (length 551 μm), completely dissected and mounted on a slide in glycerol and sealed with nail polish; collected on same date at same location as holotype; deposited in the Slovenian Museum of Natural History (Ljubljana), registration no. PMS 2014.1353.

Paratypes. 10 females, 3 males (stored in 70% alcohol); collected on 8 February 2014 at the same location as holotype and allotype; deposited in the Slovenian Museum of Natural History (Ljubljana), registration no. PMS 2014.1354. Five females, 2 males (partly damaged) on a single SEM stub; deposited in the Slovenian Museum of Natural History (Ljubljana), registration no. PMS 2014.1355.

The remaining specimens (20 females, one male) collected on 22 February 2014 at the same location as the holotype remain in authors' collections.

Description

Female, body length, measured from tip of rostrum to posterior margin of caudal rami, 609–651 μm (mean: 636 μm ; $n = 10$), elongated, width constant to end of double genital somite, last three urosomal somites slightly narrower, evenly tapering toward anal somite, colourless (Figures 1A, 2A). Body length/width ratio about 4.5; pro-some/urosome ratio 1.1; length/width ratio of cephalothorax in dorsal view about 1; cephalothorax about 22% of entire body length. Naupliar eye not discernible. Rostrum small, rounded (Figure 1B, C). Integumental windows not discernible. Posterior margins of thoracic and abdominal somites dorsally smooth (Figure 1A, E, F, G). Genital double-somite with no spines laterally or ventrally (Figures 1A, F, 2C, D, 7A). Genital complex with single large copulatory pore, sclerotized, bell-shaped; seminal receptacles small, simple and heavily sclerotized. Fused plate with reduced sixth legs positioned well above seminal receptacles (Figure 7A).

Short row of spinules laterally on fourth urosomal somite; fifth urosomal somite dorsolaterally and ventrally with continuous row of spinules, smallest in ventromedial part (Figures 1A, G, 2D, 7B, C). Anal somite laterally with short row of strong

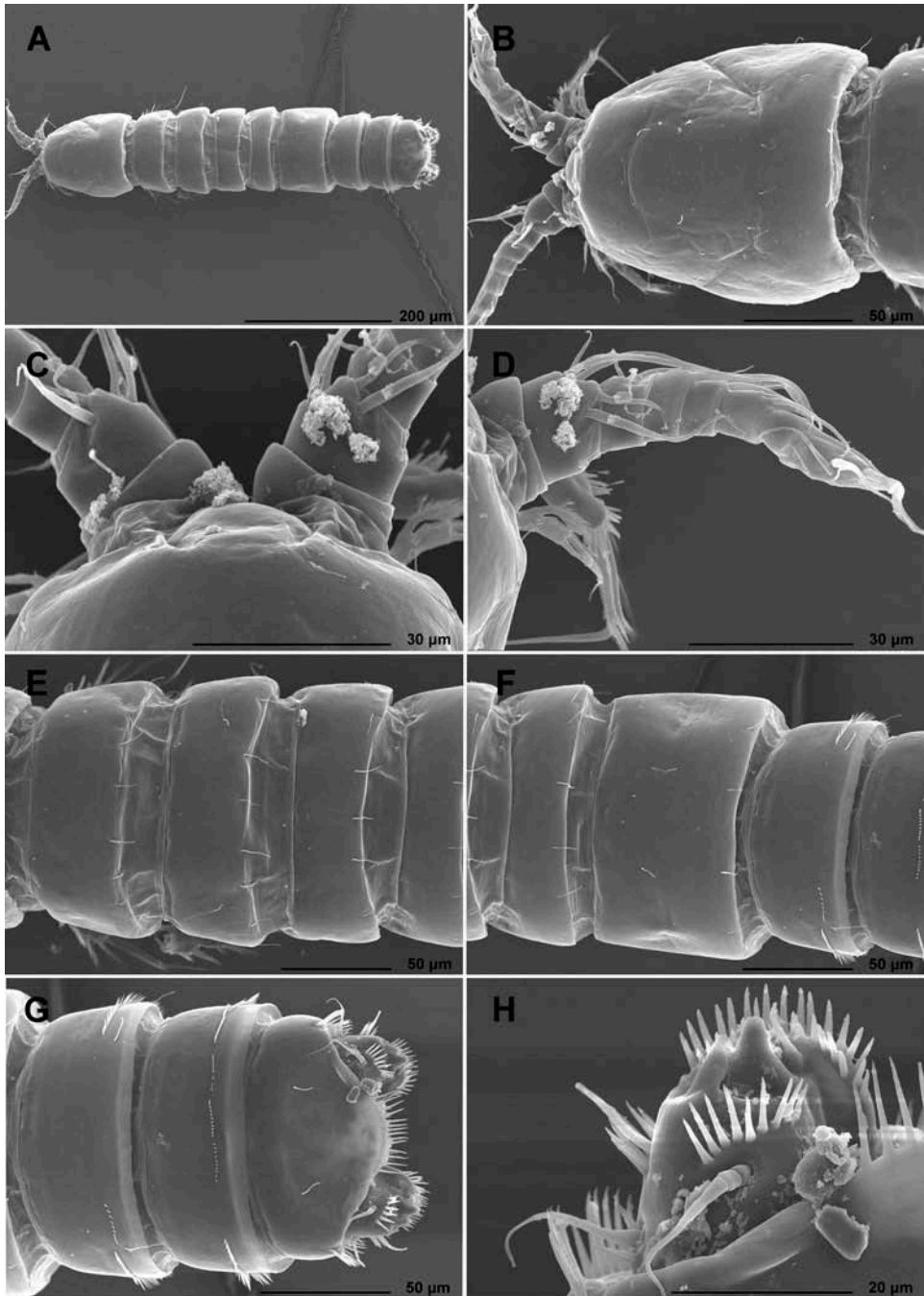


Figure 1. *Maraenobiotus slovenicus* sp. nov., SEM micrographs, paratype female 1: (A) habitus, dorsal; (B) cephalothorax, dorsal; (C) anterior part of cephalothorax, dorsal; (D) right antennule, dorsal; (E) free pedigerous somites, dorsal; (F) first three urosomites, dorsal; (G) last three urosomites and caudal rami, dorsal; (H) right caudal ramus, dorsal.

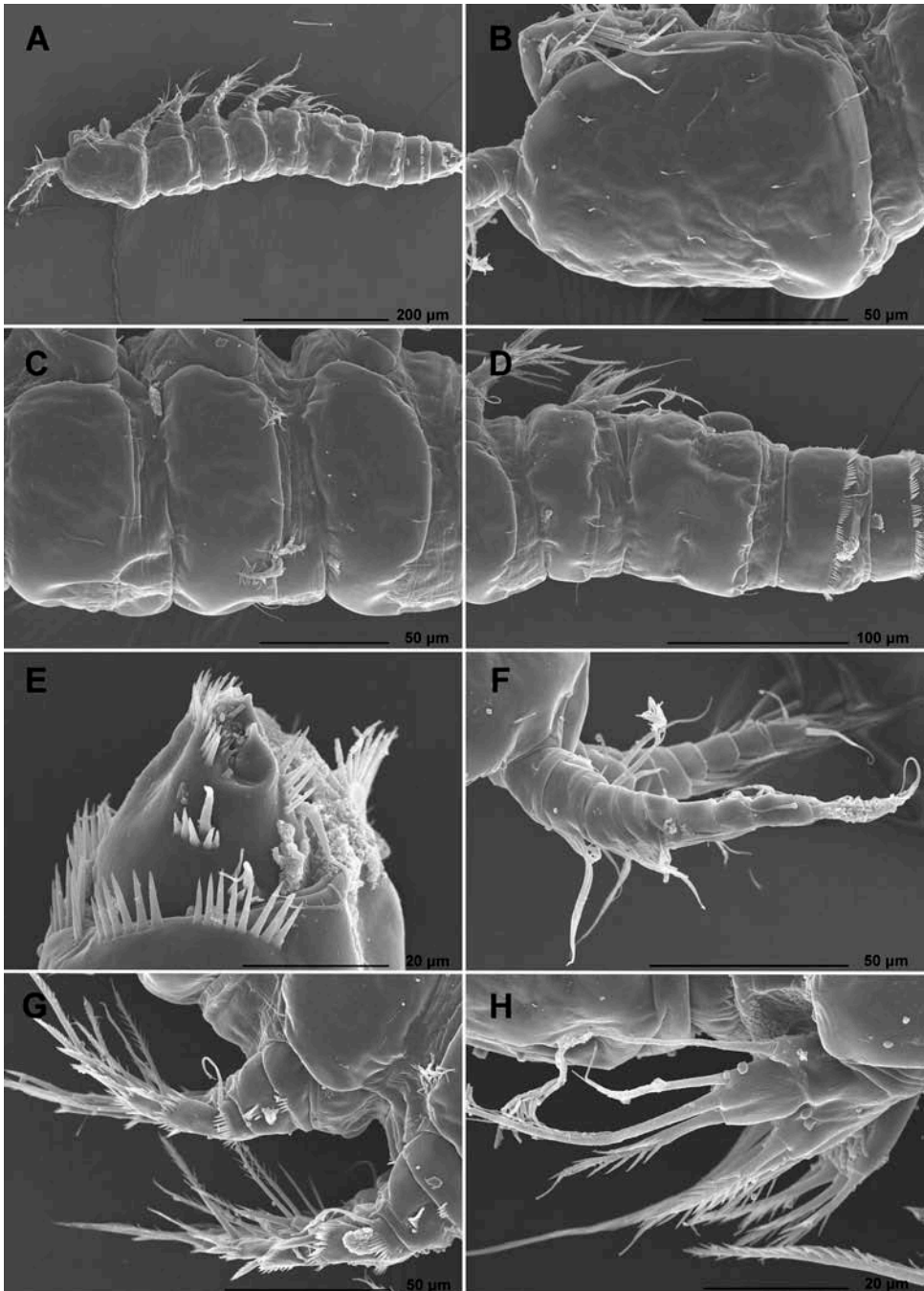


Figure 2. *Maradenobiotus slovenicus* sp. nov., SEM micrographs, paratype female 2: (A) habitus lateral; (B) cephalothoracic shield, lateral; (C) pleurons of free pedigerous somites, lateral; (D) first three urosomites, lateral; (E) anal somite and right caudal ramus, lateral; (F) antennule, lateral; (G) P3 and P4, lateral; (H) P5, lateral.

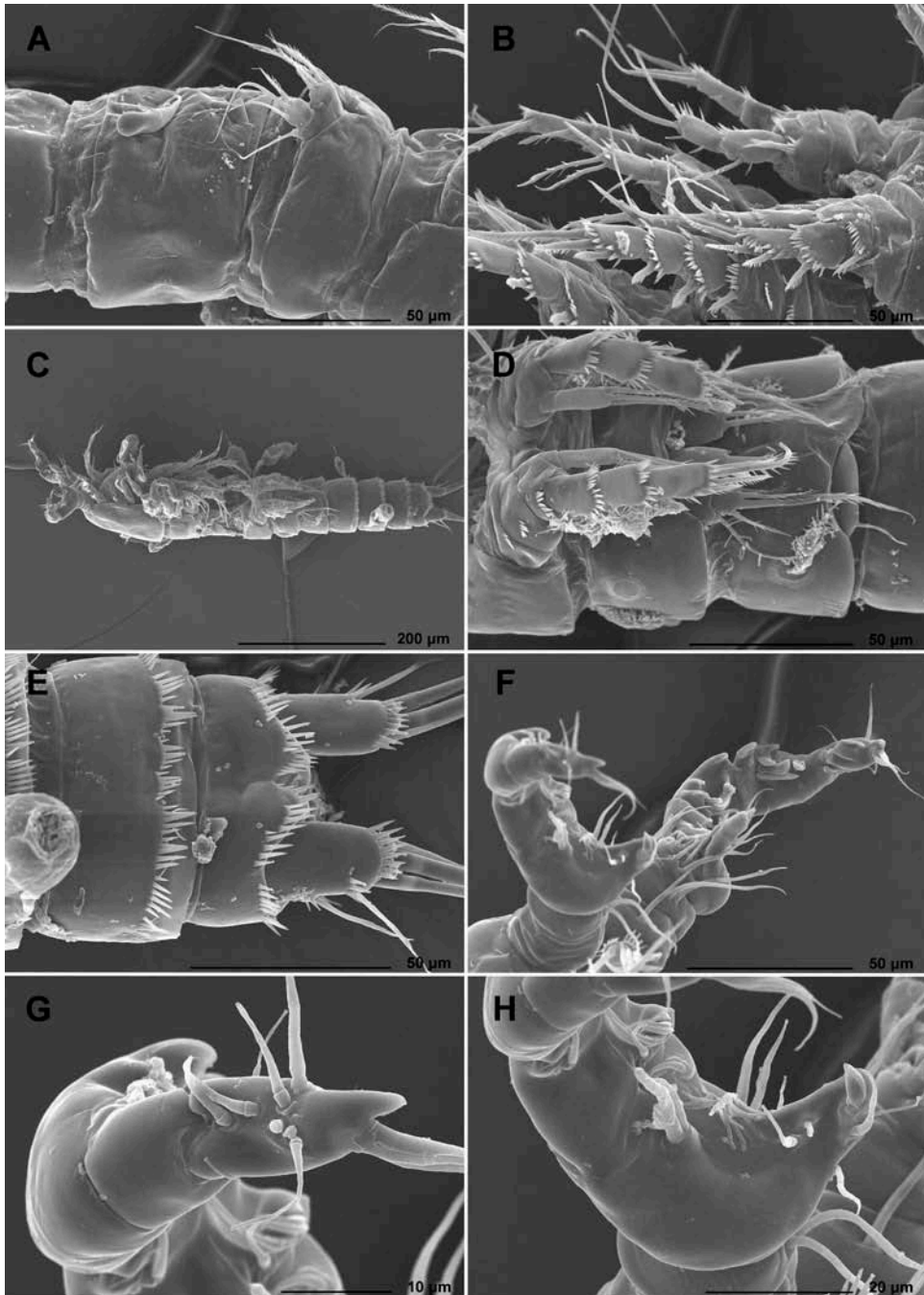


Figure 3. *Maraenobiotus slovenicus* sp. nov. (A, B) SEM micrographs, paratype female 3; (C–H) damaged paratype male 1: (A) first two urosomites and P5; (B) P1–P3, ventrolateral; (C) habitus with several large epibiotic ciliates, ventral; (D) P4–P6, ventral; (E) last two urosomites and caudal rami, ventral; (F) antennule, ventral; (G) distal part of right antennule, ventral; (H) central part of right antennule, ventral.

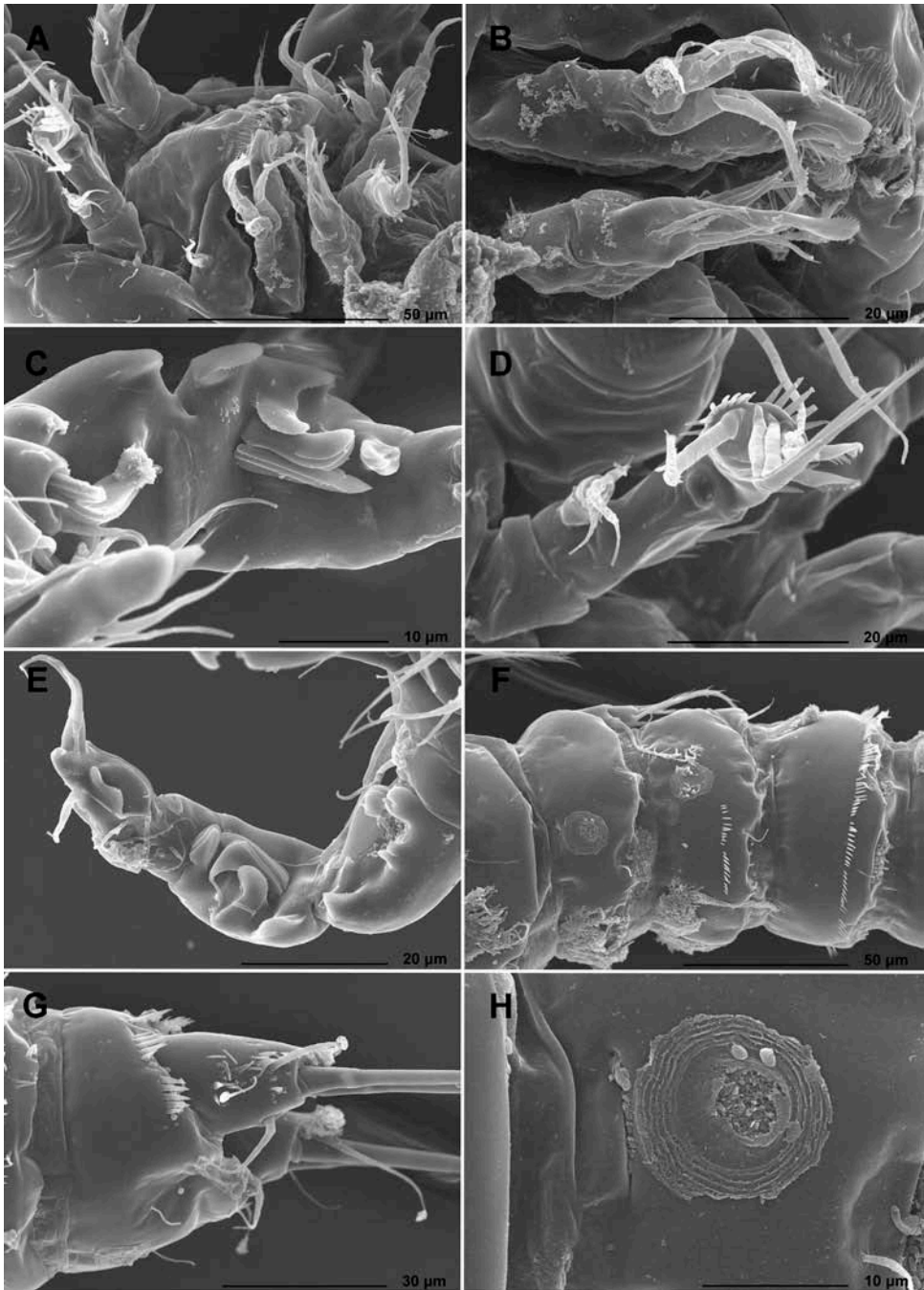


Figure 4. *Maraenobiotus slovenicus* sp. nov., SEM micrographs, (A–D) damaged paratype male 1; (E–H) paratype male 2: (A) mouth appendages, ventral; (B) maxillule and maxilla, ventral; (C) central part of left antennule, ventral; (D) antenna, ventral; (E) left antennule, lateral; (F) first three urosomites, lateral; (G) anal somite and caudal rami, lateral; (H) detail of first urosomite, with cuticular window, large pore, and sensillum, lateral.

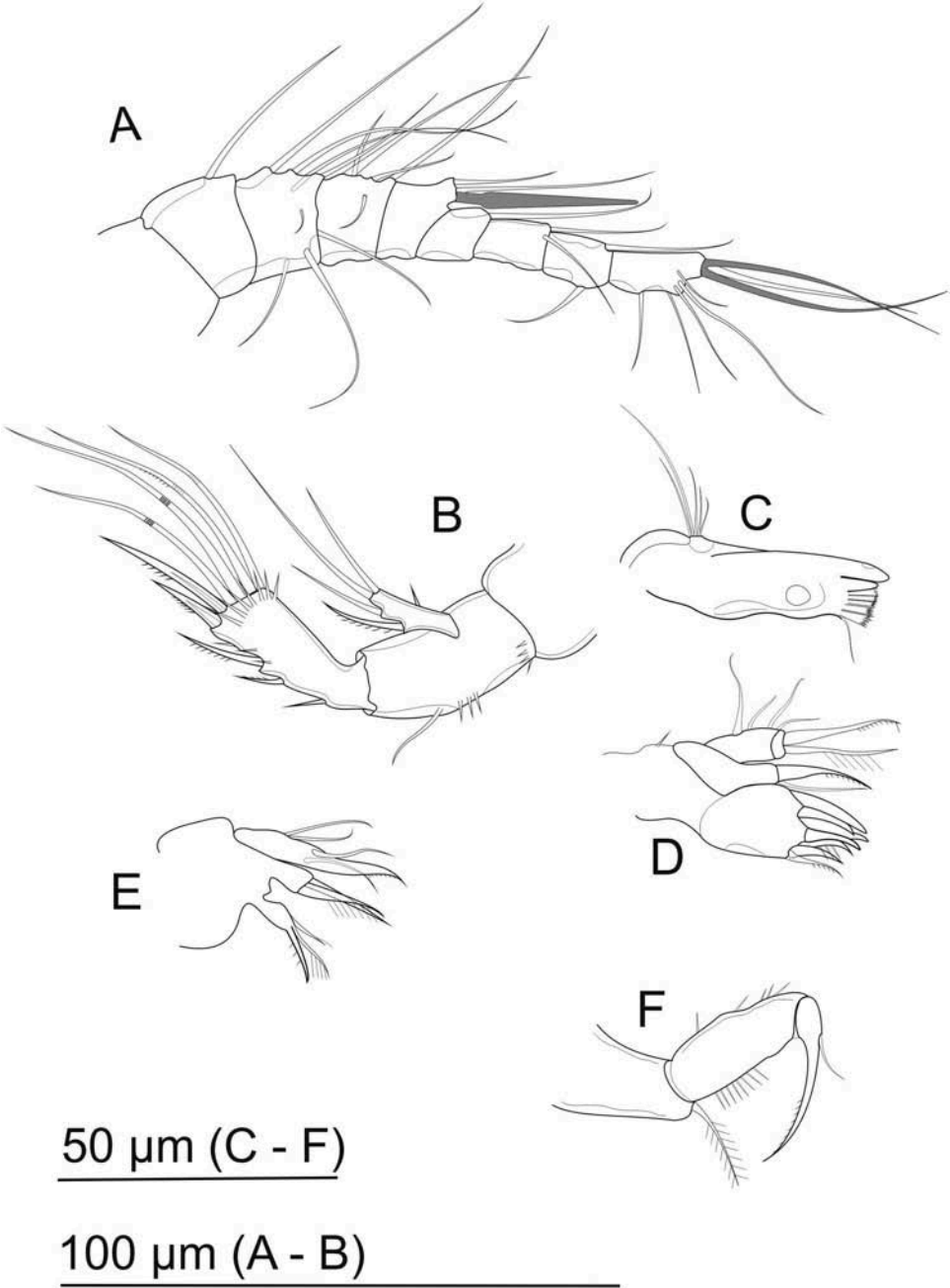


Figure 5. *Maraenobiotus slovenicus* sp. nov., line drawings, holotype female: (A) antennule, dorsal; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped.

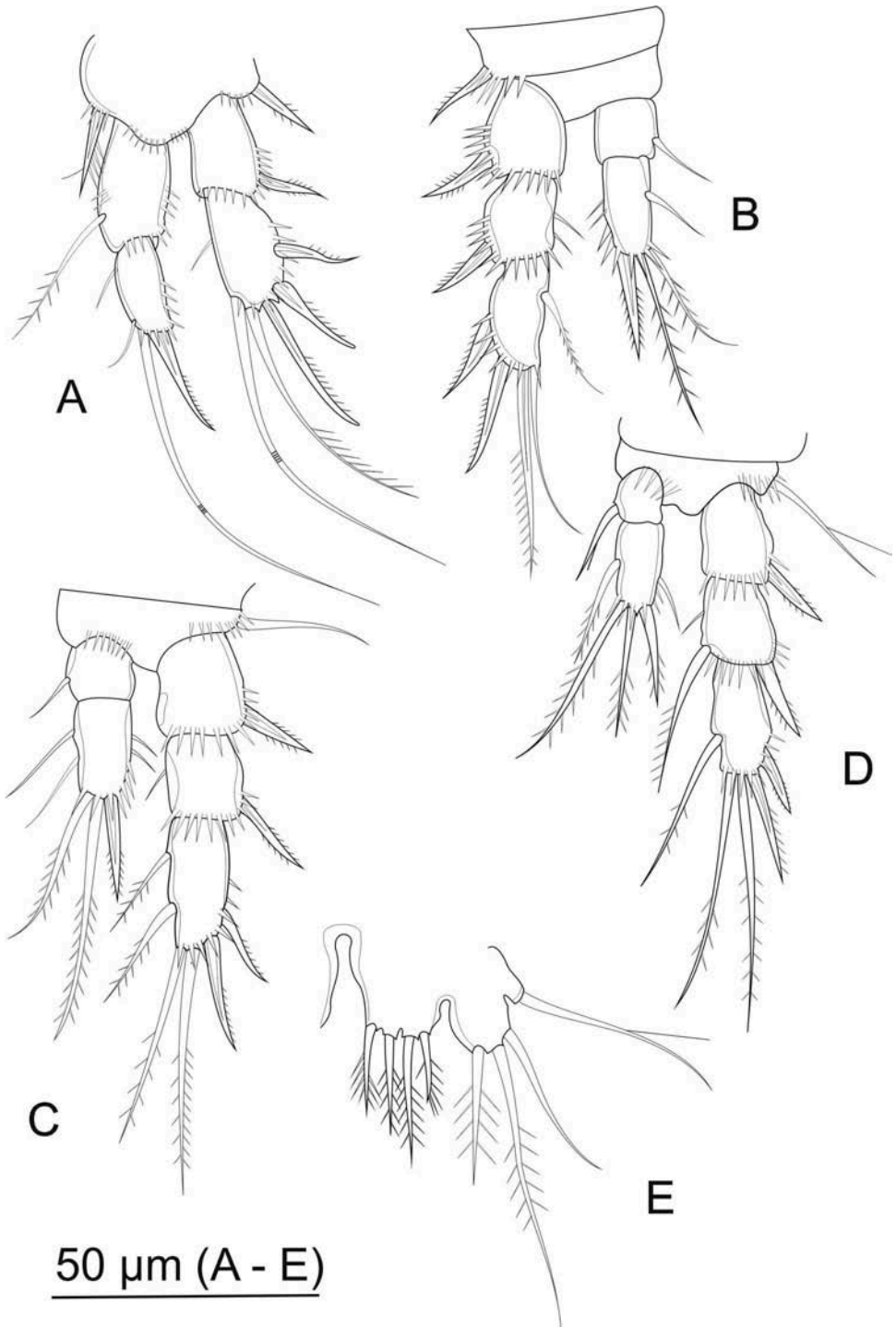


Figure 6. *Maraenobiotus slovenicus* sp. nov., line drawings, holotype female: (A) P1; (B) P2; (C) P3; (D) P4; (E) P5.

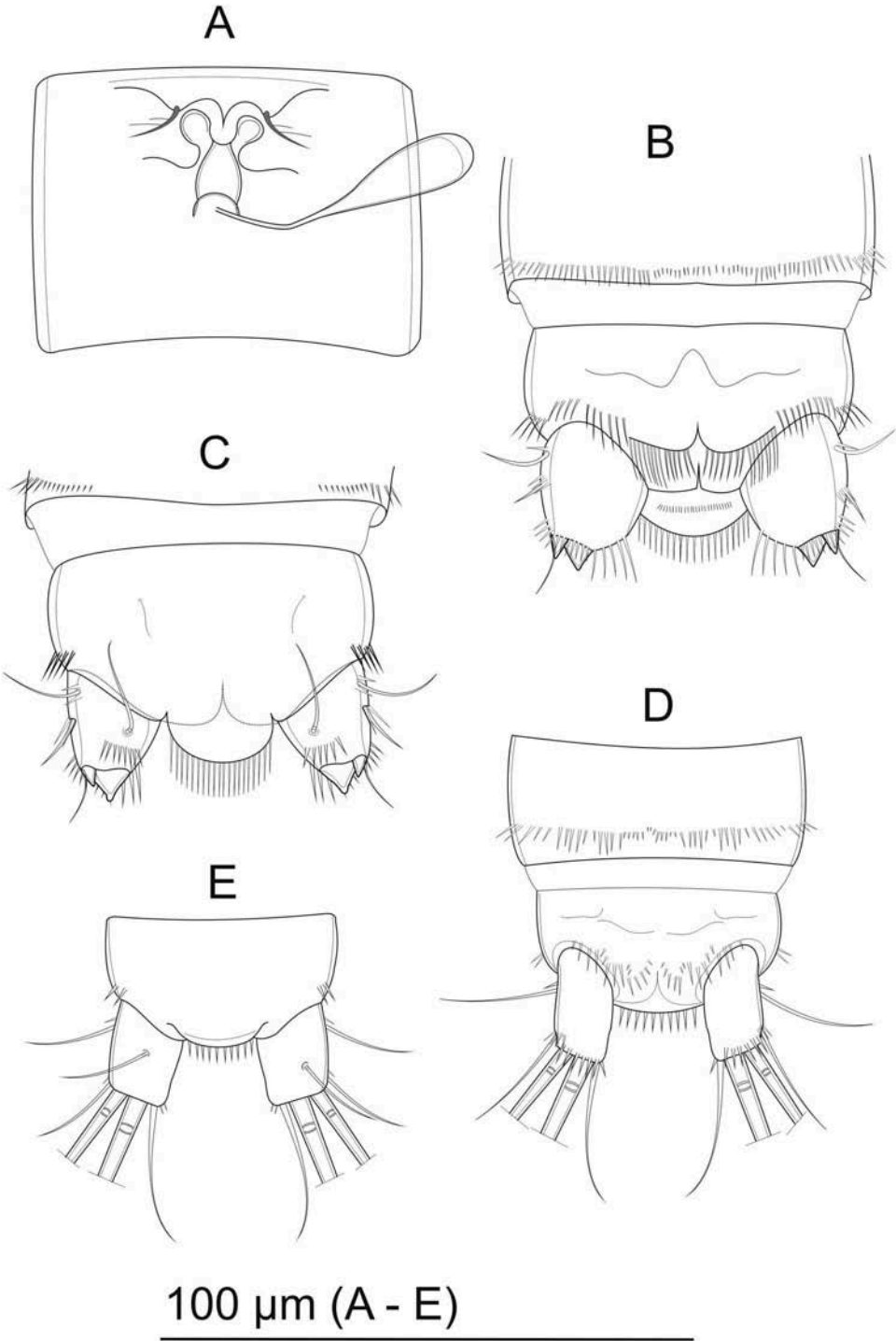
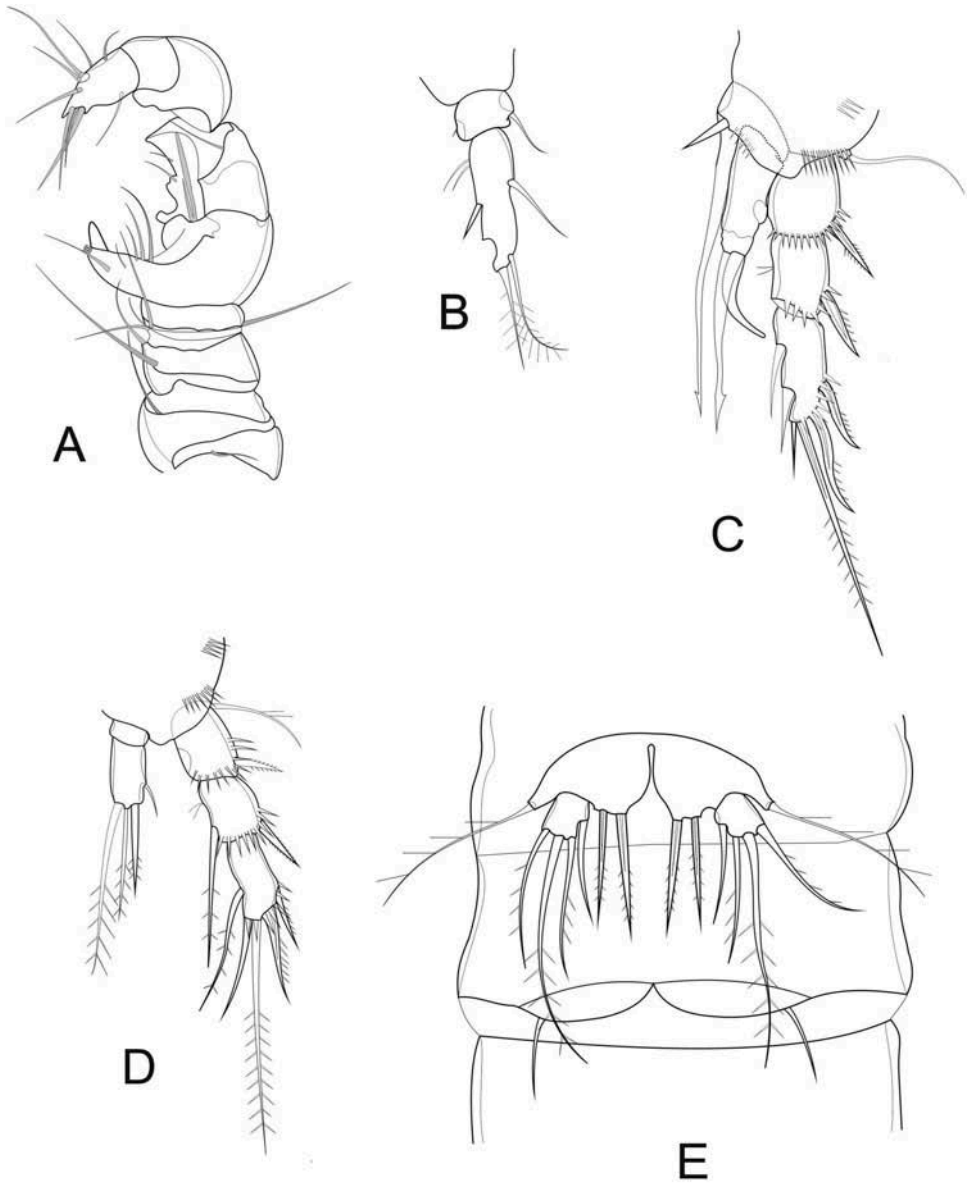


Figure 7. *Maraenobiotus slovenicus* sp. nov., line drawings, (A–C) holotype female; (D, E) allotype male: (A) genital segment with attached spermatophore, ventral; (B) last urosomite, anal somite and furcal rami, ventral; (C) last urosomite, anal somite and furcal rami, dorsal; (D) last urosomite, anal somite and furcal rami, ventral; (E) anal somite and furcal rami, dorsal.



100 μ m (A - E)

Figure 8. *Maraenobiotus slovenicus* sp. nov., line drawings, allotype male: (A) antennule, dorsal; (B) Endp P2; (C) P3; (D) P4; (E) P5 and P6.

spinules; ventrally four groups of long and slightly curved spinules (Figures 1A, G, 7B, C).

Anal operculum large, rounded, overreaching distal end of anal somite, with some 20 well developed spinules along distal margin (Figures 1A, G, 7B, C). Ventral side with additional row of minute spinules. Anal operculum about 58% of total anal somite width.

Caudal rami conical, slightly diverging, with inner and outer margins slightly convex; ramus as long as wide, with no dorsal keel (Figures 1A, G, H, 2E, 7B, C). Inner distal corner dorsally with 6–10 strong spines, ventrally inner corner with row of long and slightly curved spinules followed by smaller spinules toward outer corner. Anterolateral external accessory seta (I) slightly shorter than furcal ramus, inserted close to base; anterolateral external accessory seta (II) shorter than seta I and thin. Posterolateral seta (III) positioned below insertion of outer terminal seta (IV), shorter than seta II, very thin. Outer terminal seta (IV) reduced to minute knob, heavily chitinized. Inner terminal seta (V) reduced to minute knob, bigger than seta IV, heavily chitinized. Inner accessory seta (VI) reduced, not discernible from nearby spines. Dorsal seta (VII) slightly longer than caudal ramus, inserted on internal side, at about mid length.

Antennule (Figures 1B, C, D, 2F, 5A) relatively short, eight-segmented. Aesthetasc on fourth segment cylindrical, with rounded tip, reaching base of 8th segment. Second aesthetasc on terminal segment as long as first, slim. Both aesthetascs combined as acrothec (common base of spine and aesthetasc). Setal formula: 1.7.5.2.1.2.2.8. Length ratio of antennular segments from proximal to distal end and along caudal margin 1:2:1.4:1:1:1.4:1:2.2.

Antenna (Figures 2B, 5B) with allobasis, and robust, one-segmented Exp and Endp. Three strong spines on outer margin of Endp, increasing in length distally; terminal armature consisting of one short spine, one twice as long as short spine, and four geniculate setae. Exp with four spiniform setae, one ornamented with spinules on one margin.

Mandible (Figure 5C) short and robust, with two strongly chitinized teeth on gnathobase. Dorsal seta near gnathobase. Mandibular palp very short, fused with coxa, with five setae, one of them twice as long as the other.

Maxillule (Figure 5D) with strong and robust spines on praecoxal arthrite. Coxa with strong, chitinized spine and slim seta. Basis with strong, beak-like outgrowth, with long seta and long setules unilaterally. Exp and Endp reduced, fused with basis; each represented by two weak setae.

Maxilla (Figure 5E) two-segmented; syncoxa with 2 endites with 3 and 2 elements. Basis with strong spine and long seta. Endp reduced to three setae.

Maxilliped (Figure 5F) comprising syncoxa, basis, and one-segmented Endp. Syncoxa with seta distally. Basis three times as long as wide, with 8–10 spinules positioned near palmar margin dorsally, equal in length. Endp drawn out into strong, acutely curved claw; as long as basis and armed with several spinules in distal half; additional armature represented by a short seta.

P1 (Figures 3B, 6A) with two-segmented Exp and Endp, equal in length. Basis with strong and robust inner spiniform seta and stout outer basal spine. Exp-1 with strong outer spine; Exp-2 with two strong spines laterally, spine and two long geniculate setae terminally; inner terminal seta longer than Exp. Endp-1 with long seta on inner margin at two thirds length. Endp-2 terminally with three setae;

innermost short and soft, terminal seta long and geniculate, outer one spiniform, with spinules on outer margin.

P2 (Figures 3B, 6B) on basis with spiniform outer seta. Three-segmented Exp and two-segmented Endp. Endp as long as Exp-1 and Exp-2 combined. Exp-1 1.3 times as long as wide, with strong spine at distal corner. Exp-2 with strong outer spine. Exp-3 twice as long as wide, with two outer spines, terminal spiniform seta with strong spinules unilaterally and slim and bare seta, as long as spiniform seta. Endp-1 as long as wide, with seta on inner margin, at about two thirds of segment length. Endp-2 twice as long as wide, with seta along inner margin at half length of segment. Terminally two long soft setae, sub-equal in length; robust spiniform outer terminal seta, as long as Endp-2.

P3 (Figures 2G, 3B, 6C) with long and thin outer basal seta. Three-segmented Exp and two-segmented Endp. Endp slightly shorter as Exp-1 and Exp-2 combined. Exp-1 and Exp-2 similar to that of P2. Exp-3 with relatively weak spine on 2/3 of outer margin, robust spine subterminally and two robust setae terminally. Additional two robust setae on inner margin at 1/3 and 2/3 length of segment, respectively. Endp two-segmented; Endp-1 as in P2. Endp-2 with a row of strong spines on outer margin. Terminally two long soft setae, sub-equal in length; robust spiniform outer terminal seta, as long as Endp-2; two long and weak setae on inner margin at 1/3 and 2/3 length of segment, respectively.

P4 (Figures 2G, 6D) with outer basal seta long and thin, with additional very long and thin spinules. Three-segmented Exp and two-segmented Endp. Endp reaching about to middle of Exp-2. Exp-1 and Exp-2 similar to those of Pa and P3 but with additional robust seta on inner distal corner of Exp-2. Exp-3 twice as long as wide, with relatively weak spine located subterminally on outer margin. Terminally two long soft setae, sub-equal in length; robust spiniform outer terminal seta, shorter than Exp-3; long seta on inner margin at half length of segment, respectively. Endp-1 as wide as long, smaller as in P2 or P3 respectively. Spine on inner margin with distinct long spinules. Endp-2 with short spine on outer margin, at 2/3 of segment length. Terminally robust spiniform seta on outer position and two setae unequal in length. Seta on inner margin at mid length of segment.

P5 (Figures 2D, H, 3A, 6E) Exp and baseoendopod not distinctly separated; baseoendopodal lobe well developed, with four strong pinnate spines of unequal length; innermost three increasing in length toward outside; outermost shortest, Exp lobe longer than baseoendopodal, as long as wide, with three apical setae of unequal length; innermost shortest, with strong spinules; medial longest, with strong spinules; outer one bare. Outer lateral seta on baseoendopodal lobe long and bare, but one very long setula.

P6 (Figure 7A) fused, small, forming simple plate; each with thin seta with several long setulae.

Male, body length, measured from tip of rostrum to posterior margin of caudal rami, 524–554 μm ; average: 543 μm ($n = 4$), elongated, widest at distal part of cephalosome, rest of body slightly narrower, evenly tapering toward anal somite, colourless (Figure 3C, D, E). Naupliar eye not discernible. Rostrum small. Integumental window not discernible. Posterior margins of thoracic and abdominal somites dorsally and ventrally smooth (Figures 3D, E). Short row of small spinules laterally on first urosomal somite; continuous row of small spinules dorsally on second urosomal somite (Figure 4F); third urosomal somite dorsally with three

groups of small spinules; fourth and fifth urosomal somite dorsally with four groups of small spinules, laterally with longer spinules; fourth urosomal somite ventrally with continuous row of spines equal in length; fifth urosomal somite ventrally with continuous row of spinules unequal in length (Figures 3C, E, 7D). Anal somite laterally with short row of strong spinules; ventrally row of spines between bases of furcal rami (Figures 3E, 4G, 7D). First and second urosomite with cuticular window each; large pore next to cuticular window on first urosomite (Figures 3D, 4F, H).

Anal operculum well developed, rounded, overreaching distal end of anal somite, with about 10 well-developed spinules along distal margin (Figure 7D, E).

Caudal rami almost rectangular, slightly longer than wide, diverging; outer margin slightly convex; with no dorsal keel (Figures 3C, E, 7D, E). Ventrally row of spinules at distal part of ramus (Figures 3E, 7D). Anterolateral external accessory seta (I) thin, slightly longer than ramus, inserted at 1/3 of ramus length (Figures 4G, 7D, E); anterolateral external accessory seta (II) as long as seta I, thin; positioned at distal corner of ramus. Posterolateral seta (III) absent. Outer terminal seta (IV) about 4 times as long as seta II, with fracture plane. Inner terminal seta (V) about 2.5 times as long as seta III, straight, robust, with fracture plane. Inner accessory (VI) slightly longer than seta I. Dorsal seta (VII) slightly longer than caudal ramus, inserted on internal side, at about mid length.

Antennule (Figures 3C, F, G, H, 4C, E, 8A) relatively short, robust, nine-segmented, strongly chitinized. Geniculated articulation between sixth and seventh segments. Aesthetasc on fifth segment cylindrical, short, does not extend over fifth segment, aesthetasc on ninth segment spine-like. Both aesthetascs combined as acrothec (common base of spine and aesthetasc). Proximal part of fifth segment extended medially, with strong chitinous tooth at inner corner (Figures 3F, H, 8A). Setal formula: 0.1.1.2.9.3.0.0.9.

Antenna, mandible, maxillule, maxilla, maxilliped, P1 similar to those in female.

P2 (Figure 8B): Exp similar to female. Endp two segmented. Endp as long as Exp-1 and Exp-2 combined. Endp-1 0.75 times as long as wide, with seta on inner distal corner. Endp-2 three times as long as wide, with seta along inner margin at 1/3 length of segment. Terminally two soft setae, sub-equal in length, slightly shorter than segment; well-formed incision present on inner margin subterminally; at half length of segment on inner margin short spine, and at 1/4 two long spinules.

P3 (Figure 8C) with long and thin outer basal seta. Three-segmented Exp and two-segmented Endp. Endp reaching middle point of Exp-2. Exp-1 and Exp-2 similar to that of female. Exp-3 with relatively weak spine on 2/3 of outer margin, robust spine subterminally, long robust outer seta and short inner spiniform seta terminally. Additional two robust bare spiniform setae on inner margin at 1/3 and 2/3 length of segment, respectively. Endp two-segmented; Endp-1 with long spear-like apophysis, reaching tip of Exp-3. Endp-2 with relatively short blunt spine curving outward and spear-shaped seta as long as spear-like apophysis of Endp-1.

P4 (Figures 3D, 8D) with outer basal seta long and thin, with additional two very long and thin spinules. Three-segmented Exp and two-segmented Endp. Endp extending just beyond Exp-1. Exp armature similar to female but less robust. Endp-1 half as wide as long, with no spine/seta on inner margin. Endp-2 with short spine on outer margin, at 2/3 of segment length. Terminally spiniform seta on outer position and two setae unequal in length. No seta on inner margin.

P5 (Figures 3D, 4F, 8E) Exp and baseoendopod well separated; baseoendopod well developed, with two strong pinnate spines of unequal length; inner longer. Exp longer than baseoendopod, as long as wide, with four elements; inner three setae increasing in size toward outside; innermost seta bare; medial with unilateral spinules, outer with strong spinules bilaterally. Outermost seta as long as second innermost seta, with unilateral spinules. Outer lateral seta long with few long setules unilaterally.

P6 (Figures 3D, 4F, 8E) fused, small, forming simple plate; each with thin bare seta.

Variability

No variability was observed other than minor variation in the number of spinules on the abdominal somites.

Etymology

The new species is named after Slovenia, where the specimens were collected for the first time.

Remarks

This Slovenian new species undoubtedly belongs to the *Maraenobiotus vej dovskyi* complex, which is mostly defined by the armature formula of its appendages (Lang 1948). Its truncated female principal caudal setae would put it close to *Maraenobiotus vej dovskyi truncatus* Gurney, 1932, but a closer examination of this subspecies (which is elevated to the full specific rank below) and detailed comparison with our population reveals a number of significant differences. For example, *M. vej dovskyi truncatus* has a much shorter anal operculum than *M. slovenicus* sp. nov., which is ornamented with minute spinules (versus long spinules in *M. slovenicus*). Also, *M. vej dovskyi truncatus* has no distal lateral caudal setae in female (versus well-developed setae in *M. slovenicus*), and the transformed Endp of the male third leg has but a single apical element (versus two apical elements in *M. slovenicus*). Unfortunately, many other characters could not be compared because of a limited set of illustrations provided by Gurney (1932) for *M. vej dovskyi truncatus*. There are three other reported and illustrated populations from this complex with truncated female principal caudal setae, one from Japan (Ishida 1987) and two from Italy (Pesce et al. 1994), which we describe below as new species. However, both *M. ishidai* sp. nov. from Japan and *M. galassiae* sp. nov. from Italy (see below) have much longer and cylindrical caudal rami. *Maraenobiotus pescei* sp. nov. from Italy (see below), however, has caudal rami very similar in shape to those of *M. slovenicus*, but the two differ in the lateral armature of the caudal rami (lateral setae very reduced or absent in *M. pescei* versus well developed in *M. slovenicus*), number and size of spinules on the anal operculum (longer and fewer in *M. slovenicus*), segmentation of the antennal Exp (two-segmented in *M. pescei* versus one-segmented in *M. slovenicus*), number of apical elements on the second Endp segment of the male P3 (one in *M. pescei* versus two in *M. slovenicus*), and relative length of Endp spine on the male P5 (the inner one almost twice as long as the outer one in *M. pescei* versus nearly equal in *M. slovenicus*). Unfortunately, illustrations and descriptions of other four species are not as complete as those of *M. slovenicus*, so many morphological characters could not be compared.

Maraenobiotus ishidai sp. nov.

[partim.] *Maraenobiotus vej dovskyi* Mrázek – Ishida 1987: p. 83, fig. 14n.

Type locality

Japan, Hokkaido, Yoichi, 43.13° N, 140.44° E. Habitat data unknown.

Type material

Holotype female illustrated by Ishida (1987) in his figure 14n from the type locality, originally deposited in the author's private collection. Current location unknown. [not examined]

Etymology

The species name is dedicated to late Dr Terue Ishida, who discovered this specimen from Japan. The name is a noun in the genitive singular.

Description

Female as illustrated by Ishida (1987) in his figure 14n, as *Maraenobiotus vej dovskyi* Mrázek.

Remarks

This female specimen has truncated principal caudal setae as in *Maraenobiotus vej dovskyi truncatus* Gurney, 1932, but the caudal rami look very different in shape and size. They are cylindrical in dorsal view and almost twice as long as wide in *M. ishidai* sp. nov., while the caudal rami in *M. vej dovskyi truncatus* are almost conical in shape and about as long as wide. Also, in the latter species the distal lateral caudal setae seem to be either much reduced in size or absent, while they are well developed in the former. Finally, the anal operculum is much longer in *M. vej dovskyi truncatus* than in *M. ishidai*. There is very little chance that these very disjunct populations, with so vastly different caudal rami and anal operculum, could belong to the same species. In fact, *M. ishidai* differs so much from the other four species of *Maraenobiotus* with truncated female caudal setae, which are all European, that we believe there is a strong argument for them to be separate species. Its caudal rami are most similar in shape to those of the Italian *M. galassiae* sp. nov. (see below) and it may be plausible that the two have shared a recent common ancestor with a wide Holarctic range. Major differences involve the position of the dorsal caudal seta (nearly central in *M. galassiae* versus close to inner margin in *M. ishidai*), as well as the shape and inclination of the posterior margin of the ramus itself (convex and perpendicular to the body axis in *M. ishidai* versus straight and diagonal in *M. galassiae*). *Maraenobiotus ishidai* differs from *M. slovenicus* sp. nov. (see above) and *M. pescei* sp. nov. (see below) in the much longer and cylindrical caudal rami.

Unfortunately, we do not know which appendages illustrated by Ishida (1987) belong to this species, so they cannot be compared to other species from the *M. vej dovskyi* complex until the holotype has been found and redescribed.

Maraenobiotus pescei sp. nov.

[partim.] *Maraenobiotus vej dovskyi* Mrázek, 1893 – Pesce et al. 1994: p. 83, figs. 1–10.

Type locality

Italy, Abruzzo, L'Aquila, Gioia dei Marsi, temporary stream Fosso Perrone, a tributary of the river Sangro, epibenthic and interstitial habitat in organic detritus.

Type material

Holotype female, illustrated by Pesce et al. (1994) in their figures 1, 2, 5, 7, 9, 10; allotype male, illustrated by Pesce et al. (1994) in their figures 3, 4, 6, 8; both from the type locality, originally deposited in the Dipartimento di Scienze Ambientali, Università di L'Aquila, Via Vetoio 14, 67100 Coppito, L'Aquila, Italy. Current location the same, but condition not checked since the 2009 L'Aquila earthquake which damaged many slides (Prof. Diana M. P. Galassi, personal communication, July 2014). [not examined]

Etymology

The species name is dedicated to Prof. Giuseppe Lucio Pesce, who discovered these specimens in Italy with his collaborators. The name is a noun in the genitive singular.

Description

Female as illustrated by Pesce et al. (1994) in their figures 1–10, as *Maraenobiotus vej dovskyi* Mrázek, 1893.

Remarks

The female specimen of this Italian population has truncated principal caudal setae as in *Maraenobiotus vej dovskyi truncatus* Gurney, 1932, and the caudal rami look very similar in shape and size, except that the Italian population has slightly smaller caudal rami in proportion to the anal somite. However, *M. pescei* sp. nov. differs from *M. vej dovskyi truncatus* by much reduced (or absent) all lateral setae on the caudal rami, as well as by a much longer apophysis on the male Endp P3.

Maraenobiotus pescei differs from *M. slovenicus* sp. nov. also by very reduced (or absent) all lateral setae on the caudal rami, while the caudal rami of two other species from the *M. vej dovskyi* complex, *M. ishidaei* sp. nov. (see above) and *M. galassiae* sp. nov. (see below), are cylindrical and much longer.

Maraenobiotus galassiae sp. nov.

[partim.] *Maraenobiotus vej dovskyi* Mrázek, 1893 – Pesce et al. 1994: p. 83, figs. 18–27.

Type locality

Italy, Alto Adige, Croda di Cengles, I Laghetti, Seenlein, smaller lake, epibenthic and interstitial habitat in pebbles and coarse gravel.

Type material

Holotype female illustrated by Pesce et al. (1994) in their figures 18–27, from the type locality, originally deposited in the Dipartimento di Scienze Ambientali, Università di L’Aquila, Via Vetoio 14, 67100 Coppito, L’Aquila, Italy. Current location the same, but condition not checked since the 2009 L’Aquila earthquake, which damaged many slides (Prof. Diana M. P. Galassi, personal communication, July 2014). [not examined]

Etymology

The species name is dedicated to Prof. Diana M. P. Galassi, who discovered these specimens in Italy with her collaborators. The name is a noun in the genitive singular.

Description

Female as illustrated by Pesce et al. (1994) in their figures 18–27, as *Maraenobiotus vej dovskyi* Mrázek, 1893.

Remarks

This female specimen has truncated principal caudal setae as in *Maraenobiotus vej dovskyi truncatus* Gurney, 1932, but the caudal rami look very different in shape and size. They are cylindrical in dorsal view and almost twice as long as wide in *M. galassiae* sp. nov., while the caudal rami in *M. vej dovskyi truncatus* are almost conical in shape and about as long as wide. Also, in the latter species the distal lateral caudal setae seem to be either much reduced in size or absent, while they are well developed in the former. The caudal rami of *M. galassiae* are most similar in shape to those of the Japanese *M. ishidai* sp. nov. (see above) and it may be plausible that the two have shared a recent common ancestor with a wide Holarctic range (for major differences between them see above). *Maraenobiotus galassiae* differs from *M. slovenicus* sp. nov. (see above) and *M. pescei* sp. nov. (see above) by much longer and cylindrical caudal rami, among other things.

Discussion

As noted above, relationships among species and subspecies of *Maraenobiotus* are very complicated. In the absence of any fresh material to undertake a molecular

study, we have tried to reinterpret some old morphological data in the light of modern studies in other groups of copepods (Karanovic and Cooper 2012). Based on our study of numerous specimens of *M. slovenicus* sp. nov., we concluded that morphological variability in this population is very low. This especially refers to the truncated nature of the female caudal principal setae. However, this character was reported to be very variable in *M. vej dovskyi* s.l. (Gurney 1932; Lang 1948; Ishida 1987; Pesce et al. 1994), but the evidence for this was lacking (no sympatric forms with different caudal rami shape, except in one unsubstantiated statement by Ishida 1987). In addition to this, several subspecific categories have been described with parapatric or sympatric ranges (see Introduction), or those were implied by subsequent records, but never in the same locality. A more parsimonious explanation would be that we are actually dealing with a number of closely related but distinct species. Thus we formally elevate here to the full specific rank the following recognized subspecies of *M. vej dovskyi* Mrázek, 1893: *M. anglicus* Gurney, 1932; *M. arctica* Löffler; *M. tenuispina* Roy and *M. truncatus* Gurney, 1932.

Comparing *M. slovenicus* sp. nov. with other recognized (*M. truncatus*) and unrecognized (Ishida 1987; Pesce et al. 1994) morphotypes with truncated female principal caudal setae from the *M. vej dovskyi* s.l. complex, we conclude that they cannot be closely related. Thus we have named three new species here, based on previous illustrations (as their material was not available to us): *Maraenobiotus galassiae* sp. nov.; *M. isidai* sp. nov.; and *M. pescei* sp. nov. (see above). We conclude that this condition originated convergently probably in all cases, but at least in four instances (the Italian *M. galassiae* and the Japanese *M. isidai* may be an exception; see above). Testing this hypothesis using molecular phylogenies (as in Karanovic and Cooper 2011, 2012; Karanovic and Krajicek 2012) or those based on micro-morphological characters (as in Karanovic and Kim 2014) would be a priority for our future studies.

It is, however, unclear why this particular trait would evolve so many times in one species-complex, and why only in females and not in males. Some speculations we can offer would be a conservation of energy in the interstitial/semi-terrestrial environment, where they are not much needed, or, perhaps, to decrease mating pressure from males, because in canthocamptid harpacticoids (and many others) males grab female caudal setae with their antennules in the first act of copulation (Huys and Boxshall 1991). The unusually complicated three-dimensional structure on the male antennule in *M. slovenicus* (Figures 3F, G, H, 4C, E) is certainly well adapted for grabbing the reduced caudal rami of their females, which may be indicative of an evolutionary sexual conflict and arms races between the sexes.

Males and females of *M. slovenicus*, along with a few juveniles, appeared in a drift from a temporary spring, after a very cold and dry period in winter. This probably excludes the possibility that their origin is wet litter just next to the temporary spring. Most of specimens (males and females) were covered with dense colonies of sedentary protozoans (Ciliates), indicating that the population of *M. slovenicus* probably originated from a permanent water body inside the cave. The same phenomenon, where specimens were covered with dense colonies of epibionts, was observed on specimens of the genera *Morariopsis* Borutzky and *Bryocamptus* Chappuis from the epikarstic zone in the nearby cave Velika Pasica (Brancelj 2000; pers. obs.). However, epibionts on *M. slovenicus* were different from those on *Morariopsis dumonti* Brancelj, 2000, *Bryocamptus pyrenaicus* (Chappuis) and *B. typhlops* (Mrázek 1893), which were

exclusively Suctoria. Specific co-occurrence between epibionts and hosts indicates a long-lasting co-habitation rather than an opportunistic co-existence. At the same time, no such epibionts were observed on the accompanying copepod community.

Members of different ecological groups were collected in the drift along with *M. slovenicus*. There were few specimens of unidentified Turbellaria and Oligochaeta and numerous specimens of stygobiotic Amphipoda (*Niphargus stygius* (Schiodte)), which are typical inhabitants of springs and pools in caves. The most numerous were copepods. *Diacyclops clandestinus* (Kiefer), *D. langiudoides* (Lilljeborg), *Graeteriella unisetigera* (Graeter) and *Acanthocyclops robustus* (G.O. Sars) among Cyclopoida and *Bryocamptus pygmaeus* (Sars), *Epactophanes richardi* Mrazek, 1893 and *Moraria poppei* (Mrázek 1893) among Harpacticoida are common inhabitants of permanent groundwater habitats in fractured or porous aquifers or leaf-litter. *Speocyclops infernus* (Kiefer), *B. pyrenaicus*, *Elaphoidella millennii* Brancelj, 2009 and *M. dumonti*, all stygobionts (i.e. obligate cave dwelling species) are so far recognized as strict inhabitants of the epikarstic/vadose (i.e. unsaturated) zone (Brancelj 2000, 2002, 2009; Brancelj and Culver 2005). In springs they occur only accidentally, as a drift from epikarst (Brancelj 2002). One single female of *Parastenocaris* sp. with unknown habitat affinity was also collected there.

Such composition of the drift fauna indicates that the water from the temporary spring originates both from the epikarstic/vadose zone as well as from the local phreatic zone. The new *Maraenobiotus* species is probably a member of the phreatic (i.e. saturated) zone, because during our long-lasting sampling of the epikarstic zone in the nearby cave Velika Pasica no specimens of the new species were collected (Brancelj 2000, pers. obs.; Wei Liu and Brancelj Forthcoming 2015).

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