European Journal of Taxonomy 1086: 1–29
https://doi.org/10.5852/ejt.2026.1086.3317

europeanjournaloftaxonomy.eu
ISSN 2118-9773
2026 · Novikov A.A.

Received: 12 January 2026 • *Accepted: 11 May 2026* • *Published: 21 August 2026*

Topic editor: Magalie Castelin • *Section editor: Fabio Stoch* • *Desk editor: Pepe Fernández*

Research article

urn:lsid:zoobank.org:pub:3AAF6F39-BAD7-41E6-866B-99834A0708FA

Tatarocyclops dayanae — a new hyporheic genus and species of Cyclopidae (Copepoda, Cyclopoida) from the European part of Russia

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Abstract. A new genus and species of Cyclopidae (Copepoda, Cyclopoida) from the hyporheic zone of small rivers in Tatarstan (Russia) is described. The diagnosis of *Tatarocyclops dayanae* gen. et sp. nov. includes: female antennule 11-segmented; first to fourth swimming legs with two-segmented exopods and endopods; endopod of the fourth leg with two apical spines; and fifth leg two-segmented, not fused to the somite. The new genus shares a two-segmented fifth leg with *Reidcyclops* Karanovic, 2000, but differs from it and from other genera of the *Mixocyclops* Kiefer, 1944 group by the following combination: mandibular palp with one seta; maxilliped armature formula 2.2.1.2; first swimming leg basis with inner spine; spine formula of the second exopodal segments of the first to fourth swimming legs 2.3.3.3; third swimming leg without sexual dimorphism; fourth swimming leg endopod with two apical spines; and distal segment of the fifth leg with two setae. Among Cyclopidae with 9–11-segmented antennules, *Tatarocyclops* gen. nov. is distinctly separated by its unique combination of characters, especially the two-segmented fifth leg. The discovery of a stygobiotic cyclopid genus in the Middle Volga region aligns with recent findings of endemic amphipods in the same area and highlights a previously unexplored diversity of groundwater fauna, which is important for understanding the biogeography of Palearctic freshwater crustaceans.

Keywords. Groundwater, hyporheic fauna, *Reidcyclops*, *Speocyclops*, stygobiont, Tatarstan.

Novikov A.A. 2026. *Tatarocyclops dayanae* — a new hyporheic genus and species of Cyclopidae (Copepoda, Cyclopoida) from the European part of Russia. *European Journal of Taxonomy* 1086: 1–29.
https://doi.org/10.5852/ejt.2026.1086.3317

Introduction

The hyporheic zone, a dynamic ecotone between surface water and groundwater, is a unique and fragile transitional habitat that harbors specialized fauna. Stygobiotic and stygophilic crustaceans, particularly copepods, are key components of these communities (Sabater & Vila 1992). Their high endemism, relictual nature, and sensitivity to environmental change make them subjects of significant

ecological and biogeographical interest (Galassi 2001; Di Cicco *et al.* 2021). Among these, species of the family Cyclopidae Rafinesque, 1815, including those from the genera *Diacyclops* Kiefer, 1927 and *Acanthocyclops* Kiefer, 1927, constitute an important part of the global freshwater hyporheic fauna (Monchenko 1974).

Despite its biodiversity potential, the stygofauna of the European part of Russia remains poorly studied. Existing faunal lists, such as those for Tatarstan, record a limited number of copepod species, most of which belong to the planktonic or benthic assemblages. For instance, only 11 out of 69 recorded copepod species in Tatarstan are harpacticoids (Tokinova & Berdnik 2021), a group associated with bottom substrates. Sampling hyporheic and phreatic fauna requires specialized techniques and has therefore been largely overlooked. In the 20th century, prominent researchers of groundwater copepods in the former USSR, namely Borutzky and Monchenko, focused their efforts on regions such as Central Asia, the Caucasus, and Crimea (Borutzky 1972a, 1972b; Monchenko 1972, 1983). For the European part of Russia, available records from underground habitats predominantly comprise common surface-water species (stygoxenes), such as *Diacyclops bicuspidatus* (Claus, 1857) and *Acanthocyclops vernalis* (Fischer, 1853) (Cyclopoida, Cyclopidae) (Turbanov *et al.* 2016). The only reported true stygobiotic copepod, *Parastenocaris fonticola* Borutzky, 1926 (Harpacticoida, Parastenocarididae), was described a century ago from a well in Moscow, based on a single female specimen (Borutzky 1926), and its taxonomic status remains unclear because it has never been rediscovered. Even recent faunistic studies in the region, while noting the presence of stygobiotic taxa, report them only as unidentified morphotypes, mainly due to a shortage of taxonomic expertise. For example, an unidentified species of the family Parastenocarididae Chappuis, 1940 (Harpacticoida) was recorded from springs near Kazan (Berdnik *et al.* 2024).

This lack of knowledge in Russia stands in stark contrast to the active global exploration of groundwater copepod diversity. The period from 2010 to 2020 was particularly prolific, witnessing the description of 14 new genera of Cyclopidae worldwide, several of which from subterranean habitats (Fiers 2011; Karanovic *et al.* 2011; Totakura & Ranga Reddy 2015; Boonyanusith *et al.* 2018; Sanoamuang *et al.* 2019). Furthermore, recent studies in the Volga River basin have begun to reveal a previously undocumented stygobiont diversity, with the discovery of endemic groundwater amphipod species belonging to the genera *Volgonyx* Marin & Palatov, 2021 and *Uralocrangonyx* Marin & Palatov, 2022 (Malacostraca, Amphipoda, Crangonyctidae) (Marin & Palatov 2024a). These findings challenge the perception of the region as biologically depauperate in groundwater fauna and highlight a significant taxonomic bias: while some crustacean groups are being documented, the copepod fauna, especially Cyclopidae, in these habitats remains virtually unexplored.

Given this context, preliminary sampling of the hyporheic zone of small rivers in Tatarstan confirmed the presence of a diverse stygobiotic and stygophilic assemblage, including previously undescribed taxa. The main objective of this paper is to describe a new genus and species of cyclopid copepod collected from these habitats. This discovery not only extends the list of copepods from the region but also contributes to our understanding the biogeography and evolution of stygobiotic cyclopids in Eastern Europe.

Material and methods

The material was collected between 2020 and 2023 in the vicinity of Naberezhnye Morkvashi village (Republic of Tatarstan, Russia) (Fig. 1A–B). Hyporheic fauna was sampled using the Karaman-Chappuis method (Karaman 1935; Chappuis 1942), which involves digging a pit (50–70 cm deep) near the water's edge (Fig. 1C–D) and filtering the interstitial water that seeps into it. Water from the pit was filtered through a small plankton net (mesh size 80 μm). To remove silt, the net was rinsed carefully in the adjacent stream, avoiding direct flushing of stream water into the net. Samples were fixed in 4% formalin. A total of five samples were collected (Table 1).

Specimens were dissected under a stereo microscope, with each element being placed under a separate coverslip. Preliminary drawings were made from printed photographs, and final illustrations were prepared using Adobe Photoshop. Congo red staining and fluorescence microscopy were used to image the habitus. To stain the specimens, they were first washed in distilled water, and then kept in Congo red (1.5 mg per 1 ml) for 24 hours. Next, the crustaceans were transferred to glycerol and covered with a coverslip. For observations, we used a ZEISS Axio Imager M2 microscope with filter settings: excitation BP 460–490 nm; beamsplitter FT 495 nm; emission BP 500–600 nm. Under these conditions, Congo red fluoresces yellow, and chitin emits green autofluorescence (Novikov *et al.* 2024). Photographs were taken using z-stacking.

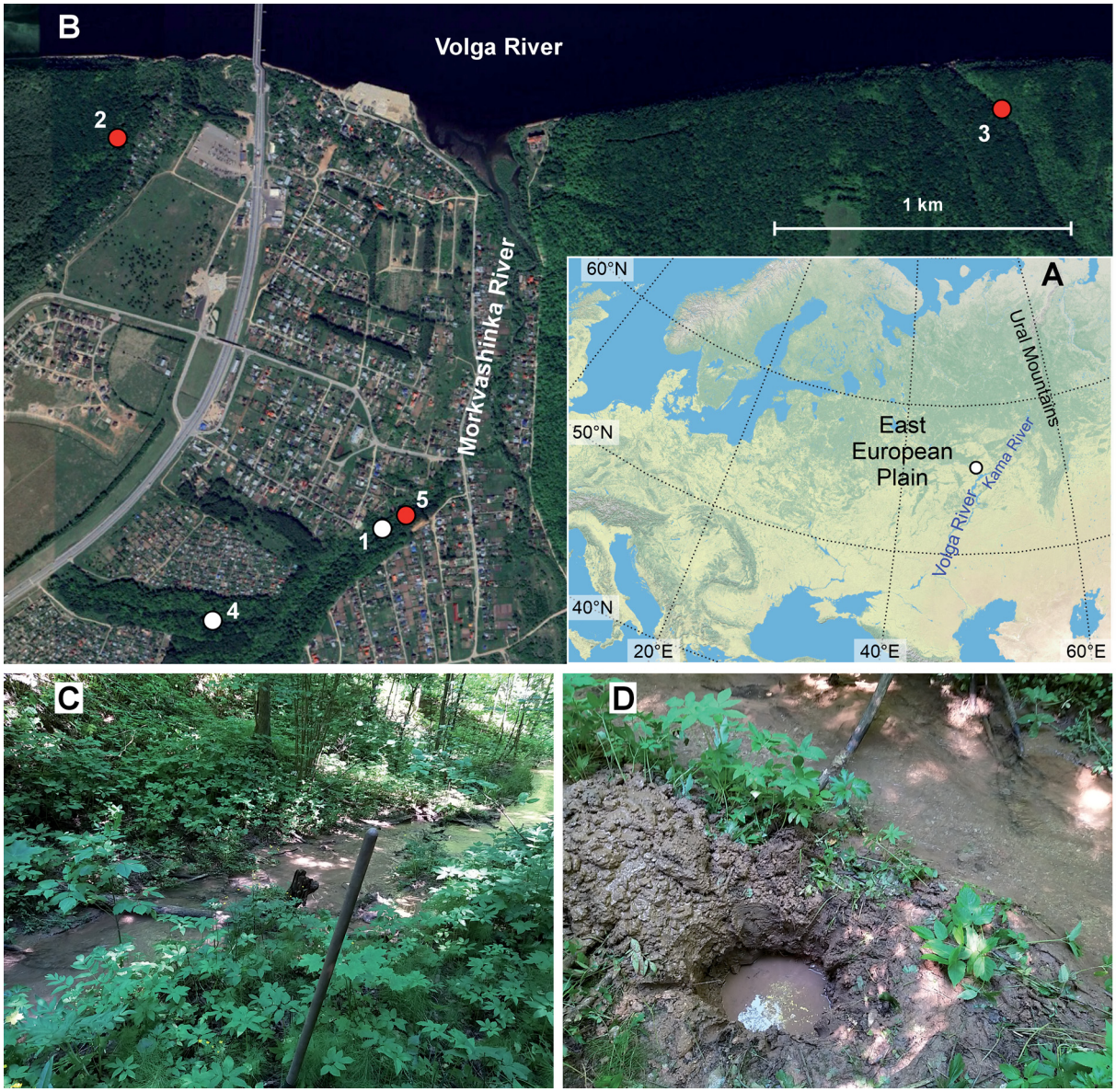

Fig. 1. Map of the study area and sampling sites. **A**. Partial map of Europe (base map: Esri) showing the position of sampling sites (white dot). **B**. Detailed map of the sampling sites near Naberezhnye Morkvashi village (base map: Google Earth); white dots: locations where stygobionts were found; red dots: locations where no crustaceans were detected or only stygophilic species occurred. **C**. Morkvashinka River at sampling site 1. **D**. The Karaman-Chappuis pit at site 1.

Table 1. List of all samples from the vicinity of the Naberezhnye Morkvashin village.

No	Latitude N°	Longitude E°	Date	Sample
1	55.76797	48.84678	17 Jun. 2020	Morkvashinka River
2	55.77972	48.83262	29 Aug. 2022	Ravine without stream
3	55.78059	48.87996	30 Aug. 2022	Stream in ravine
4	55.76538	48.83707	4 Sep. 2022	Stream flowing into the Morkvashinka River
5	55.76836	48.84804	24 Aug. 2023	Morkvashinka River

Nomenclature and descriptive terminology follow Huys & Boxshall (1991). The armature formulae of swimming legs are given according to Sewell (1949). The terms frontal and caudal to describe the armament of antennal coxobasis are used according to Van de Velde (1984). Terminology and homology of maxillary structures follow Ferrari & Ivanenko (2008). The numbering of the groups of spinules on the posterior side of the P4 coxa is given according to Einsle (1985). The term "proctodeum" is used here for the distal portion of the hindgut in the vicinity of the anus (Hołyńska 2006).

Abbreviations used in the text: ae = aesthetasc; P1–P6 = legs 1–6.

The material was deposited in the Zoological Museum of Kazan Federal University (EMKSU: VH 2002/1, VH 2002/2, VH 2002/3, VH 2002/4, VH 2002/5, VH 2002/6).

Results

Subclass Copepoda H. Milne Edwards, 1840
Order Cyclopoida Burmeister, 1834
Family Cyclopidae Rafinesque, 1815

Genus ***Tatarocyclops*** gen. nov.
urn:lsid:zoobank.org:act:F879D5E5-94A9-483D-BE5A-1CBA8717D75E

Type species

Tatarocyclops dayanae gen. et sp. nov., by monotypy.

Diagnosis

A monotypic genus. The diagnosis of the genus is identical to that of its type and only species, *Tatarocyclops dayanae* gen. et sp. nov., provided below.

Etymology

Masculine. The prefix 'Tataro-' refers to Tatarstan, where the genus was discovered, combined with the genus name *Cyclops*.

Tatarocyclops dayanae gen. et sp. nov.
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Figs 2–10, 11E

Diagnosis

Small representative of family Cyclopidae. Female genital somite and third urosomite fused, no signs of articulation between original urosomites. P6 lateral. Anal operculum triangular. Caudal rami length/width ratio 1.9. Antennule 11-segmented. Antenna without exopodal seta; second endopodal segment with six

setae. Mandible with small palp with one seta. Maxilliped four-segmented; setal formula 2.2.1.2. P1–P4 with two-segmented exopods and endopods; with coxal setae. P1 with inner spine of basis. Spine formula of P1–P4 second exopodal segments: 2.3.3.3; setae formula: 5.4.4.4. P4 second endopodal segment with outer seta, two apical spines, two inner setae. P1–P4 without sexual dimorphism. P5 two-segmented, not fused with somite; apical segment with two setae.

Etymology

The species is named after Dayana N. Sharafutdinova (Kazan Federal University), my wife, in whose home village this species was discovered.

Type material

Holotype

RUSSIA • ♀, dissected on two slides; Republic of Tatarstan, Naberezhnye Morkvashi Village, hyporheic zone of Morkvashinka River; 55.767969° N, 48.84678° E; 17 Jun. 2020; A. Novikov leg.; EMKSU VH 2002/1, VH 2002/2.

Paratypes

RUSSIA • 1 ♂, dissected on two slides; same collection data as for holotype; EMKSU VH 2002/3, VH 2002/4 • 1 ♀, dissected on one slide; same collection data as for holotype; EMKSU VH 2002/5 • 1 ♂, dissected on one slide; Republic of Tatarstan, Naberezhnye Morkvashi Village, stream flowing into the Morkvashinka River; 55.765376° N, 48.837075° E; 4 Sep. 2022; A. Novikov and D. Sharafutdinova leg.; Karaman-Chappuis pit; EMKSU VH 2002/6.

Description

Female

Habitus and measurements. Body wide and flattened (Figs 2A–C, 3A). Total body length of holotype from anterior margin of rostrum to posterior margin of caudal rami: 530 µm. Cuticle of somites slightly pitted. Cephalothorax not wider than first free somite, surface with pores and sensilla. Naupliar eye not discernible in preserved specimens. Rostrum fused with cephalothorax. Posterior margin of cephalothorax and all pedigerous somites smooth.

Urosome (Fig. 4). Consisting of fifth pediger, genital-double somite, two free urosomites and anal somite with caudal rami. All somites except anal somite on free posterior margin slightly serrated (Fig. 4). Genital-double somite composed of sixth thoracic somite and first abdominal somite; wider than long; length/width ratio 0.75; anterior part with pair of sensilla dorsally, unpaired pore dorsally and pair of pores near genital field ventrally; posterior part with unpaired pore dorsally and one pair of pores and one pair of sensilla ventrally.

P6 (Fig. 4A, C). Lateral, fused with anterior part of genital-double somite; with one long pinnate seta dorsally, one bare seta in the middle and small spiniform process ventrally. Genital field (Fig. 4B) wide, oval. Egg sacs not observed.

Third urosomite (Fig. 4A–C). With unpaired pore dorsally and pair of pores ventrally. Fourth urosomite (Fig. 4A–C) with unpaired pore dorsally. Anal somite (Fig. 4A–C) with one pair of sensilla dorsally, pairs of pores ventrally and laterally and rows of small spinules ventrolaterally; proctodeum with spinular rows. Anal operculum strongly protruding, triangular, serrated along free margin.

Caudal rami (Fig. 4A–C). Length/width ratio 1.9, with pair of pores at ¼ caudal ramus length ventrolaterally; with spinules at base of setae II and III. Seta I absent. Setae II bare, located dorsolaterally. Seta III strong, bipinnate. Apical setae IV and V (Figs 3A, 4A) long, bipinnate, with fracture planes;

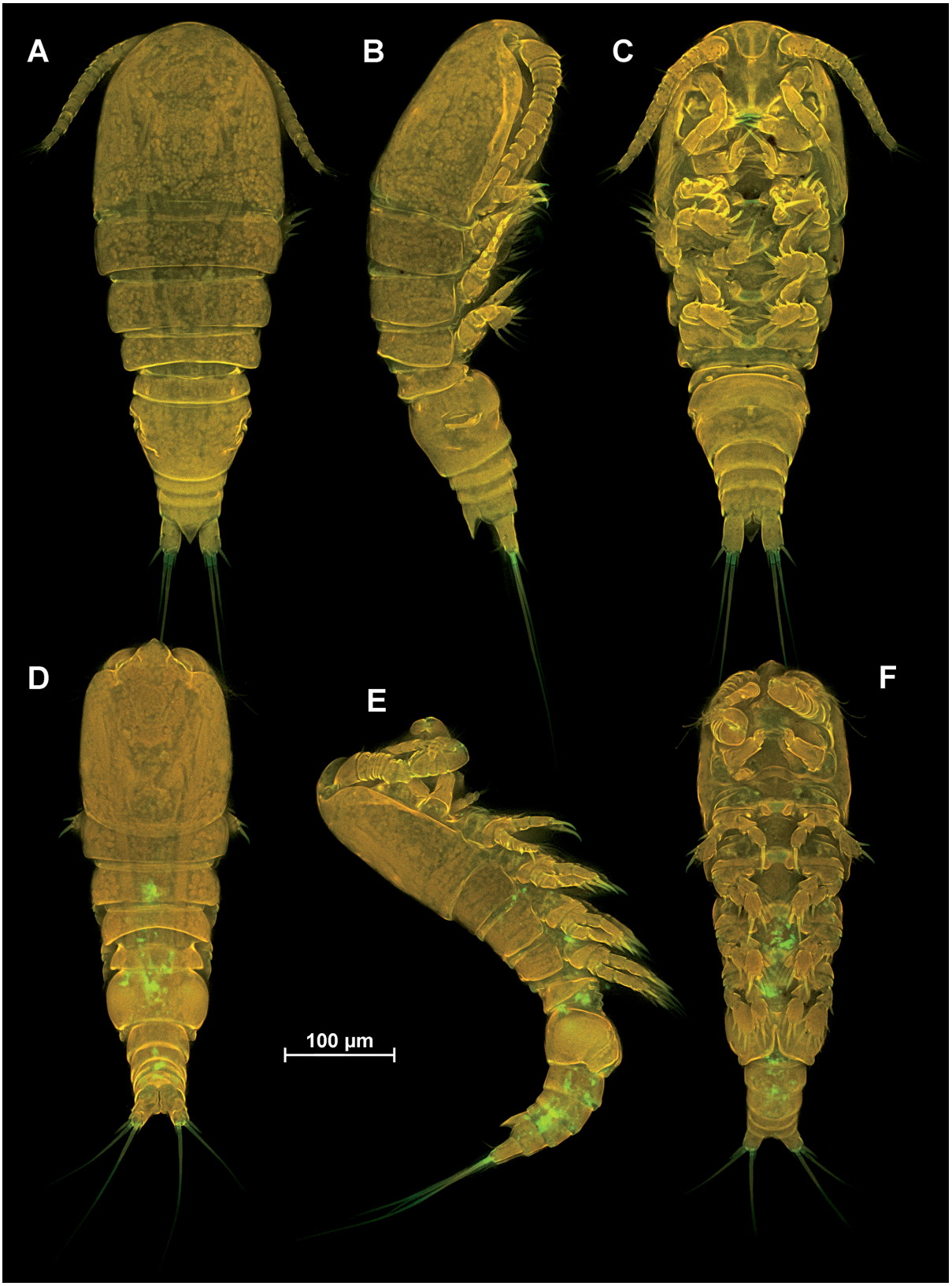

Fig. 2. *Tatarocyclops dayanae* gen. et sp. nov., habitus. **A–C**. Paratype, ♀ (EMKSU VH 2002/5). **A**. Dorsal view. **B**. Lateral view. **C**. Ventral view. **D–F**. Paratype, ♂ (EMKSU VH 2002/3–4). **D**. Dorsal view. **E**. Lateral view. **F**. Ventral view.

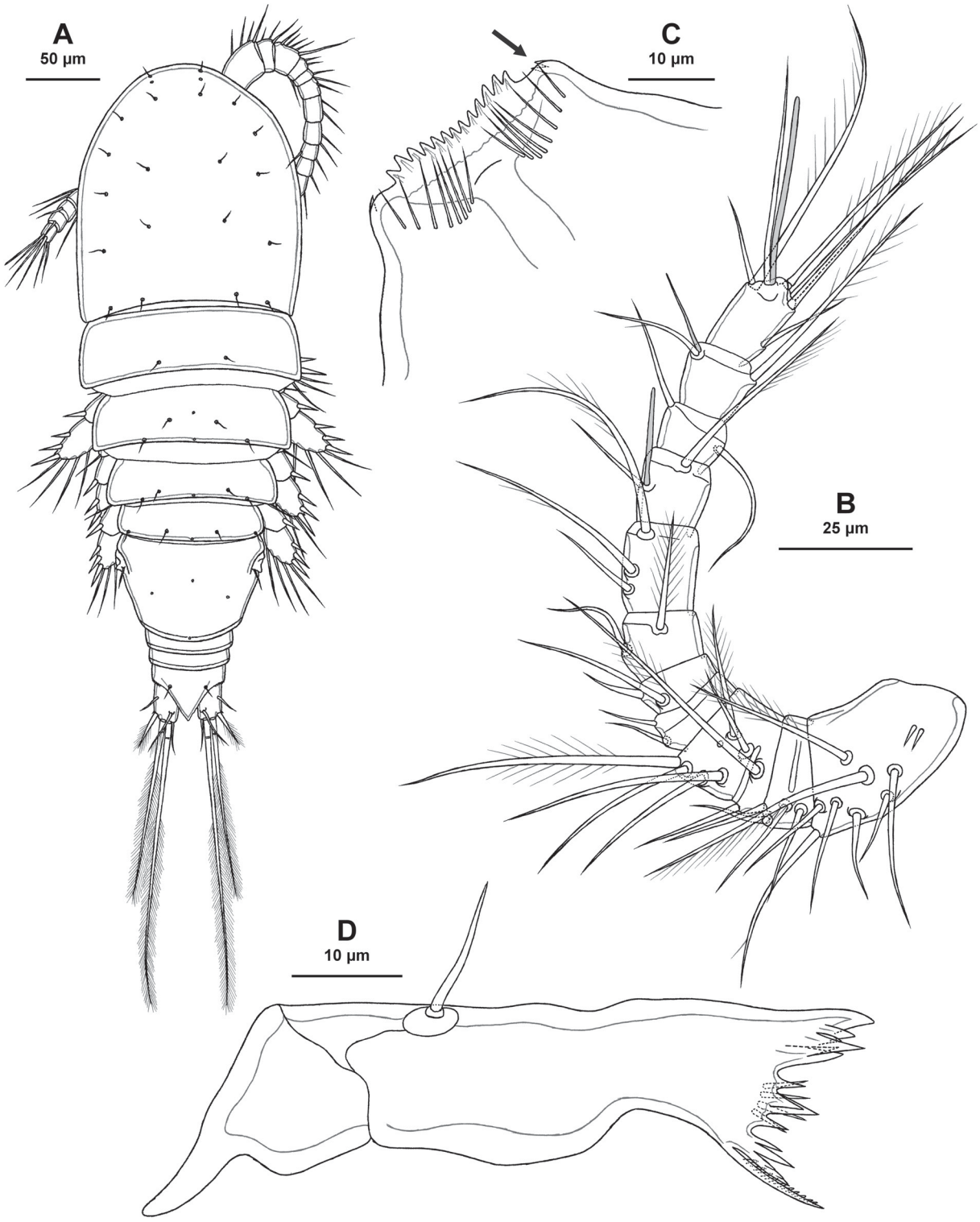

Fig. 3. *Tatarocyclops dayanae* gen. et sp. nov., holotype, ♀ (EMKSU VH 2002/1–2). **A**. Habitus, dorsal view. **B**. Antennule, posterior view. **C**. Labrum, anterior view, small lateral denticles (arrow). **D**. Mandible.

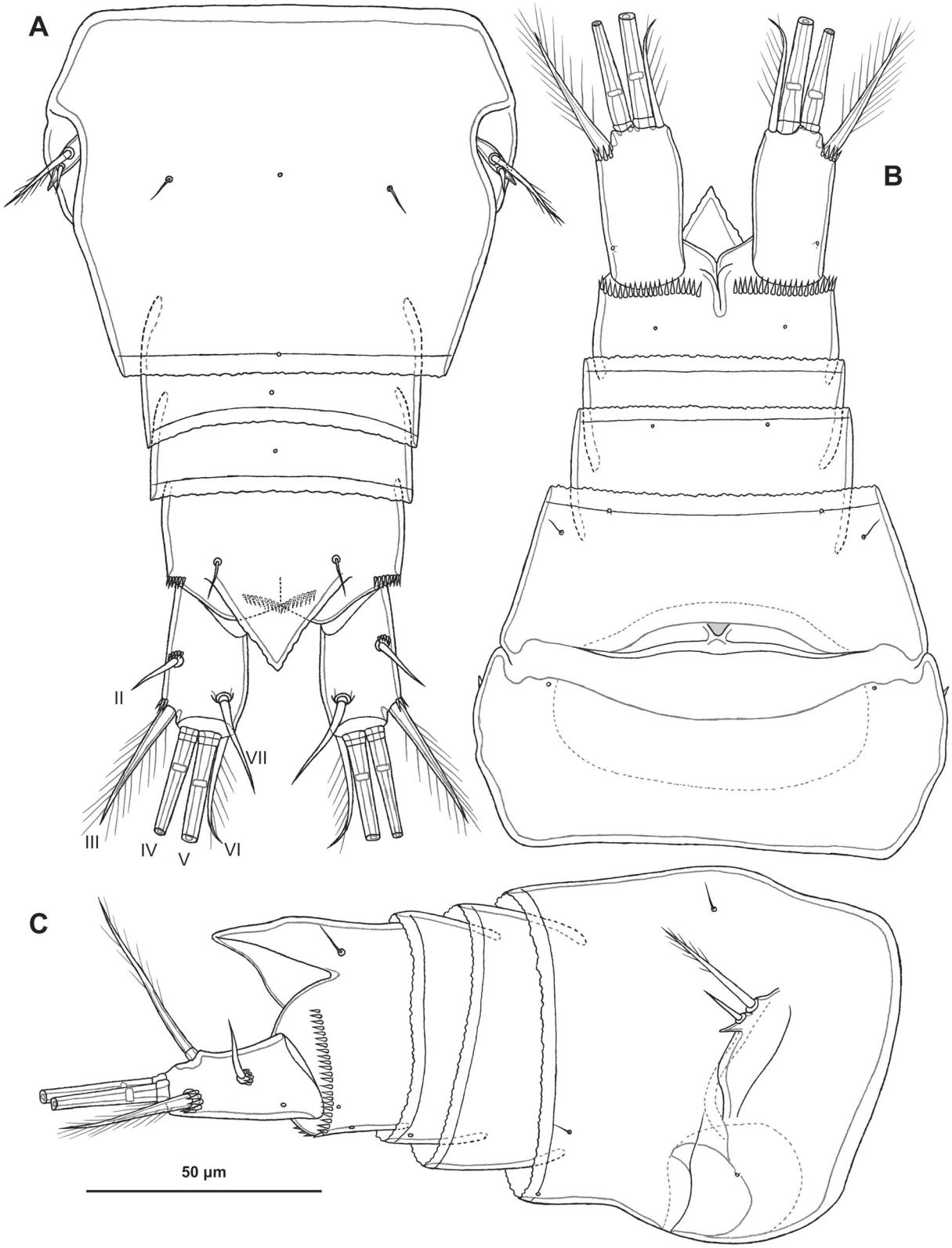

Fig. 4. *Tatarocyclops dayanae* gen. et sp. nov., holotype, ♀ (EMKSU VH 2002/1–2), second–fifth urosomites. **A**. Dorsal view. **B**. Ventral view. **C**. Lateral view.

seta V about 1.55 times as long as seta IV. Seta VI shorter than seta III. Seta VII articulated; located at ¾ caudal ramus length at inner side of ramus; slightly longer than ramus length (Fig. 4A, C).

Antennule (Fig. 3B). 11-segmented. Segment 1 with five bare and three pinnate setae and row of spinules proximally. Segment 2 with four bare setae. Segment 3 with clear semi-border between ancestral segments, with four bare and four pinnate setae, one pore (probably). Segment 4 with two small setae.

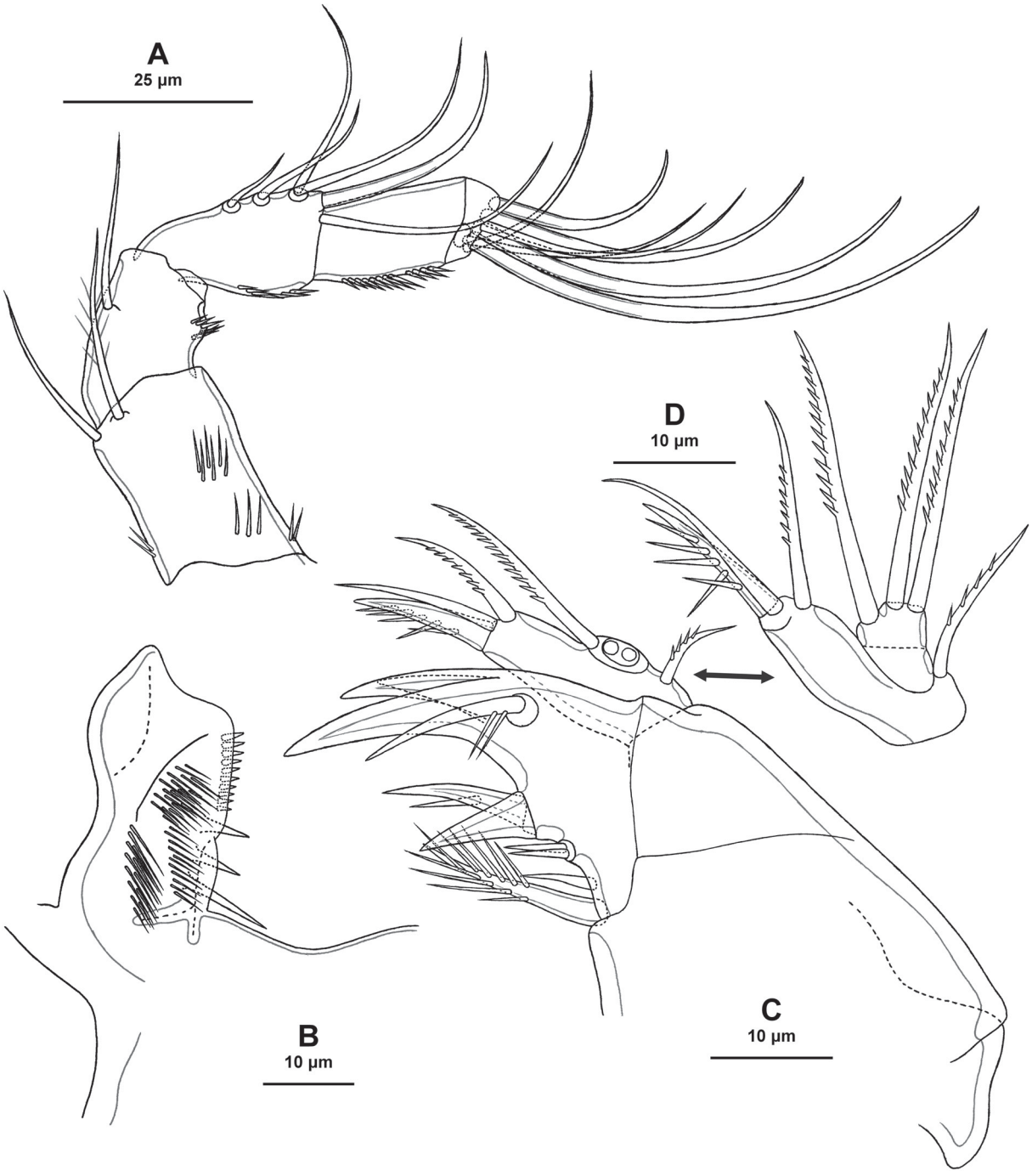

Fig. 5. *Tatarocyclops dayanae* gen. et sp. nov. **A, C–D**. Holotype, ♀ (EMKSU VH 2002/1–2). **B**. Paratype, ♀ (EMKSU VH 2002/5). **A**. Antenna, caudal side. **B**. Paragnaths, posterior view. **C**. Maxillule, posterior view. **D**. Maxillular palp, antero-lateral view.

Table 2. P1–P4 armature of *Tatarocyclops dayanae* gen. et sp. nov.

	Coxa	Basis	Exopod	Endopod
P1	0-1	1-I	I-0; II,2,3	0-1; 1,I+1,1
P2	0-1	1-0	I-0; II,I+1,3	0-1; 1,I+1,1
P3	0-1	1-0	I-0; II,I+1,3	0-1; 1,I+1,2
P4	0-1	1-0	I-0; II,I+1,3	0-1; 1,II,2

Segment 5 with one bare slender seta and one spiniform bare seta. Segment 6 with one bare and one pinnate seta. Segment 7 with proximal bare seta and two distal pinnate setae. Segment 8 with pinnate seta and aesthetasc close in base with bare seta. Segment 9 with two bare setae. Segment 10 with pinnate seta and aesthetasc close to base with bare seta. Segment 11 proximally with small bare seta; distally with four pinnate setae, one small bare seta and aesthetasc fused in base with bare seta, forming acrothek. Armature formula: 1-[8],2-[4],3-[8],4-[2],5-[2],6-[2],7-[3],8-[2+ae],9-[2],10-[2+ae],11-[6+(1+ae)].

Antenna (Fig. 5A). Four-segmented; short coxobasis and three-segmented endopod, without exopod. Coxobasis with two setae and three groups of spinules on posterior side. First endopodal segment with one seta and row of spinules on outer margin. Second endopodal segment with row of spinules along outer margin, five slender setae and one robust seta. Distal endopodal segment with two rows of spinules along outer margin, three slender and four robust setae apically.

Labrum (Fig. 3C). Trapezoidal. Anterior surface with two groups of long spinules. Distal margin with small denticles laterally and 13 blunt teeth apically.

Mandible (Fig. 3D). Composed of coxa and small palp. Palp represented by small segment with short seta. Gnathobase with cutting edge composed of three groups of teeth; spinulose seta proximally; row of four long spinules near middle group of teeth. Distal group with five teeth, middle group with four teeth, proximal group with three elongated teeth fused basally.

Paragnaths (Fig. 5B). With paired lateral lobes. Distal parts of lobes with folded outgrowths. Each lobe with three groups of setules on posterior side, row of spinules on inner margin and three long spines.

Maxillule (Fig. 5C–D). Composed of praecoxa and two-segmented palp. Praecoxal arthrite with long robust pinnate seta and small bare seta proximally; two small bare setae and two strong spines in the middle part; three strong teeth and pinnate seta distally. Palp comprising one-segmented coxobasis, one-segmented endopod and outer pinnate seta representing exopod. Coxobasis distally with two setae and one spine. Endopod with three unipinnate setae.

Maxilla (Fig. 6A). Five-segmented, composed of syncoxa, basis and three-segmented endopod. Syncoxa with endite with two long pinnate setae. Basis with two endites: proximal with one pinnate seta; distal with two pinnate setae. First endopodal segment with slender seta, strong subdistal pinnate seta and strong claw. Second endopodal segment with two strong setae, one of these serrate. Third endopodal segment with two slender setae and one strong serrate seta.

Maxilliped (Fig. 6B). Four-segmented, composed of syncoxa, basis and two-segmented endopod. Syncoxa short, with two unipinnate setae. Basis with two outer rows of spinules, row of spinules on anterior side; with two pinnate setae. First endopodal segment with long pinnate seta. Second endopodal segment with two pinnate setae.

P1–P4. Well developed, setae/spine armature as in Table 2. All setae of P1–P4 pinnate; all spines spinulose. Segments with rows of spinules near base of each spine. All exopodal segments with inner setules; all endopodal segments with outer setules.

P1 (Fig. 7A). Praecoxa naked. Coxa wide, with two distal spinular rows; one pore close to inner margin; one seta on distal inner corner. Intercoxal sclerite wide, with large lobes on distal margin, without ornamentation. Basis with pore close to outer margin, next to seta, rows of spinules at base of endopod and inner spine, inner row of setules; with long outer seta. Exopod two-segmented; first segment with spine on outer margin; second segment with one pore close to outer margin, two spines along outer margin, two setae apically and three setae along inner margin. Endopod two-segmented; first endopodal segment with row of small spinules along distal margin and one seta on inner margin; second endopodal segment with seta on outer margin, strong curved spinulose spine apically, one seta subapically and one seta on inner margin.

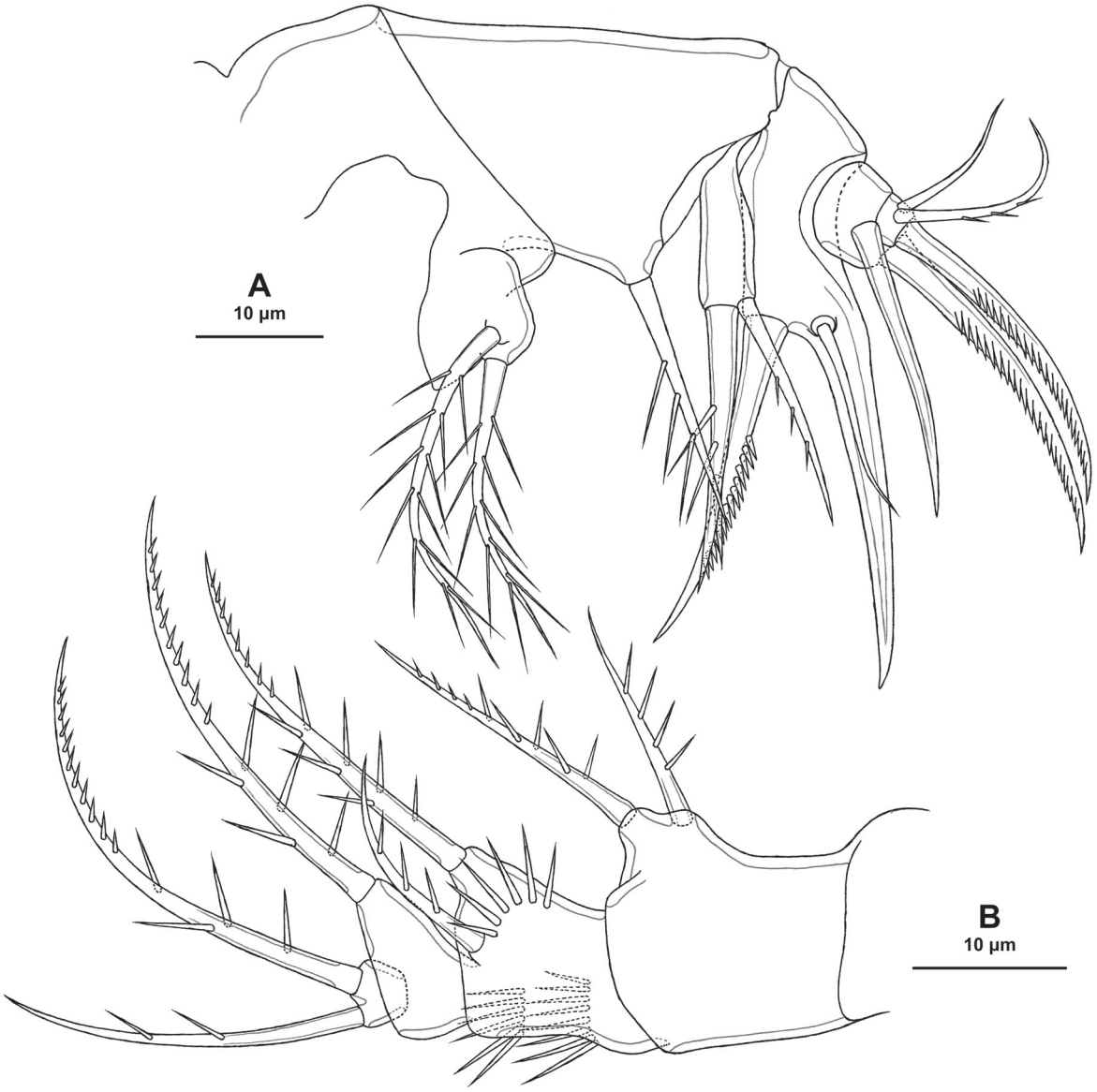

Fig. 6. *Tatarocyclops dayanae* gen. et sp. nov., holotype, ♀ (EMKSU VH 2002/1-2). **A**. Maxilla, posterior view. **B**. Maxilliped, anterior view.

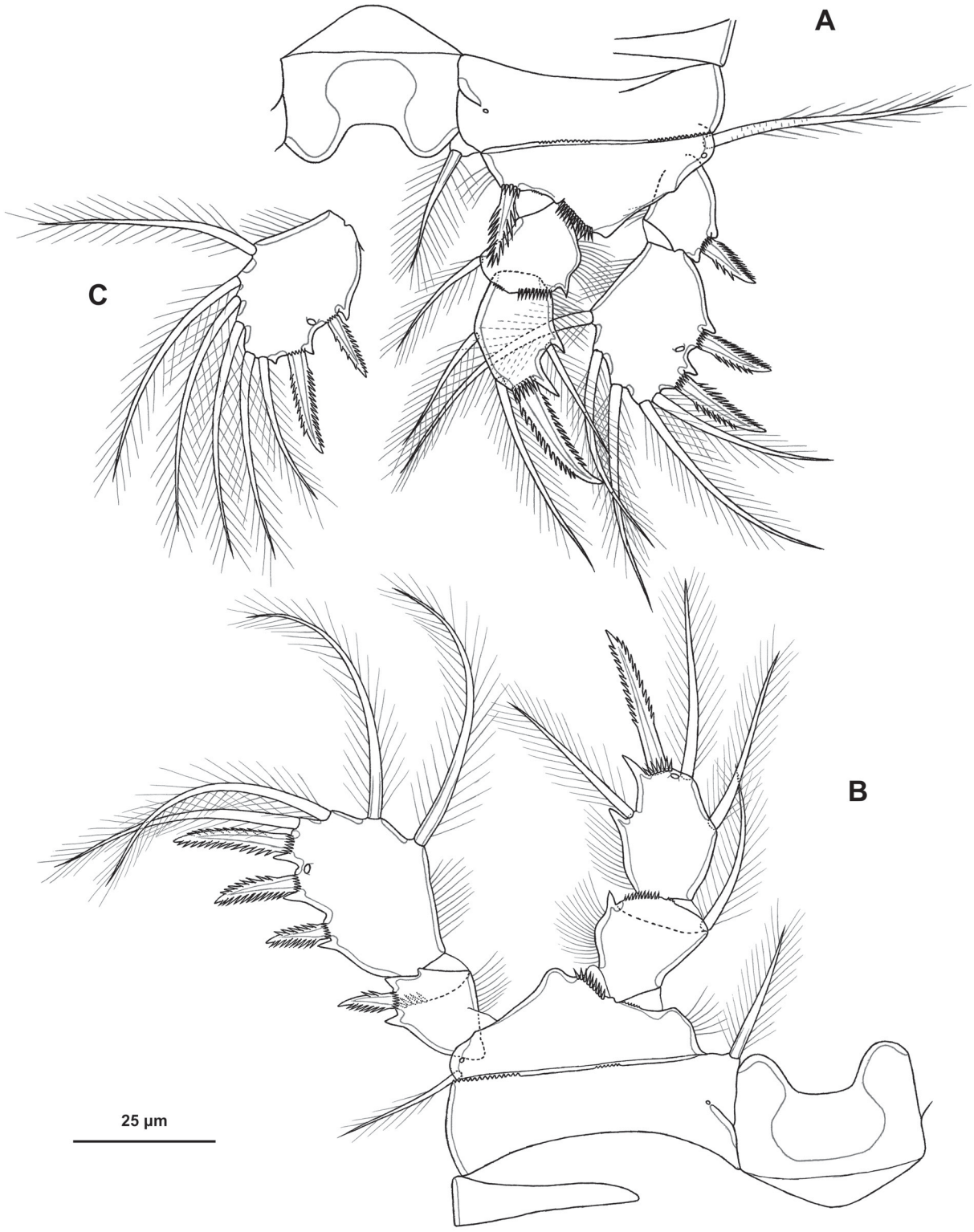

Fig. 7. *Tatarocyclops dayanae* gen. et sp. nov. **A–B**. Holotype, ♀ (EMKSU VH 2002/1-2). **C**. Paratype, ♂ (EMKSU VH 2002/6). **A**. P1, anterior view. **B**. P2, anterior view. **C**. P1, second exopodal segment, anterior view.

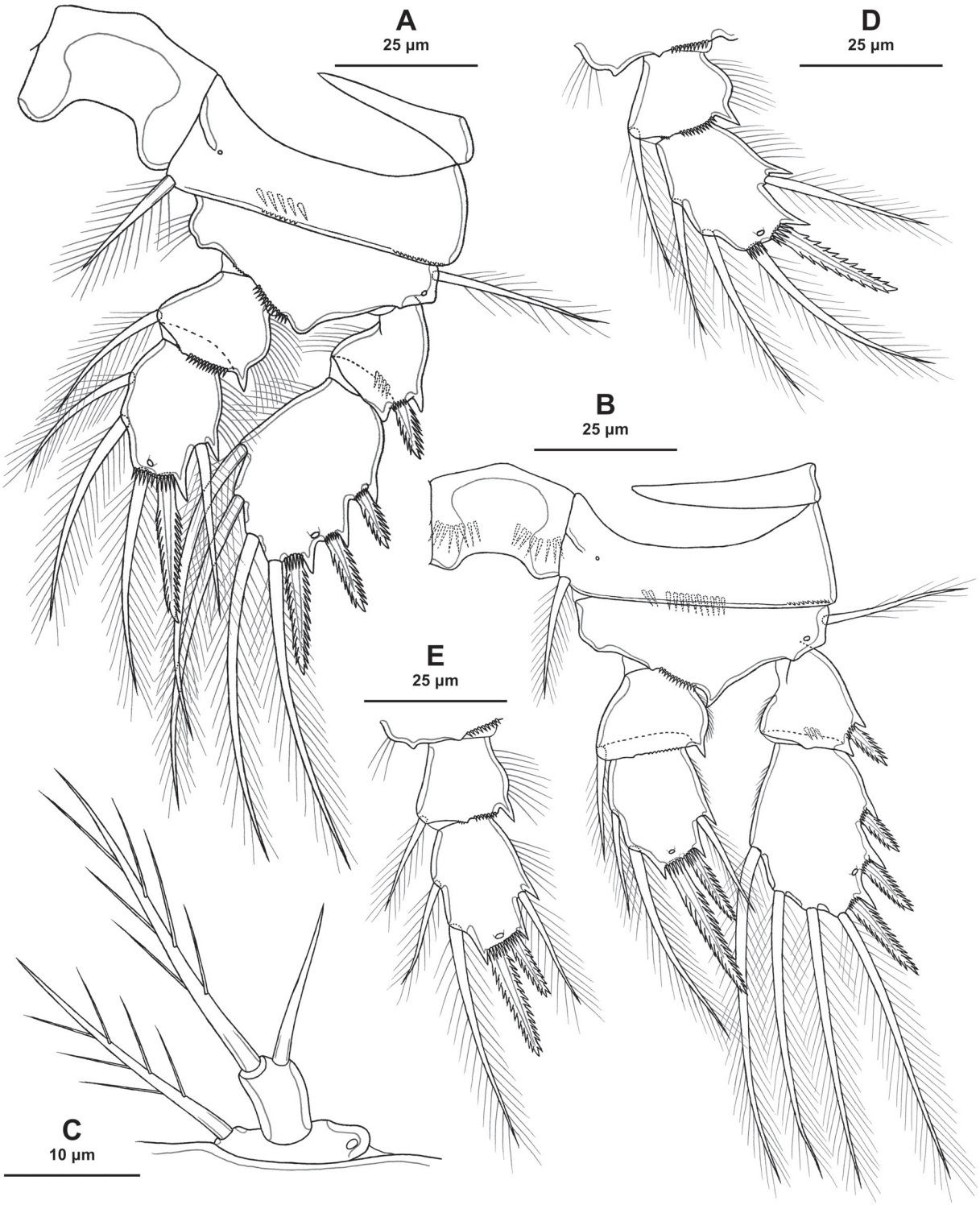

Fig. 8. *Tatarocyclops dayanae* gen. et sp. nov. **A–C**. Holotype, ♀ (EMKSU VH 2002/1–2). **D–E**. Paratype, ♂ (EMKSU VH 2002/3–4). **A**. P3, anterior view. **B**. P4, anterior view. **C**. P5, anterior view. **D**. P3, endopod, anterior view. **E**. P4, endopod, anterior view.

P2 (Fig. 7B). Praecoxa naked. Coxa wide, with two distal spinular rows; one pore close to inner margin; one seta on distal inner corner. Intercoxal sclerite wide with large lobes on distal margin, without ornamentation. Basis with pore close to outer margin, row of spinules at base of endopod, inner row of setules; with outer seta. Exopod two-segmented; first segment with distal spinular row on posterior side and spine on outer margin; second exopodal segment with one pore distally, close to outer margin, two spines along outer margin, one spine apically, one seta apically and three setae along inner margin. Endopod two-segmented; first endopodal segment with row of spinules along distal anterior margin and one seta on inner margin; second endopodal segment with seta on outer margin, one spine apically, one seta subapically, one seta on inner margin and pore subapically.

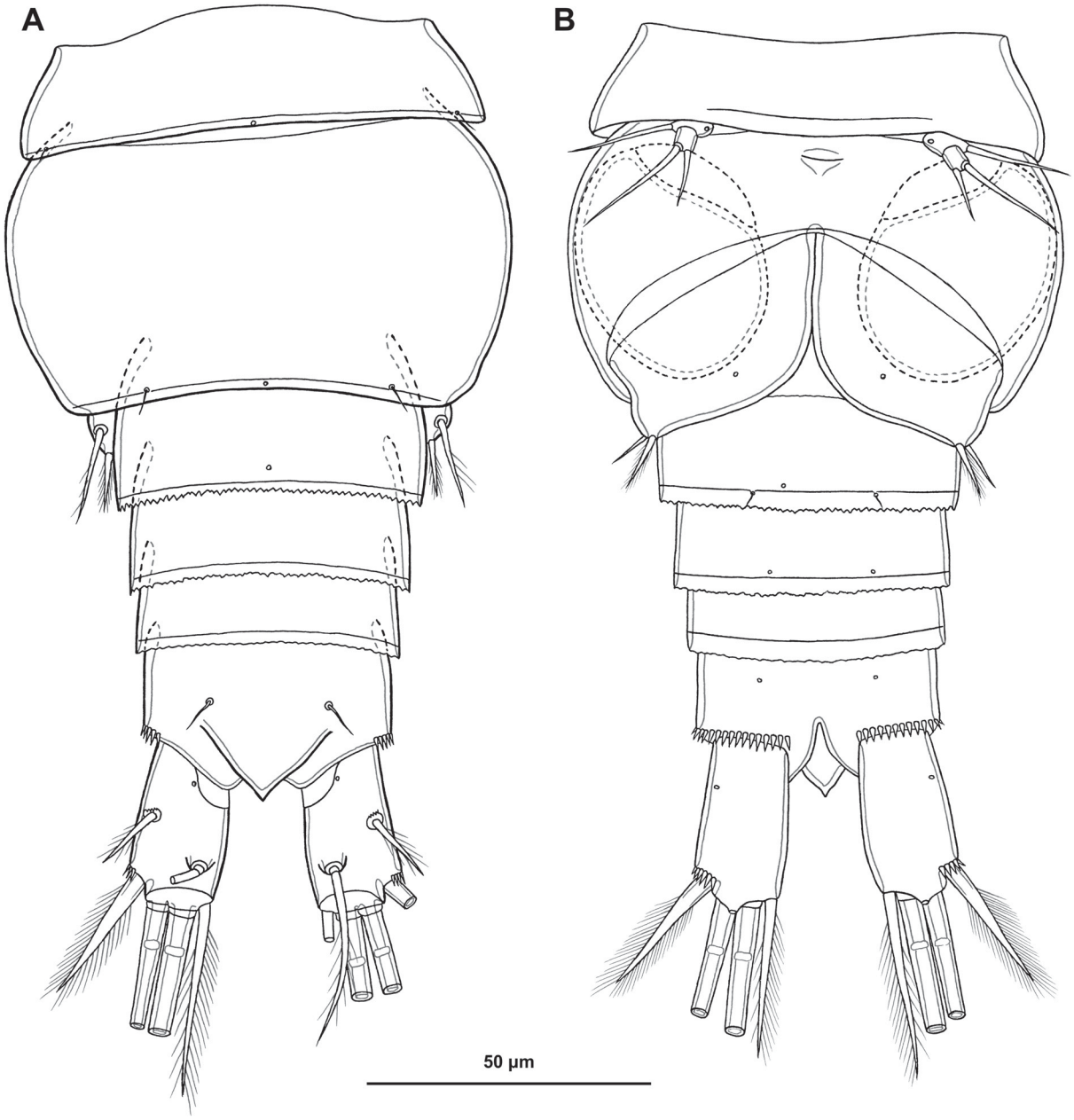

Fig. 9. *Tatarocyclops dayanae* gen. et sp. nov., paratype, ♂ (EMKSU VH 2002/6), urosome. **A**. Dorsal view. **B**. Ventral view.

P3 (Fig. 8A). Praecoxa, intercoxal sclerite, basis and exopod similar to those in P2. Coxa wide, with two rows of small spinules along distal anterior margin; row of larger spinules along distal posterior margin; one pore near inner margin and one seta on distal inner corner. Endopod two-segmented; first endopodal segment with row of spinules along distal margin, one seta on inner margin; second endopodal segment with seta on outer margin, one spine apically, one seta apically, two setae along inner margin, one pore close to distal margin.

P4 (Fig. 8B). Praecoxa without ornamentation. Coxa wide, with one pore close to inner margin; with seta on inner distal corner; anterior side with row of small spinules distal margin close to outer margin; posterior side with groups of spinules (Fig. 8C–D) along distal margin separated by short gap. Intercoxal sclerite wide, with large lobes on distal margin, with rows of spinules on posterior surface above each lobe. Basis with pore on outer distal corner, row of spinules at base of endopod; soft seta on outer margin; inner margin of basis without protrusions; distal protrusion between endopod and exopod hook-shaped. Exopod two-segmented. First segment with distal spinular row on posterior side and spine on outer margin; short setules on inner margin. Second exopodal segment with one pore close to distal outer margin, two spines on outer margin, one spine apically, one seta apically and three setae along inner margin; short setules on inner margin. Endopod two-segmented. First endopodal segment with row of spinules along distal margin, one seta on inner margin; setules along outer margin short. Second endopodal segment with seta on outer margin, two spines apically and two setae on inner margin; one pore on distal margin; setules along outer margin short; ratio of inner to outer apical spines 2.2.

P5 (Fig. 8C). Two-segmented, composed of coxobasis and exopod, without intercoxal sclerite. Coxobasis small, not fused with somite, with pinnate seta on outer margin and pore close to inner margin. Exopod with pinnate seta apically and bare seta subapically; ratio of outer to inner apical setae 2.2.

Male

Smaller than female, with narrower somites (Fig. 2D–F). Total body length of paratype from anterior margin of rostrum to posterior margin of caudal rami: 445 μm. Sexual dimorphism expressed in the antennule, genital segmentation and ornamentation, P6, length of caudal seta VI. Cephalothorax and thoracic somites as in female. P1–P5 similar to those in female, differences only in relative length of segments, setae and spines. P3–P4 endopods similar to those in female (Fig. 2D–E).

Genital somite (Figs 9A–B, 10A). With two oval-shaped spermatophores (Figs 9B, 10A) visible inside; with P6. P6 (Fig. 10A) represented by two large flaps fused to the somite; each with one pore ventrally; with long pinnate seta dorsolaterally, short pinnate seta laterally and bare seta ventrolaterally. Anal operculum shorter than in female (Fig. 9A). Inner apical seta VI longer than in female and longer than seta III (Fig. 9).

Antennule (Fig. 10C–E). 16-segmented, haplocer with geniculation between segments 14 and 15; with nine aesthetascs. Segment 1 with eight setae and three aesthetascs. Segment 2 with four setae. Segments 3, 5, 6, 7, 8 short, each with two setae. Segment 4 with two setae and aesthetasc. Segment 9 with short robust seta, long seta and aesthetasc. Segments 10 and 11 widened, each with two setae. Segment 12 with one small and one spiniform robust seta. Segment 13 with two small setae and one aesthetasc. Segment 14 elongate, with three small setae, one modified flattened seta. Segment 15 elongate, with one long seta, two modified flattened setae and small aesthetasc. Ancestral segments 16 and 17 partially fused, with eleven setae, two of which fused at base with one aesthetasc each. Armature formula: 1-[8+3ae],2-[4],3-[2],4-[2+ae],5-[2],6-[2],7-[2],8-[2],9-[2+ae],10-[2],11-[2],12-[2],13-[2+ae],14-[3+1 modified],15-[1+2 modified+ae],16-[9+(1+ae)+(1+ae)].

Variability

One of the four examined specimens (EMKSU VH 2002/6) possesses six setae on the second exopodal segment of P1 (Fig. 7C) instead of the typical five. In the same specimen, the P6 is asymmetrical: on one side it bears only two setae instead of the normal three (Fig. 10B), which is likely a developmental deformity.

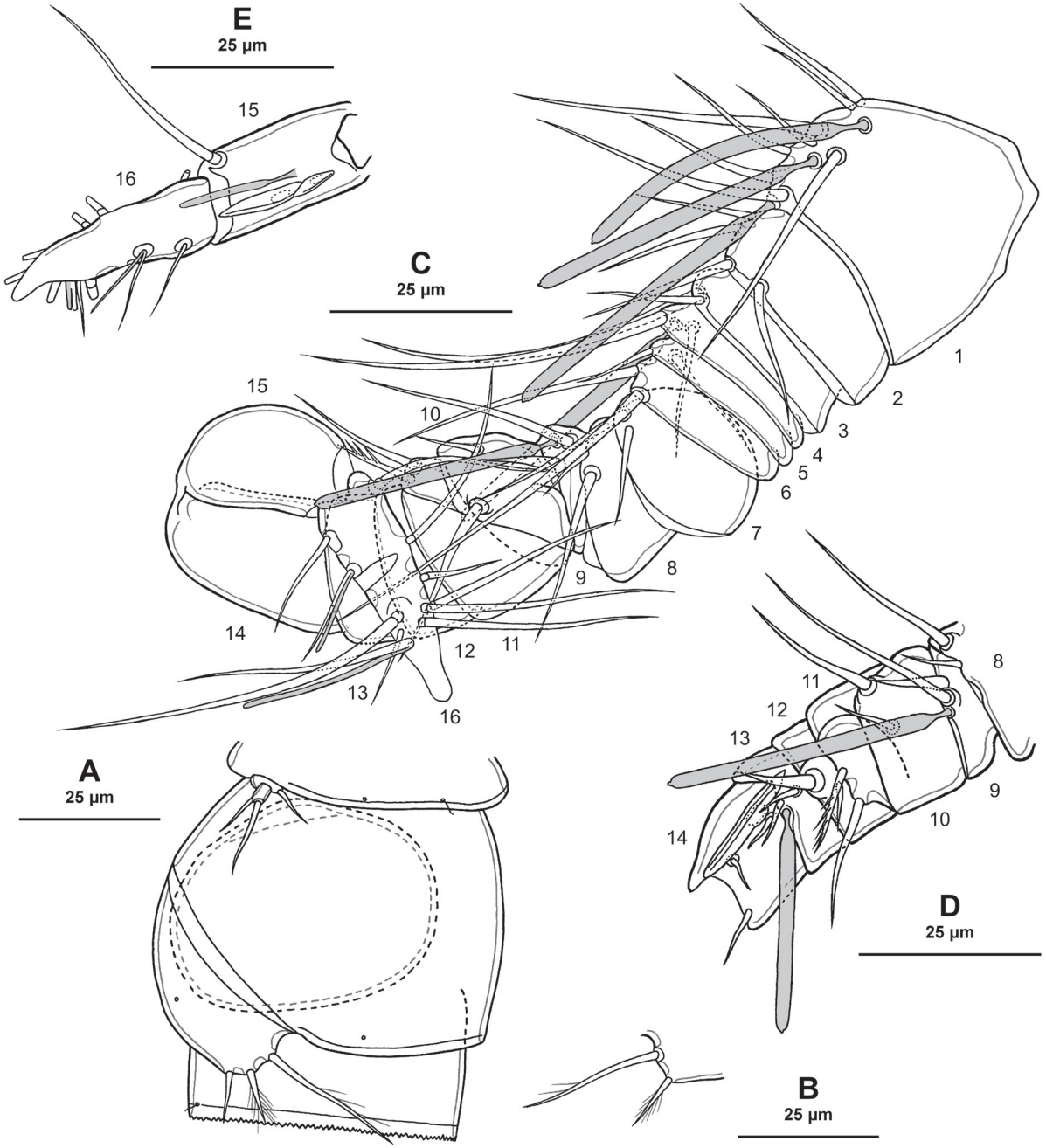

Fig. 10. *Tatarocyclops dayanae* gen. et sp. nov. **A–B, D–E**. Paratype, ♂ (EMKSU VH 2002/6). **C**. Paratype, ♂ (EMKSU VH 2002/3–4). **A**. First–third urosomites, lateral view. **B**. P6 with abnormal setation, lateral view. **C**. Antennule, dorsal view, setae are not shown on segments 12–15. **D**. Antennule, segments 8–14, anterior view. **E**. Antennule, segments 15–16, anterior view.

Fig. 11. Representatives of hyporheic fauna of crustaceans in the vicinity of the village of Naberezhnye Morkvashi. **A**. *Diacyclops crassicaudis* (Sars, 1863), ♀. **B**. *Attheyella crassa* (Sars, 1863), ♀. **C**. *Elaphoidella* cf. *elaphoides* (Chappuis, 1924), ♀. **D**. Unidentified Bathynellidae Grobben, 1905, juvenile. **E**. *Tatarocyclops dayanae* gen. et sp. nov., ♀.

Ecology

The new species was found in two out of the five collected samples (samples 1 and 4 from Table 1). It co-occurred with stygophilic copepods *Diacyclops crassicaudis* (Sars, 1863) (Cyclopoida, Cyclopidae) (Fig. 11A) and *Attheyella crassa* (Sars, 1863) (Harpacticoida, Canthocamptidae) (Fig. 11B), as well as with the stygobionts *Elaphoidella* cf. *elaphoides* (Chappuis, 1924) (Harpacticoida, Canthocamptidae) (Fig. 11C) and an unidentified species of the family Bathynellidae Grobben, 1905 (Malacostraca, Bathynellacea) (Fig. 11D).

Discussion

Placement of *Tatarocyclops* within Cyclopidae and justification for the new genus

Within the family Cyclopidae, a large group of genera is characterized by 11-segmented antennules in females and two-segmented exopods and endopods of the swimming legs in males or females (Pesce 1996). The new genus exhibits a unique combination of both highly apomorphic and plesiomorphic characters (Monchenko & Von Vaupel Klein 1999). The specific combination of a two-segmented P5 (plesiomorphy), the spine and seta formulae of the swimming legs (oligomerized segmentation and armature), and the presence of two apical spines on the distal endopodal segment of P4 (plesiomorphy) supports the establishment of a new, distinct genus.

Following the classification proposed by Pesce (1996), which is based on an 11-segmented antennule, two-segmented exopods and endopods of P1–P4, and a two-segmented P5, *Tatarocyclops* gen. nov. can be tentatively assigned to the *Mixocyclops* group. This group, as conceived by Pesce (1996), included the genera *Mixocyclops* Kiefer, 1944, *Caspicyclops* Monchenko, 1986, and some species ща *Diacyclops* and *Acanthocyclops* (some species of the latter two have since been transferred to *Reidcyclops* Karanovic, 2000 and *Monchenkocyclops* Karanovic, Yoo & Lee, 2012, respectively). *Tatarocyclops* gen. nov. can be clearly distinguished from all previously described genera. A detailed comparison with genera of the *Mixocyclops*-group is provided below.

– *Mixocyclops*. *Tatarocyclops* gen. nov. differs in (1) the armature of P5, in which both apical setae are long and well-developed, whereas in *Mixocyclops* one is a short, reduced spinule; (2) the presence of a medial spine on the basis of P1 (absent in *Mixocyclops*) (Tang & Knott 2009).

– *Caspicyclops*. The new genus differs markedly in (1) habitus, which is stouter and broader in *Tatarocyclops* gen. nov.); (2) the less reduced mouthparts: the mandibular palp is present (absent in *Caspicyclops*), the maxilliped is four-segmented (three-segmented in *Caspicyclops*), the maxillular palp bears seven setae (four setae in *Caspicyclops*); (3) armature of P1–P4: *Caspicyclops* has only one or two spines on the second exopodal segments (two or three in *Tatarocyclops*), lacks coxal setae on P2–P4, and lacks a medial spine on the P1 basis (coxal setae on P2–P4 and a medial spine on the P1 basis are present in *Tatarocyclops*) (Monchenko 1986).

– Species of *Diacyclops* with two-segmented endopods (*Diacyclops biceri* Boxshall, Evstigneeva & Clark, 1993 and *Diacyclops eulittoralis* Alekseev & Arov, 1986). *Tatarocyclops* gen. nov. differs in (1) the presence of two-segmented exopods on P2–P4 (three-segmented in *D. biceri* and *D. eulittoralis*); (2) the mandibular palp bearing one seta (three setae in *D. biceri* and *D. eulittoralis*) (Alekseev & Arov 1986; Boxshall *et al.* 1993).

– *Reidcyclops*. *Tatarocyclops* gen. nov. differs from *Reidcyclops dimorphus* (Reid & Strayer, 1994) in (1) the mandibular palp bearing one seta (three in *R. dimorphus*); (2) the absence of sexual dimorphism in the P4 exopod (the male P4 exopod is three-segmented in *R. dimorphus*); (3) the spine and seta formulae of the swimming legs (spine formula: 2.3.3.3 in *Tatarocyclops* vs 3.3.3.3/4 in *R. dimorphus*;

seta formula: 5.4.4.4 in *Tatarocyclops* vs 4.4.4.4 in *R. dimorphus*) (Reid & Strayer 1994). The new genus differs from *Reidcyclops trajani* (Reid & Strayer, 1994) and *Reidcyclops imparilis* (Monchenko, 1985) in: (1) the absence of sexual dimorphism in the P3 endopod (a modified apical endopodal spine is present in *R. trajani* and *R. imparilis* males); (2) two-segmented exopods on P3–P4 in males (three-segmented in *R. trajani* and *R. imparilis* males); (3) the absence of setae on the first exopodal segments of P1–P4 (present in *R. trajani* and *R. imparilis*) (Monchenko 1985; Karanovic 2000).

– *Monchenkocyclops*. *Tatarocyclops* gen. nov. differs in (1) the mandibular palp bearing one seta (three in *Monchenkocyclops*); (2) the long setiform element on the inner side of the P5 (the short spiniform element in *Monchenkocyclops*); (3) the two-segmented exopods on P1–P4 (vs three-segmented in *Monchenkocyclops*) (Monchenko 1972; Karanovic *et al.* 2012; Karaytuğ *et al.* 2018).

An overview of other cyclopid genera that share the 9–11-segmented female antennule and two-segmented swimming legs reveals that *Tatarocyclops* gen. nov. is distinctive in its combination of morphological characters (Table 3). Crucially, the new genus retains a plesiomorphic, two-segmented P5 that is not fused to the somite. This condition separates it from a large array of genera in which the proximal segment (and often the distal segment) of the P5 is either completely or partially fused to the somite, including *Allocyclops* Kiefer, 1932; *Anzcyclops* Karanovic, Eberhard & Murdoch, 2011; *Apalachocyclops* Fiers, 2011; *Apocyclops* Lindberg, 1942; *Brevicyclops* Totakura & Ranga Reddy, 2015; *Bryocyclops* Kiefer, 1927; *Cochlacocyclops* Kiefer, 1955; *Cryptocyclops* Sars, 1927; *Dussartcyclops* Karanovic, Eberhard & Murdoch, 2011; *Fierscyclops* Karanovic, 2004; *Fimbricyclops* Reid, 1993; *Goniocyclops* Kiefer, 1955; *Graeteriella* Brehm, 1926; *Haplocyclops* Kiefer, 1952; *Hesperocyclops* Herbst, 1984; *Hypocyclops* Fiers, 2012; *Idiocyclops* Herbst, 1987; *Korecyclops* Cottarelli, Bruno, Spena, Caccamo & Grasso, 2026; *Menzeliella* Lindberg, 1954; *Meridiecyclops* Fiers, 2001; *Metacyclops* Kiefer, 1927; *Muscocyclops* Kiefer, 1937; *Neutrocyclops* Kiefer, 1936; *Olmeccyclops* Fiers, 2012; *Palaeocyclops* Monchenko, 1972, *Pescecyclops* Karanovic, Eberhard & Murdoch, 2011, *Pilbaracyclops* Karanovic, Eberhard & Murdoch, 2011; *Psammocyclops* Kiefer, 1955; *Psammophilocyclops* Fryer, 1956; *Pseudograeteriella* Sanoamuang, Boonyanusith & Brancelj, 2019; *Pseudohesperocyclops* Brancelj, Boonyanusith & Sanoamuang, 2024; *Rybocyclops* Ranga Reddy & Defaye, 2008; *Siamcyclops* Boonyanusith, Sanoamuang & Brancelj, 2018; *Speocyclops* Kiefer, 1937; *Stolonicyclops* Reid & Spooner, 1998; *Teratocyclops* Plesa, 1981; *Thalamocyclops* Fiers & Van Damme, 2017; *Virbiocyclops* Fiers, 2012; and *Yansacyclops* Reid, 1988.

Given the absence of a molecular phylogeny and multiple morphological homoplasies, such as the independent evolution of an 11-segmented antennule in various cyclopid lineages (Schutze *et al.* 2000), the exact phylogenetic relationships of *Tatarocyclops* gen. nov. remain uncertain. Morphological similarities can be found with several genera, including *Speocyclops* and *Reidcyclops*. Among these, *Speocyclops* shares several apomorphic traits (e.g., absence of an antennal exopodal seta, six setae on the second segment of the antennal endopod, and two-segmented P1–P4 rami in both sexes). *Speocyclops* comprises about 50 species and subspecies and is likely polyphyletic (Fiers 2011). *Tatarocyclops* differs from *Speocyclops* in its maxilliped armature (2.2.1.2 vs 1.1.1.2), the presence of two apical spines on the P4 endopod (vs one), the absence of a visible dorsal border on the genital double-somite, and a completely free two-segmented P5 (proximal segment fused to the somite in *Speocyclops*). The typical exopod spine formula for *Speocyclops* is 3.4.4.3 and the seta formula is 4.4.4.3, which contrasts with the spine formula of 2.3.3.3 and the seta formula of 5.4.4.4 in *Tatarocyclops* (Monchenko 1974, 2010; Einsle 1993; Galassi & De Laurentiis 2004; Fiers 2005; Fiers & Pandourski 2008). Even in exceptional cases like *Speocyclops lindbergi* Damian, 1957 (spine formula 3.3.3.3, seta formula 5.4.4.4), the number of spines on the P1 exopod does not match that of the new genus (Damian 1957).

A possible relationship with *Reidcyclops* also deserves discussion. This genus also appears to be polyphyletic. A comparison of the species descriptions within this genus indicates that the European

Table 3 (continued on next two pages). Comparative morphology of *Tatarocyclops* gen. nov. and other cyclopid genera possessing 9–11-segmented female antennules and two-segmented P1–P4 exopods and endopods.

Genus	Antenna exopod; mandibular palp, setae	Spine formula of P1–P4 second exopodal segments	Seta formula of P1–P4 second exopodal segments	Sexual dimorphism in P3–P4 endopods	P5, number of segments; number of setae	Reference
Tatarocyclops gen. nov.	0;1	2.3.3.3	5.4.4.4	absent	2;3	original data
Allocyclops	1/0;3	3.4.4.3	5.5.5.5 5.5.5.4	absent	0;3	Fiers 2012
Anzcyclops	0;3/2/1	2.3.3.2 2.3.2.2	5.5.5.4 5.4.4.4 4.4.4.4	absent	1;3	Karanovic 2005; Karanovic *et al.* 2011
Apalachocyclops	0;3	3.4.4.4	5.5.5.5	P3, P4	1;3	Fiers 2011
Apocyclops	1;3	3.4.4.3	5.5.5.5	absent	0;3	Coelho-Botelho 1999
Brevicyclops	0;0	2.3.3.2 2.2.2.2	5.5.5.4	absent	0;3	Totakura & Ranga Reddy 2015
Bryocyclops	0;1	3.3.3.3 3.3.3.4	5.5.5.4 4.5.5.4	P3, P4	0;3	Boonyanusith *et al.* 2018; Watiroyram 2021
Caspicyclops	0;0	1.1.2.2	4.3.3.3	?	2;3	Monchenko 1986
Cochlacocyclops	?;?	3.3.3.2	?	?	1 or 0[1]	Kiefer 1955
Cryptocyclops	1;3	3.4.4.3	5.5.5.5	absent	1;2	Monchenko 1974
Dussartcyclops	0;1	2.2.2.2	4.4.4.4 4.4.4.3	P4	1/0;3	Karanovic 2003, 2004a
Fierscyclops	1;3	3.4.4.3	5.5.5.5	absent	1;3	De Laurentiis *et al.* 2001
Fimbricyclops	0;1	3.3.3.3	5.5.5.5	absent	1;3	Reid 1993a
Goniocyclops	0;?	3.3.3.2	?.4.4.4	absent	1/0;3	Kiefer 1955; Dussart 1984
Graeteriella[2]	0;2	3.4.4.4	5.5.5.5	absent	1;2	Gurney 1933; Einsle 1993
Haplocyclops[3]	0;0	2.2.2.2	5.4.4.4	P4	0;3	Totakura & Ranga Reddy 2015
Hesperocyclops	1/0;3	3.4.4.3 3.4.3.3	5.5.5.5	P4	1;3	Galassi & Pesce 1992

Table 3 (continued). Comparative morphology of *Tatarocyclops* gen. nov. and other cyclopid genera possessing 9–11-segmented female antennules and two-segmented P1–P4 exopods and endopods.

Genus	Antenna exopod; mandibular palp, setae	Spine formula of P1–P4 second exopodal segments	Seta formula of P1–P4 second exopodal segments	Sexual dimorphism in P3–P4 endopods	P5, number of segments; number of setae	Reference
Hypocyclops	0;1	3.4.4.3	5.5.5.5 5.4.4.4	absent	0;3	Petkovski 1971; Karanovic 2001
Idiocyclops	1;?	4.4.4.3	4.5.5.4	absent	1;2	Herbst 1987
Korecyclops	1;3	3.3.3.2	5.5.5.5	absent	1;3	Cottarelli *et al*. 2026
Menzeliella	?;?	3.4.4.3	?.?.?.5	?	1;3	Chappuis 1917; Lindberg 1954
Meridiecyclops	1;3	3.3.3.3	5.5.5.5	P4	1;3	Fiers 2001
Metacyclops[4]	1;3	3.4.4.3 3.4.4.2 3.3.3.3	variable	absent	1;3	Tang & Knott 2009; Karanovic *et al.* 2011
Mixocyclops	0;1	2.3.4.4 2.3.3.3	4.3.3.3	absent	2;3	Chappuis 1951; Tang & Knott 2009
Muscocyclops	0;0	2.3.3.2	5.4.4.4	absent	1;3	Rocha & Bjornberg 1987
Neutrocyclops	1;?	3.4.4.3	5.?.?.5	absent	0;2	Lowndes 1934
Olmeccyclops	0;1	2.3.3.2	4.4.4.3	?	0;3	Fiers & Jocque 2013
Palaeocyclops	?;0	2.3.3.3	5.5.5.4	P3, P4	0;3	Monchenko 1972
Pescecyclops	1/0;3	3.3.3.3	5.5.5.5	absent	1;3	Karanovic 2004b
Pilbaracyclops	0;3	3.3.3.3 3.3.3.2	5.5.5.5	absent	1;3	Karanovic 2006
Psammocyclops	1;3	3.3.3.3	5.4.4.4	absent	0;3	Fiers 2012
Psammophilocyclops		3.3.3.3 2.2.2.2	5.5.5.4	P3, P4	0;3	Lee & Chang 2012
Pseudograeteriella	0;3	3.3.3.3	5.5.5.4	P4	0;2	Sanoamuang *et al.* 2019
Pseudohesperocyclops	1;3	3.4.3.3	5.5.5.5	absent	1;3	Brancelj *et al.* 2024
Reidcyclops[5]	0;3/1/0	3.4.4.4 3.3.3.4/3	5.5.5.5 4.4.4.4	P3/absent	2;3	Monchenko 1985; Reid & Strayer 1994; Karanovic 2000

Table 3 (continued). Comparative morphology of *Tatarocyclops* gen. nov. and other cyclopid genera possessing 9–11-segmented female antennules and two-segmented P1–P4 exopods and endopods.

Genus	Antenna exopod; mandibular palp, setae	Spine formula of P1–P4 second exopodal segments	Seta formula of P1–P4 second exopodal segments	Sexual dimorphism in P3–P4 endopods	P5, number of segments; number of setae	Reference
Rybocyclops	0;0	2.2.2.2	5.5.5.4 5.4.4.3	P4	0;3	Totakura & Ranga Reddy 2015
Siamcyclops	0;3	3.3.3.2	5.5.5.5 5.5.5.4	P3, P4	0;3	Boonyanusith *et al.* 2018; Watiroyram & Koompoot 2024
Speocyclops	0;1/0	3.4.4.3 3.3.3.3 2.2.2.2	5.4.4.4 4.4.4.4 4.4.4.3 3.4.4.3	absent	1/0;3/2	Damian 1957; Monchenko 1974, 2010
Stolonicyclops	0;2	2.3.3.3	5.4.4.4	absent	0;3	Reid & Spooner 1998
Teratocyclops	1;3	3.4.4.3	5.5.5.5	absent	1;3	Iepure & Defaye 2003
Thalamocyclops	0;1	3.3.3.3	5.5.5.4	P3, P4	0;3	Fiers & Van Damme 2017
Virbiocyclops	1;3	3.3.3.2	5.5.5.5	P4	0;3	Fiers 2012
Yansacyclops	1;3	3.4.4.3	5.5.5.5	absent	0;3	Reid 1988

? — unknown or not reported.

[1] Basal seta arises from pediger 5; other elements unknown.

[2] Data are given for species with two-segmented P1–P4 rami: females of *Graeteriella unisetigera* (Graeter, 1908) and *G. boui* Lescher-Moutoué, 1974.

[3] Data are given for the species with two-segmented P1–P4 rami: *Haplocyclops primitivus* Totakura & Ranga Reddy, 2015.

[4] Antennule segmentation within the genus ranges from 9 to 13.

[5] Males of *Reidcyclops trajani* (Reid & Strayer, 1994) and *R. imparilis* (Monchenko, 1985) have three-segmented exopods on P3–P4; those of *R. dimorphus* (Reid & Strayer, 1994) have a three-segmented exopod only on P4. Females of *R. imparilis* are unknown.

species *R. trajani* (the type species) and *R. imparilis* differ substantially from *R. dimorphus* from Florida. They differ in the spine and seta formulae of the P1–P4 exopods and endopods, the presence or absence of sexual dimorphism in the P3 endopod, the structure of the mandibular palp, and the armature of the maxilliped (Monchenko 1985; Reid & Strayer 1994; Karanovic 2000). In our opinion, *R. dimorphus* is morphologically closer to the North American genus *Rheocyclops* Reid & Strayer, 1999, particularly to *Rheocyclops carolinianus* Reid, 1999 and *Rheocyclops virginianus* (Reid, 1993) (Reid 1993b; Reid *et al.* 1999). However, based solely on published descriptions, we cannot state this with certainty.

Regarding the European species of *Reidcyclops* (*R. trajani* and *R. imparilis*), their morphological similarity to *Tatarocyclops* gen. nov. is indeed stronger than their similarity to other genera. It is possible that *Tatarocyclops* represents a clade within the European lineage of *Reidcyclops*. Conversely, it is equally plausible that *Reidcyclops* itself (in its current circumscription) might be a clade within the large and heterogeneous genus *Diacyclops*. In the absence of molecular data and given the widespread homoplasy of reductive characters (Schutze *et al.* 2000), we cannot reach a definitive conclusion about phylogenetic relationships.

A new genus in the European part of Russia: anomaly or pattern?

The discovery of *Tatarocyclops dayanae* gen. et sp. nov. in the Middle Volga region raises the question of whether it is an isolated find or part of a broader biogeographic pattern. Our sampling revealed that the obligate groundwater fauna (including *E.* cf. *elaphoides*, an unidentified species of Bathynellidae, and *T. dayanae*) was present only in the perennial streams of the Morkvashinka River system. In contrast, intermittent streams that dry up annually yielded only stygophilic species such as *D. crassicaudis* and *A. crassa*. This suggests that the stygobiotic assemblage relies on stable hydrological connections to deeper groundwater systems.

Tatarocyclops dayanae gen. et sp. nov. represents the fourth endemic species and only the second endemic genus of crustaceans described from the Middle Volga region. This finding aligns with a recent series of discoveries. Notably, several endemic species of stygobiotic crangonyctid amphipods — *Volgonyx dershavini* (Behning, 1928), *Volgonyx behningi* Marin & Palatov, 2024, and *Uralocrangonyx zhiguliensis* Marin & Palatov, 2024 — have been described from groundwater habitats along the Volga River and in the Zhiguli Mountains (Marin & Palatov 2021, 2024a, 2024b). The concurrent discovery of a West European-affiliated harpacticoid (*E.* cf. *elaphoides*) (Apostolov 2010) further indicates a potentially ancient and diverse stygofauna with complex biogeographic origins.

If the morphological similarities between *Tatarocyclops* gen. nov. and European species within genera such as *Speocyclops* and *Reidcyclops* reflect true phylogenetic affinities, one might speculate that Eastern Europe could have served as a refugium for ancient crustaceans lineages, given the poor dispersal capacity of stygobiotic crustaceans. However, similar morphological reductions (oligomerization of segments and setae) are known to evolve convergently in unrelated groundwater taxa under comparable selective pressures (Monchenko & Von Vaupel Klein 1999). Therefore, the observed similarities could also be homoplastic.

This work aims to draw attention to a region that, despite being relatively well-studied with respect to its surface-water fauna, harbors significant and previously undocumented biodiversity within its groundwater ecosystems. Given the availability of established and effective methods for sampling stygofauna, we hope to encourage further taxonomic exploration. The riverbanks of the Volga-Kama region, particularly where streams incise karstified bedrock, appear highly promising for future discoveries (Golovatch *et al.* 2018). Uncovering this hidden diversity is essential for understanding the evolution and biogeography of Palearctic freshwater fauna.

Acknowledgements

I am deeply grateful to my wife, Dayana N. Sharafutdinova (Kazan Federal University), for introducing me to the village of Naberezhnye Morkvashi, where this species was discovered. I also thank the editor of the World Register of Marine Species (WoRMS) database, Dr T. Chad Walter, whose assistance in providing numerous articles on various cyclopid genera was invaluable for comparative analyses.

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