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Morphology and zoogeography of the burrower-like gammarid *Gammarus koshovi* (Bazikalova, 1946) (Crustacea, Amphipoda, Gammaridae) – An overlooked and poorly known species in the Siberian fauna

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Abstract. A comprehensive survey of several lakes in the Tuva Republic of Russia yielded, besides the ubiquitous *Gammarus lacustris*, the discovery of a small freshwater, lacustrine amphipod not previously recorded in this area. A comparative study of the Tore-Khol Lake gammarid population, probably conspecific with *Gammarus koshovi* (Bazikalova, 1946) originating from Khubsugul Lake, was conducted. The species, *G. koshovi*, is characterized by a specific habitus: a small-sized compact body, all limbs shortened, carpi of pereopods (PIII and PIV) reduced, coxal plates broad, and pereopod dactyli sturdy. It has been suggested that juveniles of the euryoecious *G. lacustris* or other large species could be confused with the relatively small *G. koshovi*. Consequently, we decided to present the distribution of gammarid species throughout south Siberia and Mongolia, referring to the sequences of works primarily by Soviet authors, which may be hard to access by international readers. We discuss affinity with related groups, distribution, and ecology of *G. koshovi* to better understand their evolution. Additionally, the zoobenthic species diversity of widely represented groups in the ecosystems of Tore-Khol Lake is briefly reviewed. An identification key for the Siberian *Gammarus* with 10 species is provided.

Keywords. Malacostraca, taxonomy, Uvs Nuur Basin, Mongolia, first record.

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Introduction

The territory at the southern end of Central Siberia is rich in various mountain pools (more than 430 lakes) lying within the Sayan Province of the Lena-Yenisei subregion of the Palearctic (Leontyev 1957). The

fluctuating geological history of the region (Misar 1997) and a significant variety of natural landscapes (Sanders *et al.* 2021) created a wide variety of aquatic biotopes (rivers, springs, takyrs / playas) and ephemeral rivers, as well as a wide variety of invertebrate species that inhabit them. However, it should be noted that the amphipod fauna of the southern region of Central Siberia, and especially Tuva, is practically unknown (Dgebuadze *et al.* 2010; Kirova 2019). Currently, our study is a first report for more than a century of amphipod research in Siberia.

The genus *Gammarus* J.C. Fabricius, 1775 is a large Holarctic/Sino-Indian epigeal/subterranean group of amphipods that is typically found to be morphologically monotonous at high latitudes (Culver *et al.* 1995), with a number of distinctly divergent narrowly localized endemic species at the southern border of the range (Sidorov *et al.* 2018; Zheng *et al.* 2020). However, the historical reasons for this distribution are not entirely known. Despite the obvious inconsistencies in morphological distances between recent species and parphyly within the group, the genus *Gammarus* reveals a certain unity and is known from at least the Oligocene-Eocene era (Hou *et al.* 2011). Earlier, in a series of publications, it was shown that the amazingly diverse endemic amphipod fauna of Baikal Lake, consisting of more than 354 species (Takhteev 2019), had radiated from a putative *Gammarus*-like ancestor in the Oligocene (28 Mya), coinciding with the formation of the lake (Ogarkov *et al.* 1997; Sherbakov *et al.* 1999; MacDonald *et al.* 2005; Hou & Sket 2016).

As part of the inventory of the genus *Gammarus* J.C. Fabricius, 1775 inhabiting Siberia, samples from three different lakes of Tuva were collected. Two were small limnetic pools containing the ubiquitous *Gammarus lacustris* G.O. Sars, 1863, whereas in the dune subsaline lake Tore-Khol (also known as Döröö Nuur), a population of a poorly known species, *Gammarus koshovi* (Bazikalova, 1946) (sometimes misspelled as ‘*kozho*vi’, ‘*kozhowi*’, or ‘*kozovi*’), was apparently discovered. This species was described by A.Ya. Bazikalova in 1946 and originally placed in the now defunct genus *Rivulogammarus* S. Karaman, 1931. Type material of *G. koshovi* was either lost or not deposited, and the original description of the species by Bazikalova (1946) was so lacking in detail that its correct taxonomic status has remained problematic. It is noteworthy that *G. koshovi* was previously known only from the Mongolian Lake Khubsugul (Hövsgöl) that holds some endemic species of the purely Baikalian flocks (Kozhova *et al.* 1994; Martens & Segers 2009) and its discovery in Lake Tore-Khol not only significantly expanded its range, but also raised additional questions.

Lake Tore-Khol is located in the northeastern part of the Ubsunur Basin (1148 m a.s.l.), 20 km south of Erzin. The lake was formed as a result of damming one of the tributaries of the Tes-Khem River by a ridge of moving sands, the Eder-Elesin. The dimictic steppe lake has exclusively subterranean inflow and an underground outflow, dominance of picoplanktic cyanobacteria, and strong calcite precipitation (Walther *et al.* 2020). It is oligotrophic, with a tendency towards being mesotrophic at the drainage area, with the following properties: total area 72 km², approximately 7 m mean depth (max. 26–27 m, according to some sources 38.8 m), slightly subsaline (0.6–0.7 g/L), Mg/Ca–HCO₃ type, T 18.5°C (at max. depth T 6°C), conductivity 0.71 mS/cm, and pH 8.85–9.2. It has sandy sediments with a different silting thickness overgrown with *Chara* sp. and *Potamogeton pectinatus* L., and a wide reed belt of *Phragmites australis* (Cav.) Steud. in places. Fishes include *Oreoleuciscus* sp. and *Esox lucius* Linnaeus, 1758 (artificially populated) (Zaika & Makarov 2000; Flößner *et al.* 2005; Paul 2012; Dulmaa 2013; Kalnaya *et al.* 2018). This is the only lake declared in 1982 as a natural monument of republican significance with some areas later included in the protected zone of the ‘Ubsunurskaya Kotlovina’ Biosphere Reserve – a World Heritage Site of UNESCO since 2003 (Arakchaa & Laidyp 1994).

Considering the importance of finding this species in constructing the general zoogeography of the genus *Gammarus*, we also attempted to provide a brief description of the freshwater fauna of Tore-Khol Lake in highlighting the common species with Khubsugul.

Historical review

In 1851, J.F. Brandt reported on *Gammarus* in the Nachiki hot spring basin on E Kamchatka, which he believed was indistinguishable from *Gammarus pulex* (De Geer, 1778) (Brandt 1851). *Gammarus ermanni* Milne-Edwards, 1840 was mentioned among others reported in Kamchatka's thermal spring by H. Milne-Edwards in 1840, and was subsequently assigned to the genus *Crangonyx* Spence Bate, 1859 (Bate 1862; Karaman 1991). In a historical retrospective for Siberia, the indication of the binomial name *Gammarus pulex* is not unexpected. For example, a wide geographical distribution of this species was reported by R.K. Maak (1886) according to the results of the expedition of 1853–1855 to Angara, Lena, Vilyui, in the Ural region, Pyasina (Taimyr), in the vicinity of Olenek, beyond the Arctic Circle (see also Gerstfeldt 1858). Probably the binomen '*Gammarus pulex*' was used as a collective name for any species of *Gammarus*, *Eulimnogammarus* Bazikalova, 1945, or *Pallasea* Spence Bate, 1862, and even *Synurella* Wrzeźniowski, 1877 that are usually common in these areas (see Stebbing 1906; Martynov 1930; Lepneva 1933). Later, in Mongolia, B.I. Dybowsky (1901) found *G. pulex* off the northern shore of Lake Khuvsgul, later referred to as *Gammarus lacustris* G.O. Sars, 1863 (Karaman 1991). In addition to this species, two more are known from Lake Khubsugul: *Gammarus koshovi* Bazikalova, 1946 (Erbaeva *et al.* 1990; Kozhova *et al.* 1994) and *Gammarus hanhi* Safronov, 2006 (Kozhova *et al.* 2000; Safronov 2006).

Studies of the hydrobiology of the lakes of the Ubsunur Basin do not cover an extended period. On the fauna of gammarids inhabiting the freshwater lakes of the Ubsunur depression, in particular Tore-Khol Lake, the information is either absent (Zaika 1993; Zaika & Makarov 2000) or short (Dolgin & Yalysheva 2008; Yalysheva 2010). Paul (2012) provides data on the euryhaline *G. lacustris* that stands as a typical component of the bottom fauna in salt lakes. In general, it should be noted that *G. lacustris* (partially identified as '*Gammarus* sp.', '*Gammaridae*', or '*gammarids*') is a permanent component of the various aquatic biotopes of Tuva and Mongolia, often dominating the lotic and lentic communities (Dulmaa 1979; Gundriser *et al.* 1986; Shcherbina & Ayuushsuren 2007; Kosterin & Zaika 2011; Maasri & Gelhaus 2012; Dgebuadze 2013; Matafonov 2014; Ayuushsuren & Shcherbina 2015; Prokin *et al.* 2019); however, despite the identification of this species, its morphological and genetic profile remains unknown.

Other species of the genus *Gammarus* in Siberia, not mentioned above, that are known include: *Gammarus korbuensis* Martynov, 1930; *Gammarus teletzkensis* Martynov, 1930; *Gammarus angulatus* (= *Gammarus ocellatus angulatus* Martynov, 1930) from the mountain river Korbu and Teletskoye Lake; *Gammarus angustatus* Martynov, 1930 from the stream in the Inya River basin, Ob' River near Novosibirsk (Martynov 1930); *Gammarus pellucidus* Gurjanova, 1930 from the Ladeysky riffle at the Yenisey (sandbank) (Gurjanova 1930); *Gammarus barnaulensis* Schellenberg, 1937 (locus typicus is unknown), which A. Schellenberg indicated from Barnaul (Tomsk) in lakes, Burgusutai (W Siberia), which has led to confusion (Schellenberg 1937); *Gammarus dabanus* Tachteev & Mekhanikova, 2000 from mountain streams of the northern macroslope of the Khamar-Daban Ridge (Tachteev & Mekhanikova 2000); a suggested juvenile specimen of *Gammarus* sp. in Gurjanova (1930) from the Yenisey near Nyasha and a channel of the Yenisei near Khudonogovo (Gurjanova 1930).

Material and methods

Sampling

Specimens of gammarids were collected with a Petersen bottom grab sampler and a common hand net in three lakes of the territory of the Tuva Republic of Russia (see Fig. 1): Tore-Khol Lake, a small freshwater lake near Shara-Nur Lake and 'Dashtyg' alpine lake (see below). Samples were fixed and stored in a ca 80% ethanol solution.

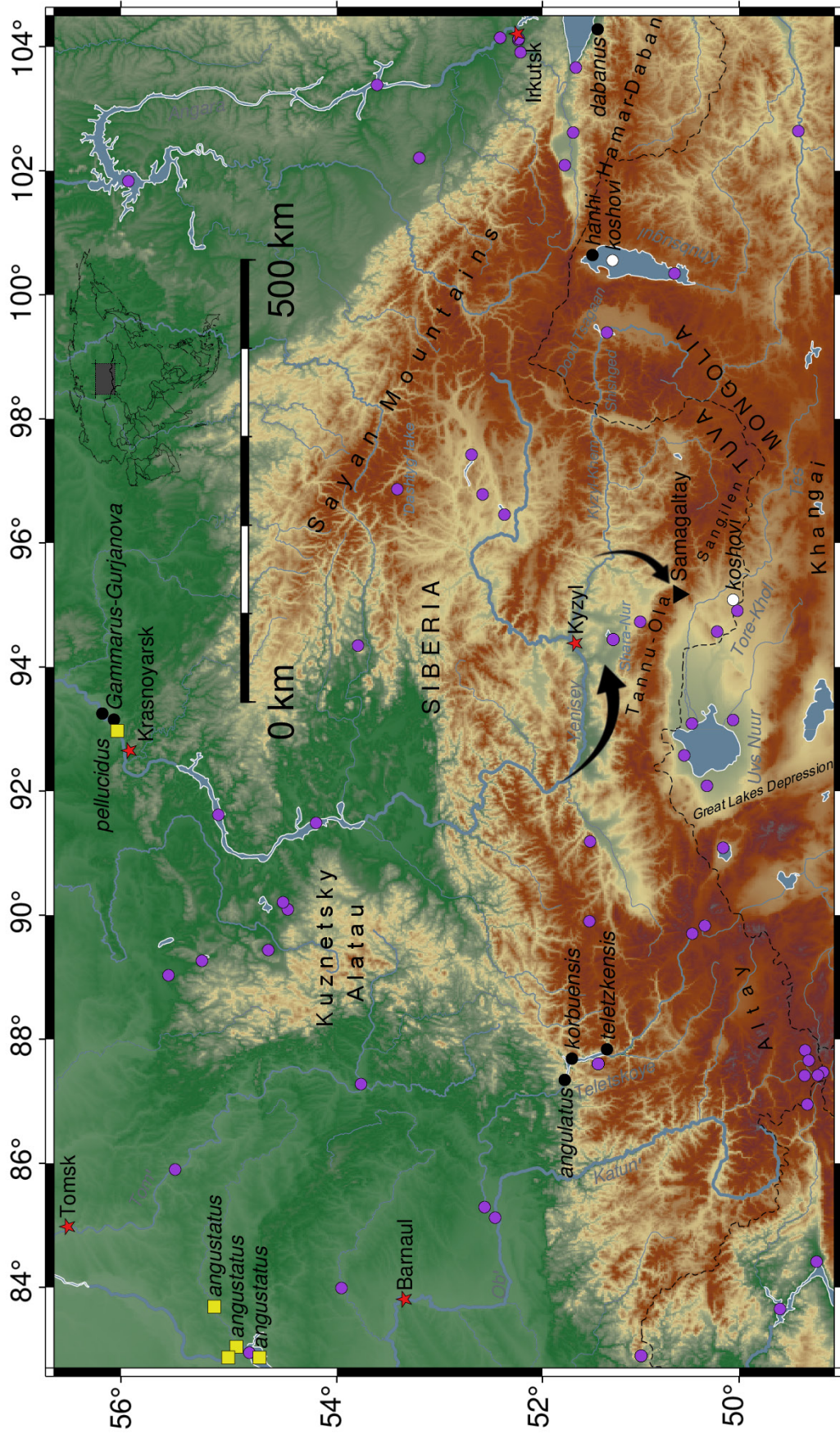


Fig. 1. Distribution map of *Gammarus* J.C. Fabricius, 1775 in Siberia. *G. koshoi* (Bazikalova, 1946) in Tore-Khol and Khubsugul Lakes (empty circles); *balcanicus* group (yellow squares); *pulex* group (filled circles) with *G. lacustris* G.O. Sars, 1863 (purple circles) coinciding with the entire Siberian part of the group's range. A contour line overview (top right) shows principal study area. Each point may represent 1–3 closely adjacent localities (for further explanation, see text).

Morphology

Specimens were dissected using a dissecting microscope Lomo MBS-9 and mounted on microscope slides in polyvinyl lactophenol (PVL) and stained with methylene blue (Sigma-Aldrich Company, Inc.); dissected appendages were then covered with a coverslip and edged by clear nail polish. Prior to dissection, body length (BL) was recorded by holding the specimen straight and measuring the distance along the dorsal side of the body from the base of the first antennae to the base of the telson. All pertinent morphological structures were drawn using a Carl Zeiss NU-2 compound microscope equipped with a drawing device as modified by Gorodkov (1961). The nomenclature for setal patterns on article 3 of the mandibular palp follows the standard described by Karaman (1970) and Stock (1974). A geographical map (Fig. 1), with the location of the sampling sites, was constructed with the open source software Generic Mapping Tools, GMT ver. 4.5.14. The description given here is based on the type series which is deposited in the private collection of D.A. Sidorov (prefix DAS).

Results

Taxonomy

Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Amphipoda Latreille, 1816
Superfamily Gammaroidea Latreille, 1802 (Bousfield 1977)
Family Gammaridae Leach, 1814
Genus *Gammarus* J.C. Fabricius, 1775

Gammarus koshovi (Bazikalova, 1946)
Figs 2–5

Rivulogammarus koshovi Bazikalova, 1946: 677, text-fig. (original description).

Rivulogammarus koshovi – Barnard 1958: 72. — Karaman 1991: 41.

Gammarus koshovi – Barnard & Barnard 1983: 467. — Erbaeva *et al.* 1990: 56. — Kozhova *et al.* 2000: 104. — Safronov 2006: 210.

Diagnosis (both sexes)

Compact, small-sized amphipod with well-developed eyes; coxal plates spacious (especially coxae 4 and 5); appendages comparatively short; antennae short and stout; peduncle articles 1–3 of antenna I comprise 33% of its total length, accessory flagellum 2-segmented with terminal article greatly reduced; antenna II with rare long setae on ventral face, males with calceoli; pereopods III and IV with clusters of setae on articles 4–6 posteriorly, carpi shortened; pereopod dactyli III–VII strong; uropod III endopodite somewhat shorter than exopodite, all margins with mix of setae of different length. BL = 8.0 mm (♀♀), 7.5 mm (♂♂).

Material examined (new records)

RUSSIA – **Tuva Republic** • 2 ♀♀ (BL = ca 8.0 mm); Tore-Khol Lake, isthmus; 50°02'42.6" N, 94°59'53.5" E; 6 m depth; 24 Jun. 2013; E.N. Yalysheva leg.; silted sand; DAS 16-013 • 2 juv. (BL = ca 5.0 mm); near Tore-Khol Lake, not far from recreation center; 50°06'02.4" N, 95°08'50.5" E; 7–8 m depth; 14 Aug. 2011, 27 Jun. 2015; E.N. Yalysheva leg.; silt; DAS 16-013 • 1 ♂ (BL = ca 7.5 mm); Sharlaa; 50°01'32.6" N, 95°03'28.4" E; 3 m depth; 13 Aug. 2011; E.N. Yalysheva leg.; silted sand; DAS 16-013 • 1 ♀ (BL = ca 8.0 mm); same collection data as for preceding; DAS 16-013 • 2 juv. (BL = ca

5.0 mm); same collection data as for preceding; DAS 16-013 • 1 ♀ (BL = ca 8.0 mm, damaged); site Yurty; 50°04'44.6" N, 95°08'38.5" E; 2 m depth; 28 Jun. 2015; E.N. Yalysheva leg.; silted sand; DAS 16-013.

Description

Female

SIZE. BL = 8.0 mm (oostegites developed, setose, bearing 13–15 small-sized eggs).

GENERAL BODY MORPHOLOGY (Figs 2A, 3A, 4G, 5A–B). Body stout, clearly setose with minute setules. Head with inferior antennal sinus moderate, subrounded, eyes pigmented. Pleon armed with dorsal setae. Coxal plates I–IV broad, lateral margins strongly overlap neighboring plates, distal margins rounded, with 2 short setae each, coxae II–III tapering distally, coxa IV lobate; coxal plates V–VII broad (especially, plate V). Coxal gills II–VII stalked and saccular, coxal gill VII smallest. Oostegites II–V (brood plates) of gammarid shape, well developed, oblong, plates II–IV broad, plate V the smallest. Posterior margin of epimeral plates I and II convex, not produced, with 3 setules each, distoposterior corner of plate I small, slightly produced, ventral margin with cluster of setae distoanteriorly; distoposterior corner of plate II strongly produced, with 4 long setae distoanteriorly; plate III strongly produced, but less than plate II, only with 2 spines on ventral margin and 3 long setae distoanteriorly. Urosomites with mediodorsal elevations, armed with groups of 2 spines and 1–3 setae, spine formula I–III is: 2–2–2 // 2–2–2 // 2–0–2. Telson shorter than uropod III peduncle; its width 88% of length, completely cleft, lobes apically with 2–3 notched spines accompanied by 3 long setae, laterally 1 spine or seta.

ANTENNAE (Figs 2A, 3B–C). Antenna I 40% of body length, peduncle articles in relation 1:0.6:0.35, flagellum of 17 articles, which are approximately twice as long as wide; accessory flagellum of 2 articles (1 long + 1 reduced); peduncle articles with short setae on ventral face and apically, articles of main flagellum with short setae, each flagellar article bearing minute aesthetasc, shorter than setae. Antenna II 67% of antenna I length, peduncle articles (4–5) slightly longer than flagellum; peduncle articles 4–5 bearing rare long setae on ventral face and short setae in 10 clusters along their entire lengths; flagellum modestly equipped with short setae, no calceoli.

MOUTH PARTS (typical gammarid, Fig. 3D–K). Mandibular palp with article 2 the longest, with 9 stiff setae, article 3 bearing 3 A-setae, 3 B-setae, 16 D-setae and 4 E-setae. Maxilla I asymmetric, palps broad, apically with ca 5 or 6 strong spines accompanied by thin setae; outer lobe with 12 subequal pectinate spines with ca 6 denticles each. Maxilla II inner plate with oblique row of 30 plumose setae on inner margin. Maxilliped basal endite (= inner plate) with 3 simple strong cuspidate spines on distal margin (+1 spine located subdistally); rest without peculiarities.

GNATHOPODS (Fig. 2B–C). Gnathopod I basis stout with long simple setae on anterior and posterior margins; carpus (article 5) triangular, $0.7 \times$ as long as propodus; propodus ovate, palm oblique, straight with cutting margin developed (no spines on medial face) and armed with 4 distally notched spines at defining angle; posterior margin as long as palm, bearing 4 sets of moderate setae; dactylus with 1 seta on outer face. Gnathopod II larger than gnathopod I; basis stout with long simple setae on anterior and posterior margins; carpus (article 5) $0.73 \times$ as long as propodus; propodus narrow, subrectangular, palm subtransverse, slightly concave, with cutting margin developed (spines on medial face lacking) and armed with 2 distally notched spines at defining angle; posterior margin twice as long as palm with ca 5 sets of setae; dactylus similar to that of gnathopod I.

PEREPODS (Fig. 4A–E). Pereopods III–IV subsimilar, but pereopod III densely covered with sets of moderate (as long as article widths) setae along posterior margins of articles 4–6; carpi (articles 5) reduced, about $0.6 \times$ as long as corresponding propodus, each with 1 set of very long setae apically. Pereopods V–VII strong, subsimilar, pereopod VI as long as pereopod VII; basipodites shortened, besides basipodite VII

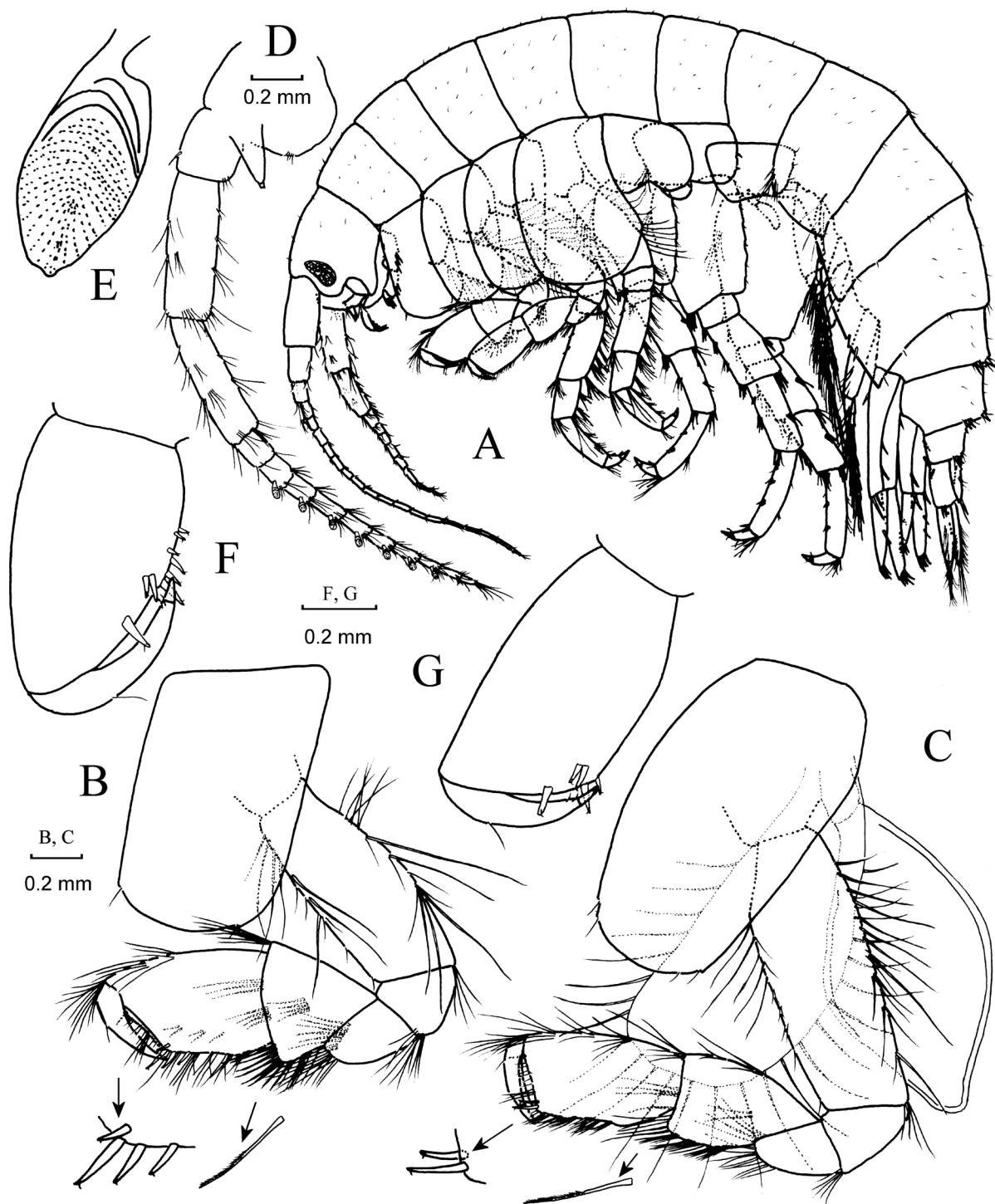


Fig. 2. *Gammarus koshovi* (Bazikalova, 1946), DAS 16-013. A–C. ♀, 8.0 mm. A. Habitus, lateral view. B. Gnathopod I. C. Gnathopod II. — D–G. ♂, 7.5 mm. D. Antenna II. E. Antenna II, calceolus ($\times 2800$). F. Gnathopod I, setation omitted. G. Gnathopod II, setation omitted.

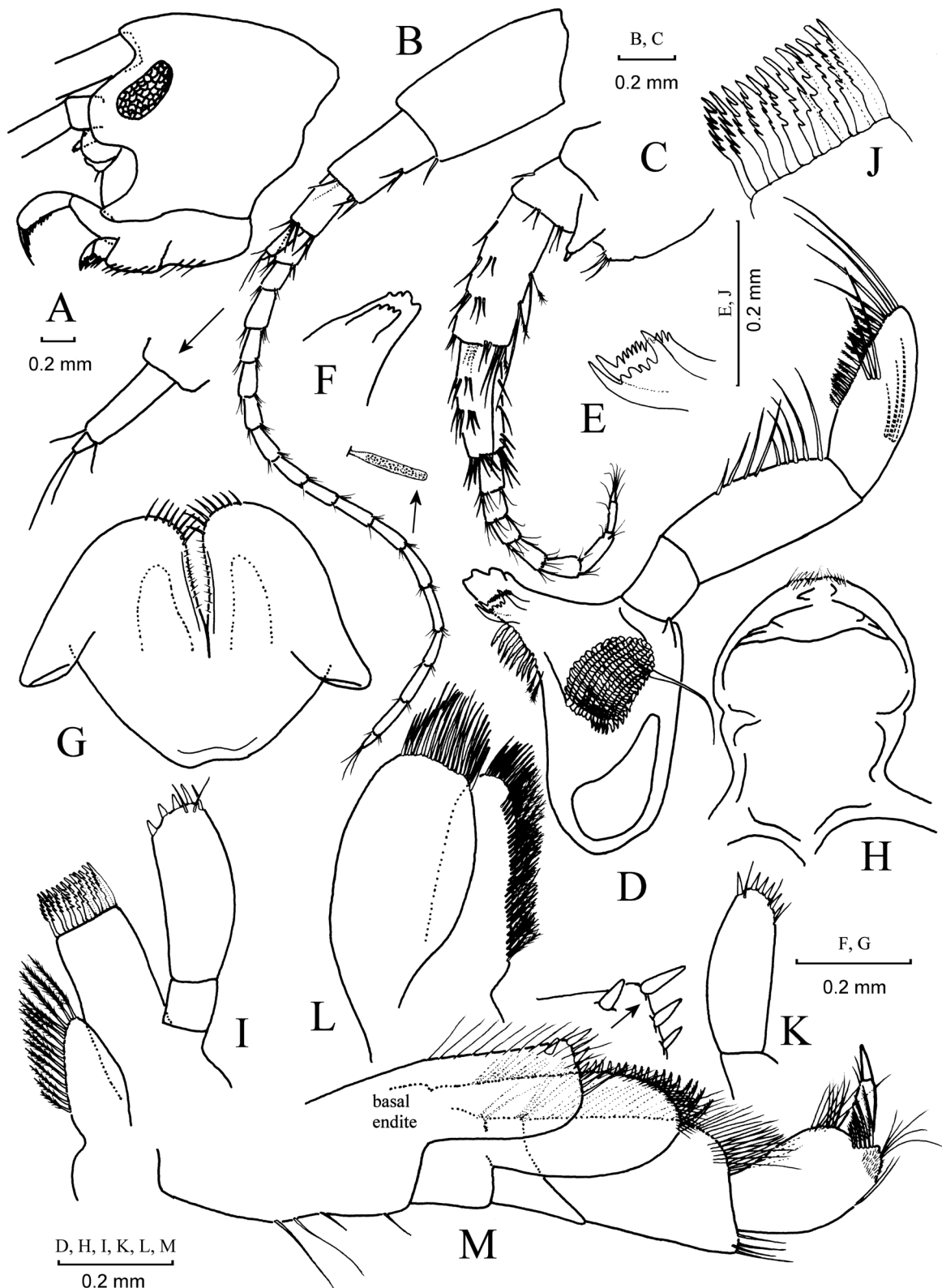


Fig. 3. *Gammarus koshovi* (Bazikalova, 1946), DAS 16-013, ♀, 8.0 mm. **A.** Head. **B.** Antenna I. **C.** Antenna II. **D.** Mandible, right. **E.** Mandible, lacinia mobilis ($\times 600$). **F.** Mandible, left (part.). **G.** Lower lip. **H.** Upper lip. **I.** Maxilla I, right. **J.** Maxilla I, outer plate ($\times 600$). **K.** Palp of maxilla I, left. **L.** Maxilla II. **M.** Maxilliped.

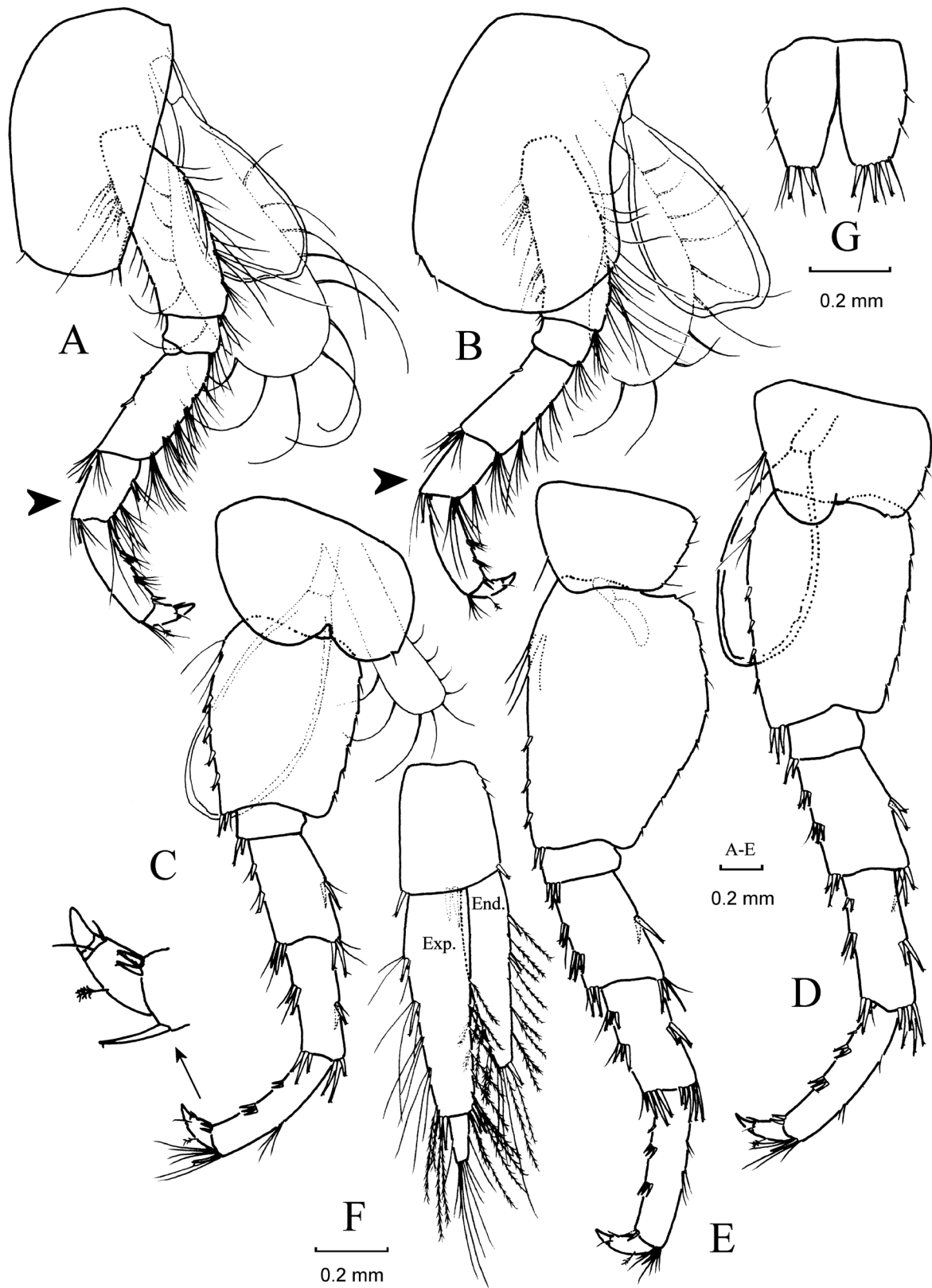


Fig. 4. *Gammarus koshovi* (Bazikalova, 1946), DAS 16-013. **A–E.** ♀, 8.0 mm. **A.** Pereopod III. **B.** Pereopod IV. **C.** Pereopod V. **D.** Pereopod VI. **E.** Pereopod VII. — **F–G.** ♂, 7.5 mm. **F.** Uropod III. **G.** Telson. Black arrowheads indicate reduced carpi.

with convex posterior margins, tapering distally, with 3 small spines and a tuft of setae along anterior and over 9 small setae along posterior margin; articles 4–5 with 4 or 5 pairs of paired spines along margins; dactylus ca 35% of propodus (article 6) length, with a short nail.

PLEOPODS AND UROPODS (Fig. 5C–H). Pleopods ordinary, rami subequal in length, segmented with 12–14 articles and fringed with plumose setae; peduncle with groups of thin setae, each retinacula two-hooked, accompanied by 1–2 slender simple stiff setae. Uropods I–II peduncles approximately reaching the end

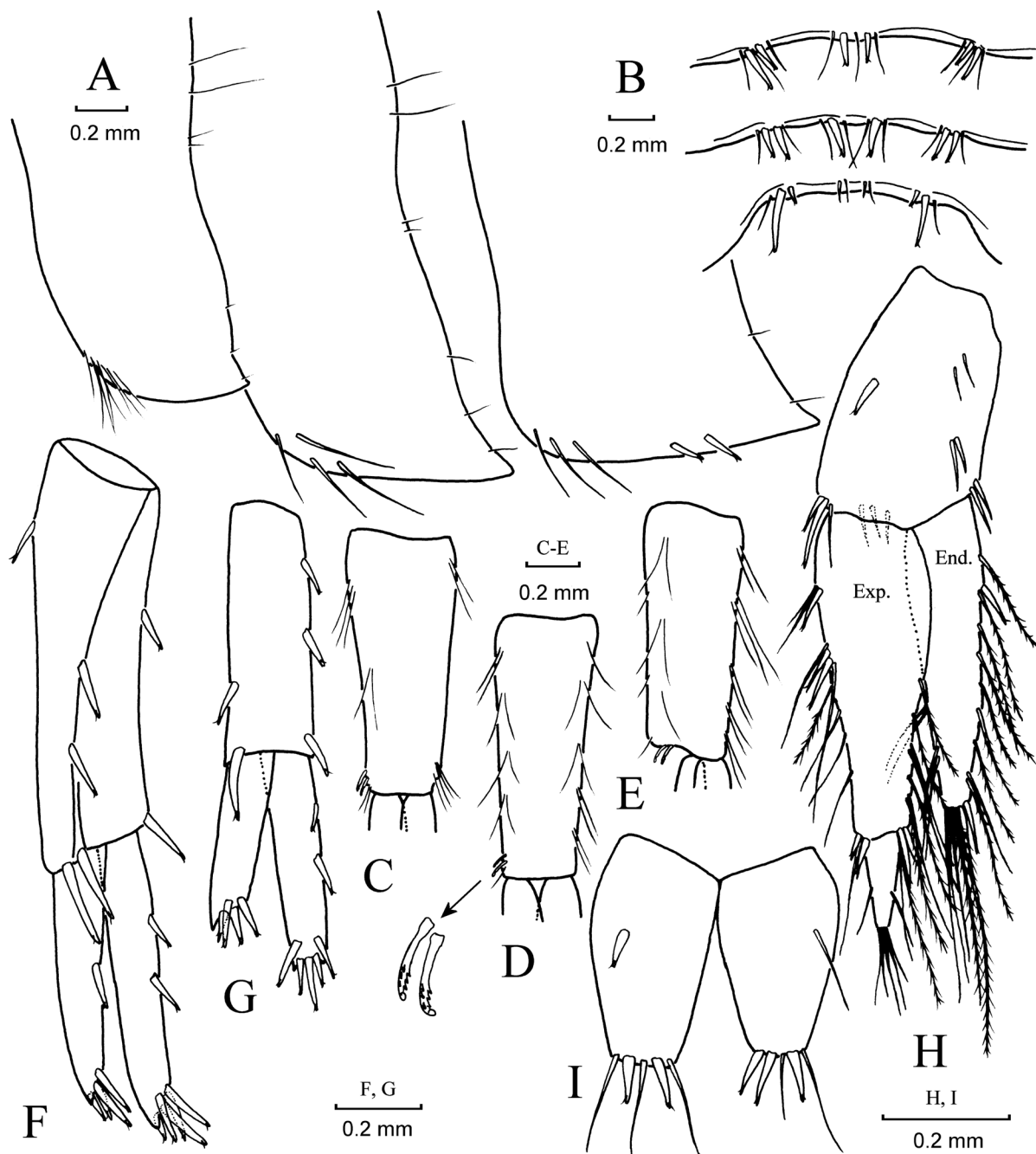


Fig. 5. *Gammarus koshovi* (Bazikalova, 1946), DAS 16-013, ♀, 8.0 mm. **A.** Epimeral plates I–III. **B.** Urosoma, dorsal view. **C–E.** Pleopods I–III (part.). **F.** Uropod I. **G.** Uropod II. **H.** Uropod III. **I.** Telson.

of uropod III peduncle, uropod I rami slightly beyond end of uropod III; peduncles with ca 4 or 6 spines along edges, uropod I with 1 basofacial spine, with 1 or 2 single spines along rami, with 3 apical and 2 subapical spines. Uropod III peduncle with 1 facial spine and 4 stiff setae and ca 8 weak spine-setae on apical margin; endopodite (= inner ramus) comprises 90% of exopodite (= outer ramus) length, with cluster of 1 spine and very long setae apically; terminal article of exopodite long, with tuft of short setae apically; both rami with moderately dense marginal brushes with mix of relatively long simple and plumose setae.

Male

Single, apparently subadult male, with habitus smaller (BL = 7.5 mm) and more slender; flagellum of antenna II with 10 articles, each with calceoli of gammarid type (type 1) (Lincoln & Hurley 1981); gnathopods subsimilar to those of female, but propodi heavily armed at defining angle, each palm bearing 1 mid-palmar spine; uropod III weakly fringed with setae; in all other characters similar to female.

Variation

Not observed.

Taxonomic remarks

The enigmatic *G. koshovi* (Bazikalova, 1946) was collected in Lake Khubsugul of northeastern Mongolia (Fig. 1) and was reported in several previous publications (see Erbaeva *et al.* 1990; Safronov 2006; Dulmaa 2009), which has now necessitated a comparative study of this species with that in the remote Tore-Khol population of the Uvs Nuur Basin. *Gammarus koshovi* from Khubsugul was described rather superficially; a holotype was not deposited, which complicates detailed comparison. Furthermore, actual sampling of the Khubsugulian gammarids was not possible for correct comparisons. Although the original *G. koshovi* vs that in the Tore-Khol population exhibit differences, their pattern and variability are not clear (Table 1). Nevertheless, we consider these two forms to be closely related and belonging to the same lineage and united by the following: common fossorial morphotype (compact body, abbreviated antennae, spacious coxal plates, and strong, short pereopods with robust dactyli), presence of calceoli in antenna II of males, armament and gnathopod shape in both sexes, armament of urosomal segments, furnishing of pereopods, uropods, and telson. Bazikalova (1946) ignored the morphology of the carpi of pereopods III and IV. Additionally, her indication that antenna I comprised 25% of the entire body length with the number of articles 11–12 (♂♂) and 8–12 (♀♀) for 7–8 mm long specimens is doubtful. It should be noted that *G. koshovi* is related to *Gammarus* sp. in Gurjanova (1930) described from Yenisey's riffle (downstream of Krasnoyarsk) based on several juvenile specimens with well-developed marsupial plates. Gurjanova (1930) compared the Yenisey form with juveniles of *G. pulex* (= *G. lacustris* G.O. Sars, 1863) from Karelia and the Polar Urals (see also Kessler 1868) and found them sharply different. Among the Central Asian members of *Gammarus* (Martynov 1935), the Tuvan-Mongolian *G. koshovi*, because of its small size, gravitates to a poorly distinguishable species from the springs of Turkestan, but the forms described by Martynov, despite their small size, still possess elongated antennae and not shortened pereopods, and are clearly distinguishable by their reduced eyes (see also *Gammarus parvioculatus* Sidorov, Hou & Sket, 2018 in Sidorov *et al.* 2018: 445). Furthermore, there is no close similarity with species of the highly diversified Altay and Tian-Shan group of *Gammarus* (Zhao *et al.* 2017; Zheng *et al.* 2020). This indicates that the territory of Siberia/Mongolia, possibly the basin of the middle Yenisey, is inhabited by a small burrower-like form of *Gammarus*, the origin and phylogenetic relationships of which are unresolved.

Accompanying fauna

Mollusca, Ostracoda (subfossil, represented by separate valves), Coleoptera, larvae of Chironomidae and Ephemeroptera.

Table 1. Comparison of character differences of *Gammarus koshovi* (Bazikalova, 1946) from two lacustrine populations.

Feature	Locality	
	Tore-Khol Lake	Khubsugul Lake
Antenna I covers	40% of body length	25% of body length
Antenna I, primary flagellum with	19 ♂, 16–17 ♀♀ articles	11–12 ♂♂, 8–12 ♀♀ articles
Antenna II, flagellum with	10 ♂, 7–8 ♀♀ articles	6–7 ♂♂, 4–6 ♀♀ articles
Pereopods V–VII, along posterior margins of basipodites	from 5 to 9 setae	from 14 to 16 setae
Epimeral plates I–III	I (set of setae disto-anteriorly), II (setae disto-anteriorly), III (2 spines)	I (a row of setae along ventral margin), II (setae cover 2/3 along ventral margin), III (spines absent)
Telson, lobes apically	with 2–3 spines each	with 4 spines each

Distribution and ecology

Previously recorded from the area of Pupok Island in Khubsugul Lake (Fig. 1), a burrower-like gammarid form that dwells on silty sand at a depth of 15–16 m (Bazikalova 1946). Details of its biology in Khubsugul are lacking (Dulmaa 2009), but for Bazikalova to rely on the ‘burrowing morphotype’ implies its fossorial behavior. We have no direct observations of the burrowing behavior of the species, except that the samples were collected by bottom grabs in the Tore-Khol on muddy bald patches devoid of vegetation.

Gammarus lacustris G.O. Sars, 1863

Gammarus lacustris G.O. Sars, 1863: 207 (original description).

Gammarus pulex sibiricus – Kiseleva 1920: 15 (lakes of Ob’ basin).

Gammarus pulex – Sars 1901: 133 (NE Mongolia); 1903: 233–261 (Siberia, Kazakhstan, Mongolia, Tibet). — Pirozchnikov 1929: 70 (Yenisey, upstream of Krasnoyarsk). — Lepneva 1930: 135 (around Biysk); 1933: 151 (Altay lakes). — Karaman 1991: 38 (see for full synonymy).

Material examined (new records)

RUSSIA – **Tuva Republic** • 3 ♀♀ (oostegites developed, some brooding the eggs), 15 ♂♂ (BL = up to 14.0 mm); small freshwater lake, southward of Shara-Nur Lake, near shepherd’s camp; 50°13′29.4″ N, 94°32′32.1″ E; 2–5 m depth; 12 Aug. 2011; E.N. Yalysheva leg.; yellowish silt, sapropelic mud with smell of hydrogen sulfide, plant residues (*Phragmites australis*); DAS 16-014 • 1 ♀ (BL = 17.0 mm); ‘Dashtyg’ taiga lake, upper reaches of Yenisey (source of Dashtyg-Aryg Stream), Todzha; 53°25′12.2″ N, 96°51′52.7″ E; 0.5 m depth; 4 Aug. 2010; E.N. Yalysheva leg.; middle of lake, boulders, rubble, fouling, depressions between stones slightly silted; DAS 16-015.

Remarks

Considering the outstanding morphogenetic polymorphism (Sket *et al.* 2019) and the very wide distribution of Holarctic/Sino-Indian *G. lacustris* in the water bodies of Siberia (Tuva) and Mongolia (Fig. 1), it is highly probable that juveniles of this species can be misidentified as small species, such as *G. koshovi*. However, *G. lacustris* was absent in our samples from Tore-Khol, which we associated, first of all, with partial acidification of waters in the Russian part owing to the increased anthropogenic pressure because of intensive grazing, fishing, and other economic activities. It was previously reported that *G. lacustris*

critically avoids water environments with pH < 5 (Moiseenko & Yakovlev 1990). However, the exact reasons for this observation remain to be solved.

Distribution and ecology

Mostly inhabits the pluvial lakes of the region (Fig. 1), though it is also observed in lakes of the Baikal Rift Zone (previous indications in Baikal are accidental, in Stom & Timofeev 1999; but see Vereshchagina *et al.* 2021). Kamaltynov (2009) reported the following data: common at depths of 0–7 m, on pebbles with sand and detritus, silted sand, flooded woods, remains of vegetation, and abundant in aquatic plant thickets. Inhabits thermal springs with temperatures up to 23°C and mineralization up to 340.5 mg/L. Inhabits small lakes and rivers of the Baikal basin, in the Baikal and Transbaikal regions (including the Irkutsk and Bratsk reservoirs), adjoining water bodies of the Yenisey and Ob', lakes in the Vilyui region of Yakutiya, lakes in the interfluvium of the Lena and Aldan rivers, Bauntovskye lakes, lakes in Mongolia (Khubsugul and Selenga basin, lakes and streams of Darhat Valley, Uvs Nuur Basin, Great Lakes Depression, and Valley of Lakes) (Dybowsky 1901; Sars 1901; Greze & Greze 1958; Bezmaternykh 2008; Kamaltynov 2009; Østbye *et al.* 2018; Tolomeev *et al.* 2018). Paul (2012) indicated that *G. lacustris* inhabits the Mongolian part of Tore-Khol Lake.

Key to the Siberian species of *Gammarus* (based on adults of both sexes)

Gammarus barnaulensis Schellenberg, 1937 is not included in the key as the original description does not provide appropriate morphological features.

1. Body and appendages ordinary, length more than 8.0 mm 2
– Body compact, appendages shortened, length up to 8.0 mm (burrowing group*) 9
2. Species with dense setation on pereopods III–IV and uropod III (*pulex* group) 3
– Species with poorly setose pereopods III–IV and uropod III (*balcanicus* group) 8
3. Pereopod dactyli long, slender 4
– Pereopod dactyli short, stout 5
4. Urosomal segments moderately armed *G. lacustris* G.O. Sars, 1863
– Urosomal segments richly armed *G. hanhi* Safronov, 2006
5. Uropod III endopodite inner face with setae 6
– Uropod III endopodite inner face naked *G. teletzkensis* Martynov, 1930
6. Epimeral plates II–III, ventral margins without setae, with spines 7
– Epimeral plates II–III, ventral margins with a row of long setae *G. angulatus* Martynov, 1930
7. Antenna I slightly more than half of body length *G. korbuensis* Martynov, 1930
– Antenna I distinctly less than half of body length *G. dabanus* Tachteev & Mekhanikova, 2000
8. Antenna I, main flagellum up to 28 articles *G. angustatus* Martynov, 1930
– Antenna I, main flagellum with 34–35 articles *G. pellucidus* Gurjanova, 1930
9. Telson, lobes apically with 4 spines *G. koshovi* (Bazikalova, 1946)
– Telson, lobes apically with 1 or 2 spines *Gammarus* sp. in Gurjanova (1930)

* Conventionally proposed group to which we additionally assign *Gammarus* sp. in Gurjanova (1930).

Discussion

During a detailed and comparative study of the lacustrine amphipod fauna in Inner Asia, a remote population of the poorly known *Gammarus koshovi* (Bazikalova, 1946), which was previously known only from the flowing Lake Khubsugul, was discovered. The history of lake formation in Inner Asia and the evolutionary transformations that they underwent are closely related to global processes throughout the Mesozoic-Cenozoic epoch (Gladkochub & Donskaya 2009; Shuvalov 2013). Khubsugul Lake is the largest and deepest freshwater lake in Mongolia and the second largest (after Lake Baikal) in Inner Asia. It is associated with Baikal by a common origin and confinement to the Baikal Rift Zone, a common history of development, and modern ‘arctic’ runoff through the Egiin and Selenga Rivers (AOW – Arctic Ocean Watershed in Maasri & Gelhaus 2012). The discovery of a small burrower-like form of the genus *Gammarus* raises a number of questions, viz., why is *G. koshovi* absent in Baikal Lake and in other pools of its catchment area, and does it claim the role of a supposed ancestor for Palearctic forms? The burrowing lifestyle and special fossorial morphology is a fairly common phenomenon among marine amphipods, such as Haustoriidae Stebbing, 1906 (Bousfield 1970), as well as freshwater amphipods like the Baikal *Micruropus* Stebbing, 1899, *Crypturopus* Sowinsky, 1915 (Bazikalova 1962; Takhteev 2000), and the Caspian *Pontogammarus* Sowinsky, 1904, and *Niphargoides* G.O. Sars, 1894 (Copilaş- Ciocianu & Sidorov 2021). However, it is rather unique for lacustrine amphipods of the genus *Gammarus*. Amongst 264 described species of the genus *Gammarus*, no lacustrine burrowing forms are known (Horton *et al.* 2021).

A number of endemic species in the Mongolian Khubsugul are prescribed a common genetic relatedness with the Baikalian groups. However, this has not been confirmed for gammarids, indicating their independent origin in these lakes (Kozhova *et al.* 2000; Goulden *et al.* 2006). Khubsugul has a less diverse set of biotopes and is much younger than Baikal, with the beginning of sedimentation expected to be no older than the Pliocene (Zorin *et al.* 1989). The ancient Mongolian multi-lake area in the Neogene is characterized by a developed lake-river system and is fed by numerous large rivers originating in the neighboring mountain structures of Khangai (Tes, Dzavkhan), Altay (Khovd, Bulgan), Khingan (Khalkhin), and Khentei (Kerulen) (Shuvalov & Deviatkin 2013). Prozorova & Zasyapkina (2010) analyzed the distribution of *Odhneripisidium* Kuiper, 1962 and had the opinion that a shallow-water molluscan fauna formed in the flowing areas of the basin of a giant paleolake that existed in the Neogene up to the Late Pliocene (Florensov 1968). Herein, our original data for the Tore-Khol concerns only amphipods (2 spp.). However, it is known that the fauna of the lake is quite distinctive, although it mainly contains the typical inhabitants of the lentic environments of Inner Asia. Among others, the following elements are known: sponges (Spongillidae) (Wiens *et al.* 2009), taxonomically rich zooplankton (Flößner *et al.* 2005; Kirova *et al.* 2020), Oligochaeta, and amphibious Insecta (Trichoptera, Ephemeroptera, Chironomidae), mostly represented by taxa indicating a Palearctic distribution (Zaika & Makarov 2000; Paul 2012). In numerous springs surrounding the lake, the following are common – Odonata, Plecoptera, Turbellaria, water boatman bugs (Corixidae), and water beetles (Dytiscidae) (Zaika 2011). Therefore, a couple of species are common to both lakes Tore-Khol and Khubsugul – *Anisus* (*G.*) *terekholicus* Prozorova & Starobogatov, 1997, also known from Nogoön and Durgun Lakes, and the aforementioned *G. koshovi* (Bazikalova, 1946) (see Kozhova *et al.* 1994; Prozorova & Starobogatov 1997; Sitnikova *et al.* 2011). The presence of the widespread amphipod *G. lacustris* in these lakes, as well as the taxonomic status of the Khubsugulian *G. hanhi* Safronov, 2006, requires further confirmation.

An interesting observation by Belostotsky (1958) is that it is likely that from the Jurassic (Mesozoic) to the Pleistocene (Cenozoic) era, the upper part of the Yenisey basin was discharged into the Ubsunur system through the Samagaltay passage (located between Tannu-Ola Ridge and the western spurs of Sangilen Upland) (Fig. 1). This point of view is supported by a number of authors (Izzatullaev & Starobogatov 1985; Tshernyshev 2010; Lukashov & Smoktunovich 2018). However, based on some elusive similarity of the Yenisey *Gammarus* sp. in Gurjanova (1930) and *G. koshovi*, along with the unclear taxonomic status

of the former, such an observation does not seem obvious. However, if the Yenisey acts as a ‘faunistic donor’ for the Ubsunur Basin, it is an interesting observation that the basin, as the largest endorheic basin (CAIW – Central Asian Inland Watershed in Maasri & Gelhaus 2012), accumulates peripheral biodiversity.

It is well known that amphipods are amazingly plastic in terms of adaptations to various environmental conditions (they occupy all types of biotopes from oceanic trenches to the interstitial areas of sandy beaches and cave pools), show response to habitat drying (Gilbert *et al.* 2018), and have an effective ability to survive (Thorp & Rogers 2011) and disperse (Rachalewski *et al.* 2013). The unlimited dispersal ability of epigeal gammarids within drainage areas (Altermatt *et al.* 2014) in contrast to increased diversification rates due to isolation through mountain barriers (Hou *et al.* 2014), in combination with multiple rearrangements of the hydrographic networks of Inner Asia during the historical period (Zherikhin 2003; Zabelin & Zaika 2021) could have positively affected the expansion of a species range. Therefore, we assume that upon careful research, *G. koshovi* will also be found in other lakes of the region.

Finally, we have concluded that an excessive presence of ‘gray spots’ in gammarid taxonomy significantly violates the accuracy of biogeographic information at a global scale. According to rough estimates, more than 80% of the described species of the genus *Gammarus* inhabiting the crucial region of Central Asia, Siberia, and the Far East need to be re-examined, and the number of undescribed species cannot be properly estimated.

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