



Three new remarkable amphipod species (Crustacea: Gammaridae) from springs and subterranean waters of Central Asia

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Abstract

Three new species of the family Gammaridae—*Gammarus troglomorphus*, sp. n., *G. parvioculatus*, sp. n. from Lebap Province of Turkmenistan and *Tadzocrangonyx alaicus*, sp. n. from Batken Region of Kyrgyzstan are described and illustrated. Morphological studies of a closely related Turkmenistan population of *G. cf. subaequalis*-Garlyk, probably conspecific with *Gammarus subaequalis* Martynov, 1935 was provided. The affinity of new species to concerned taxa is discussed. To define phylogenetic position of mentioned species DNA barcode data are obtained. *Gammarus troglomorphus* and *G. parvioculatus* are close neighbors but exceedingly different morphologically. *Gammarus troglomorphus* is a troglobiont; *G. parvioculatus* is an eutroglophile, but with exception of slightly smaller eyes, not troglomorph. Both found only within small areas in the extreme East of Turkmenistan. *Gammarus cf. subaequalis*-Garlyk seems to extend from the same region far into the eastern Kyrgyzstan.

Key words: Amphipoda, Gammaroidea, taxonomy, new species, mtDNA, Central Asia

Introduction

The amphipods of Central Asia have been studied insufficiently for a long time. Taking into account a perplexing paleogeographical history of the region (e.g., Atamuradov 1994) and the high degree of ruggedness of its landscape, it is hard to obtain a complete picture of the region's fauna, its origin and biogeography. Perhaps the first important and significant event was the finding of *Issykogammarus hamatus* Chevreux, 1908 from the brackish mountain lake Ysyk-Köl (Issyk-Kul, Isiq-Köl) in Tian-Shan (Chevreux 1908). Further, the most extensive layer of research was carried out by the Soviet authors on the territory of the former Soviet republics when some interesting species of amphipods were discovered as *Tadzocrangonyx schizurus* (Birštejn, 1948) (syn. *Crangonyx s.*) from the Kondara valley in Tajikistan (Birštejn 1948), its relative *T. setiferus* (Birstein et Ljovuschkin, 1972) (syn. *Crangonyx s.*) from a spring in Kyrgyzstan (Birstein & Ljovuschkin 1972), *Bogidiella ruffoi* (Birstein et Ljovuschkin, 1968) from some springs (incl. our samples) in the eastern Turkmenistan (Birstein & Ljovuschkin 1968). A few representatives of the genera *Sarothrogammarus* Martynov, 1935, *Comatogammarus* Stock, 1971 and *Barnardiorum* Iwan et Löbl, 2007 (syn. *Tadzhikistania*) also have been noted previously in several regions of Central Asia (Ruffo 1958; Karaman 1969a, b; Karaman 1971; Stock 1971; Barnard & Barnard 1983; see also Birstein & Ljovuschkin 1965). Information on the distribution of the Caspian relict amphipod fauna is largely heterogeneous and fragmented (Behning 1938; Birštejn 1945a; Stock 1974; Kulkina 1990; Sidorov *et al.* 2013). A variety of representatives of the genus *Gammarus* Fabricius, 1775 have been more extensively studied and described in the region (see Martynov 1930, 1935, 1936; Birštejn 1935, 1945b, 1948; Martynov & Behning 1948; Karaman & Pinkster 1977; Sidorov, 2012). The subterranean amphipod fauna is poorly known or virtually poor in Central Asia (Kulkina 1992; Holsinger 1993). Thus, for example stygobiotic representatives of *Gammarus* have not been mentioned so far except that some poorly defined 'subtaxa' of the poorly known *Gammarus turanus*

Martynov exhibit 'small' eyes (Martynov 1935). Troglomorph and certainly troglobiotic are both *Tadzocrangonyx* spp., while some small-eyed *Sarothrogammarus* group species are also often mentioned as occurring in caves (Barnard & Barnard 1983).

As a part of inventory of the amphipod fauna of Central Asia the expeditional studies have been conducted in the region during the field mission to Kyrgyzstan (in 2012) and to Koytendag State Nature Reserve of Turkmenistan (in 2015) resulted in collection of the three remarkable new species of *Gammarus* and supposedly *Tadzocrangonyx* as described below.

Material and methods

Sampling. Gammarids were sampled in springs by a hand net. Samples were fixed and stored in ethanol 96% with a small amount of glycerol added; such animals are appropriate for DNA analyses and still not too rigid for morphological study. Single specimens for DNA analysis were partly dissected and some muscle tissues or small body parts taken for analysis. The rest of the body, including all taxonomically relevant parts, has been retained as voucher specimens for subsequent morphological study.

Morphology. Specimens were dissected using a dissecting microscope Lomo MBS-9 and mounted on microscope slides in polyvinyl lactophenol (PVL) and methylene blue stain (Sigma-Aldrich Company, Inc.); dissected appendages were then covered with a coverslip and edged by clear nail polish. Prior to dissection, body length 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. An extremely calcified specimen was subjected to the procedure mitigating the rigidity of the cuticle. 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 term 'defining angle' (or 'palmar angle') of the gnathopod refers to the angle formed at the end of the palm and beginning of the posterior margin or the point at which the tip of the dactylus closes on the propodus (Birstein 1941; Holsinger 1974). The nomenclature for setal patterns on article 3 of the mandibular palp follows the standard described by Karaman (1970) and Stock (1974). Materials are deposited at the zoological collection of the Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani and in the research collection of D.A. Sidorov (DAS prefix) at East Asia terrestrial biodiversity center, Vladivostok.

Molecular methods. A partial fragment of the mitochondrial cytochrome c oxidase subunit I (MT-COI) was proposed as a crustacean barcode (Costa *et al.* 2007; Hou *et al.* 2009). The primers used are LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.* 1994). Genomic DNA extraction, amplification, and sequencing procedures were performed as in Hou *et al.* (2007). All sequences have been submitted 11 Dec. 2017 [<http://www.ncbi.nlm.nih.gov/>] to GenBank (accession numbers MG655627–MG655630).

Species descriptions

Order Amphipoda Latreille, 1816

Family Gammaridae Leach, 1814

Genus *Gammarus* Fabricius, 1775

Gammarus troglomorphus, sp. n.

Figures 1A, 2–5

Material examined. Holotype specimen NC181: male, 12.4 mm; collapse sinkhole (sink-lake) Suuv Oyuk, 37.596778, 66.405500, 360 m a.s.l., near Garlyk (Karljuk), Köýtendag District, Lebap Province, Turkmenistan, leg. 29 May 2015 by B. Sket, M. Pereladov and B. Zimmerman. Paratype NC182: female, 11.5 mm, oostegites developed, setose, bearing 19 medium-sized eggs; same data as holotype.

Diagnosis. A medium sized, pigmentless and eyeless *Gammarus* with conspicuously elongated appendages; epimera expanded acute, II sickle shaped; urosomites with dorsal laterally compressed bulges; pereopod VII and uropod I reaching close to tips of uropod III; spines of maxilla I outer lobe densely serrated; uropod I–II rami smooth; uropod III, endopodite little shorter than exopodite, all margins densely setose.

GenBank accession number: MG655628 for isolate 513GtroglomTUM.

Etymology. Specific epithet '*trogloformus*' refers to the adaptive cavernicolous morphological features.

Description. GENERAL BODY MORPHOLOGY (Figs 1A, 3F, G, 4I). A stout, weakly setose *Gammarus* without dark body and eye pigmentation. *Body* length up to 12.4 mm. *Head* with short and rounded, up-down symmetric genal plates. *Pereon* and *pleon* not armed, without dorsal setae. *Coxal plates I–IV* with rounded distal margins, with 2–4 setae each, coxae II–III tapering distally, IV lobate. *Branchia* II wide, III–IV narrower, all larger than coxal plates. *Epimeron I* disto-posteriorly only slightly produced, without spines or setae. *Epimeron II* disto-posteriorly very strongly produced, the entire plate nearly sickle shaped; with 2 weakly developed spines disto-anteriorly and 2 small setae along posterior margin. *Epimeron III* strongly produced, but less than epimeron II; only with 2 small spines on its distal margin. *Urosomites* with laterally compressed medio-dorsal elevations, with groups of (1-) 2 spines and (0-) 1 seta; median groups on top of elevations and withdrawn anteriorly; spines formula I–III is: 2–2–2 // 1–2–1 // 2–2–2. *Telson* narrow, its width 75% of length; split to 80% or deeper; lobes apically with 2–3 spines and 3 long setae, laterally single groups of 2 setae. ANTENNAE (Figs 1A, 2A, B). *Antenna I* 75% of body length, peduncle articles in relation 10:8:5, flagellum of 33 articles, which are approximately twice as long as wide; accessory flagellum of 2 long articles. Peduncle articles with setae only apically, they are less than 10 and very short and fine; such is also the setation of flagellar articles, each flagellar article bearing aesthetasc, shorter than setae. *Antenna II* 45% of antenna I length, its long peduncle articles and flagellum in relation 10:11:19; articles 4–5 with less than 10 groups of 2–6 small setae (in each group) along their entire lengths; flagellum modestly equipped with short setae; no calceoli. MOUTH PARTS (typical gammarid, Figs 2C–J). *Mandibular palp* with article 2 the longest, with 2 short and 5 longer setae, article 3 with only 2 inner groups of 4 setae each. *Maxilla I* asymmetric, palps narrow, apically with ca. 5 strong setae or spines. Outer lobe with 10 subequal, densely pectinate spines with ca. 20 denticles. *Maxilla II* and *maxilliped* without peculiarities. GNATHOPODS (Figs 3A, B). *Gnathopod I* article 6 narrow and poorly setose, palmar angle in its middle, article not pear-shaped; short facial setae in ca. 5 groups of 1–3, setae along posterior and palmar margins up to twice longer, but up to 5 groups of setae along posterior margin with only 2–5 setae each; palmar spines weak; article 5, distal half of posterior margin with 6 groups of short setae, parallel with anterior one. *Gnathopod II* articles 5–6 elongated, their posterior margins parallel with anterior ones; article 5 with 8 groups of posterior and 2 groups of facial setae, anteriorly only with the distal setae; article 6 narrow, with moderately inclined palmar margin, with 8 facial groups of 1–5 setae; one slender spine between dactylus and the slender palmar spine, posterior margin with 7 groups of setae which are half shorter than the article width. PEREOPODS (Figs 1A, 4A–E). *Pereopods III–IV* with ca. 6–7 only modestly dense groups of stiff setae on articles IV–VI posteriorly, setae lengths on 4–5 up to double article width, on VI shorter; dactylus approximately 30% of article 6 length, nail ca. 40% of dactylus length. *Pereopods V–VII* elongated, their lengths relation 10:11:11, the VII if extended, reaching tips of uropod III, 70% of body length; bases (articles 2) narrow, only slightly tapering distally; disto-posterior lobes very short, acute; posterior margin in VI–VII straight, in V slightly concave, ending distally in small rectangular and acute lobes; anterior margins with 2–3 spines in their distal halves. Along each, anterior and posterior margins of article 4 2–4 pairs of spines, in article 5 there are 4–6 single or paired; dactyli ca. 20% of article 6 length, nails ca. 35% of the entire dactylus long. PLEOPODS AND UROPODS (Figs 3C–E, 4F–H). *Pleopods* normal, retinacles of 2 hooked and 1–3 sharp spines. *Uropods I–II* very long, peduncles with 2 short facial and some apical spines, uropod I with a basofacial spine; rami shorter than the peduncle, only with very short apical spines; peduncles reaching close to the uropod III peduncle end, rami beyond the middle of uropod III rami. *Uropod III* peduncle twice as long as wide, only with some spines distally; exopodite with a minute article 2, with moderately long plumose setae along both margins; endopodite ca. 85% of exopodite long, similarly setose, but outer row with simple setae.

Female. Body 11.5 mm long. *Antenna I* with 31 articles. *Gnathopods* (Figs 5A, B) similar as in male, just slightly more setose. *Oostegites* (Figs 5B–E) comparatively narrow, II 30% as wide as long, III–V narrower, marginal setae in posterior oostegites as long as the plates wide. *Pereopod V* basipodite with a slightly produced acute disto-posterior lobe. *Uropod III* and *telson* (Figs 5F, G) in all characters similar as in male, just smaller and less richly setose.

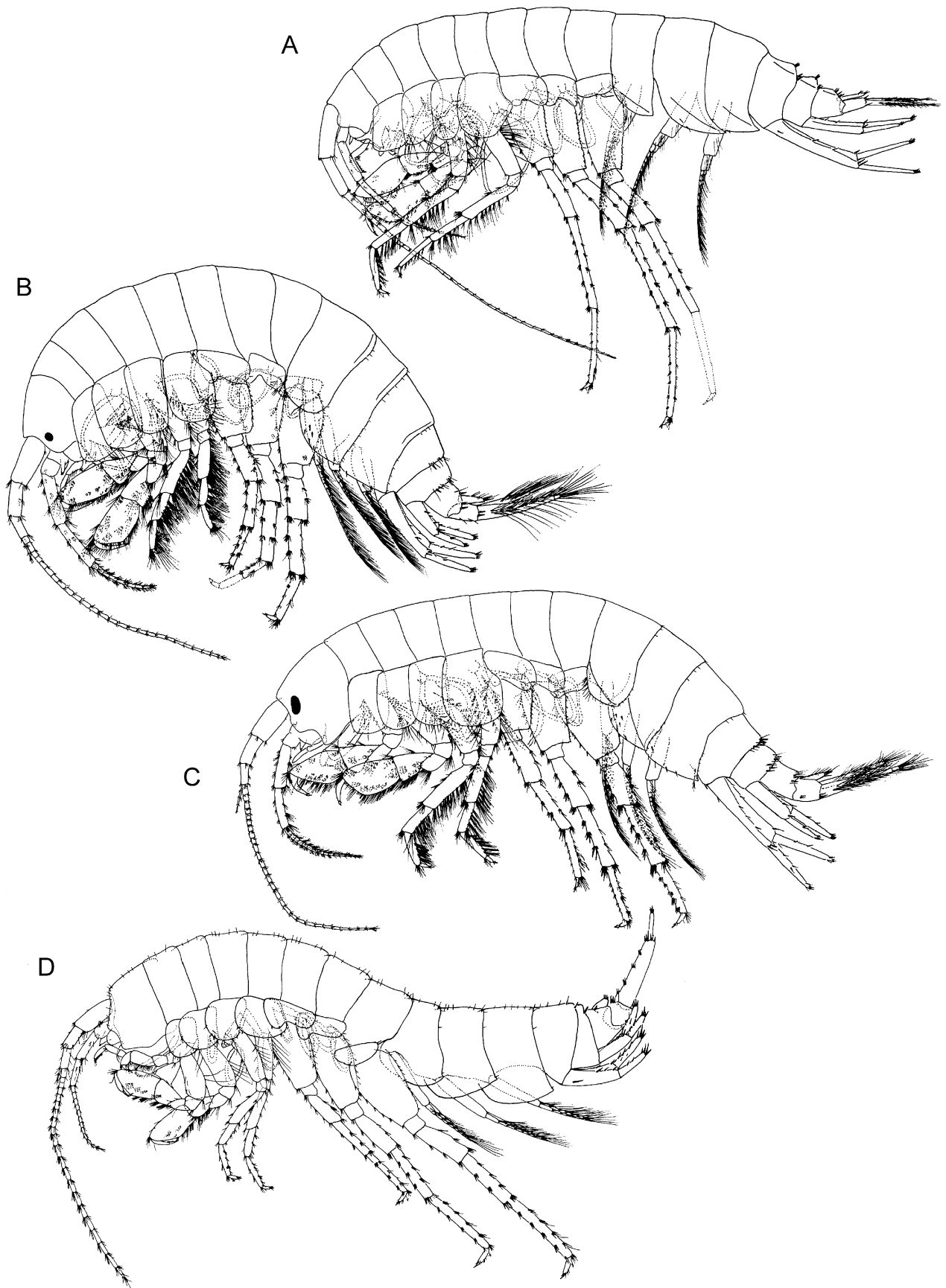


FIGURE 1. Habitus of examined specimens: (A) *Gammarus troglomorphus*, **sp. n.**; (B) *Gammarus parvioculatus*, **sp. n.**; (C) *Gammarus* cf. *subaequalis*-Garlyk; (D) *Tadzocrangonyx alaicus*, **sp. n.**

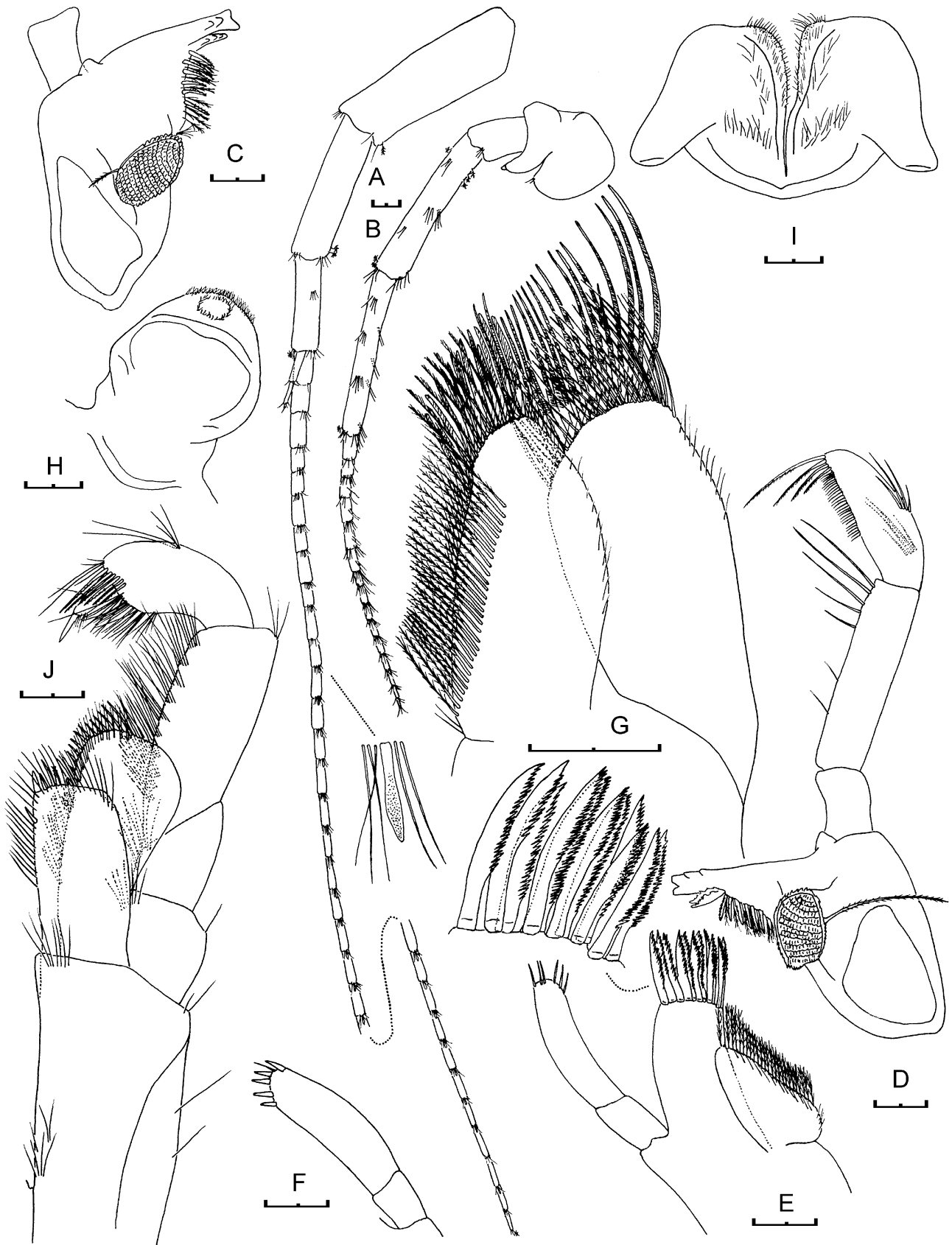


FIGURE 2. *Gammarus troglomorphus*, sp. n., male, 12.4 mm, holotype NC181: (A) antenna I; (B) antenna II; (C) mandible, left; (D) mandible, right; (E) maxilla I, left; (F) palp of maxilla I, right; (G) maxilla II; (H) upper lip; (I) lower lip; (J) maxilliped. Scale bars 0.2 mm.



FIGURE 3. *Gammarus troglomorphus*, sp. n., male, 12.4 mm, holotype NC181: (A) gnathopod I; (B) gnathopod II; (C) pleopod I; (D) pleopod II, part; (E) pleopod III, part; (F) epimeral plates; (G) urosoma, dorsal view. Scale bars 0.2 mm.

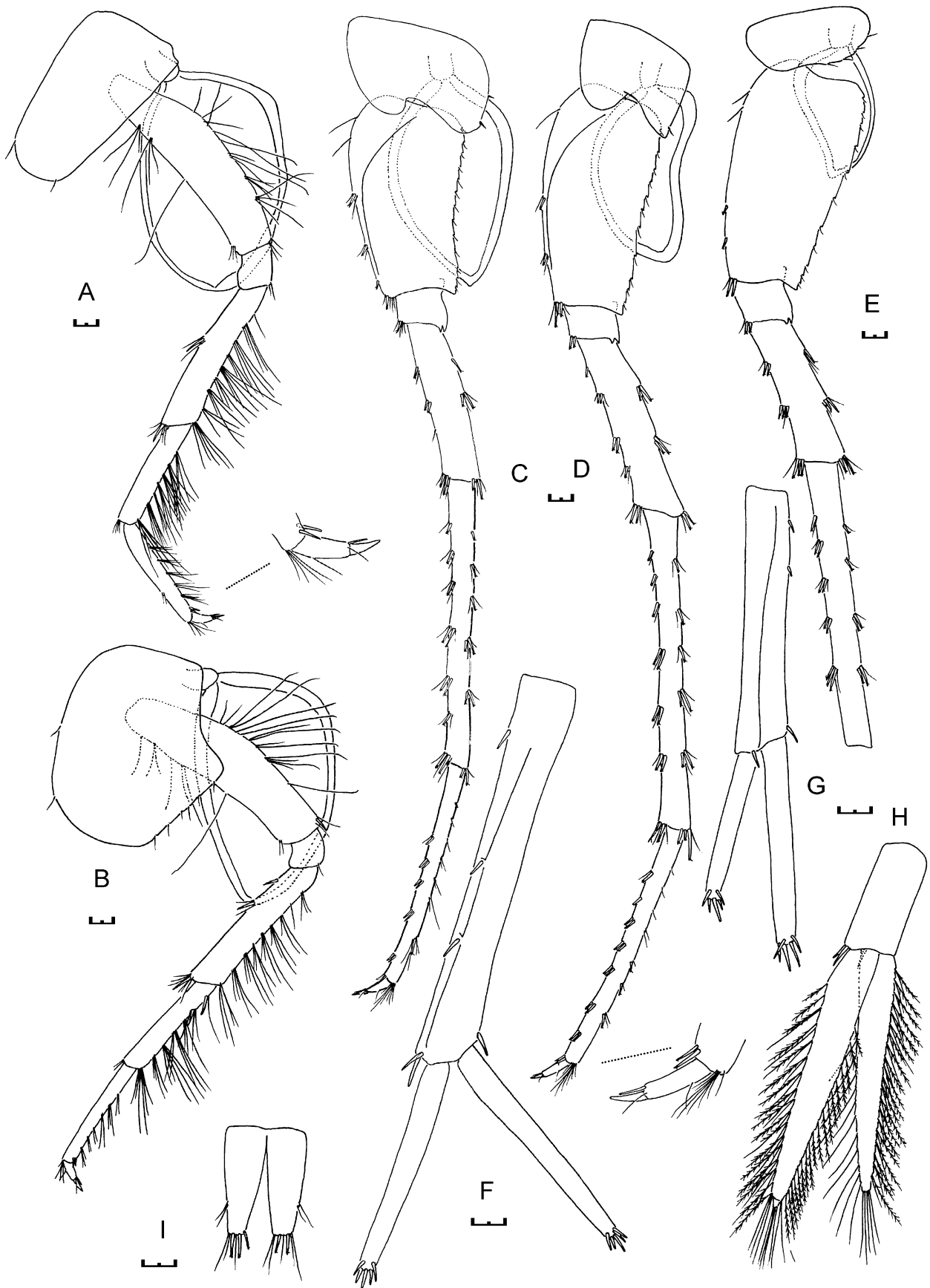


FIGURE 4. *Gammarus troglomorphus*, sp. n., male, 12.4 mm, holotype NC181: (A) pereopod III; (B) pereopod IV; (C) pereopod V; (D) pereopod VI; (E) pereopod VII; (F) uropod I; (G) uropod II; (H) uropod III; (I) telson. Scale bars 0.2 mm.

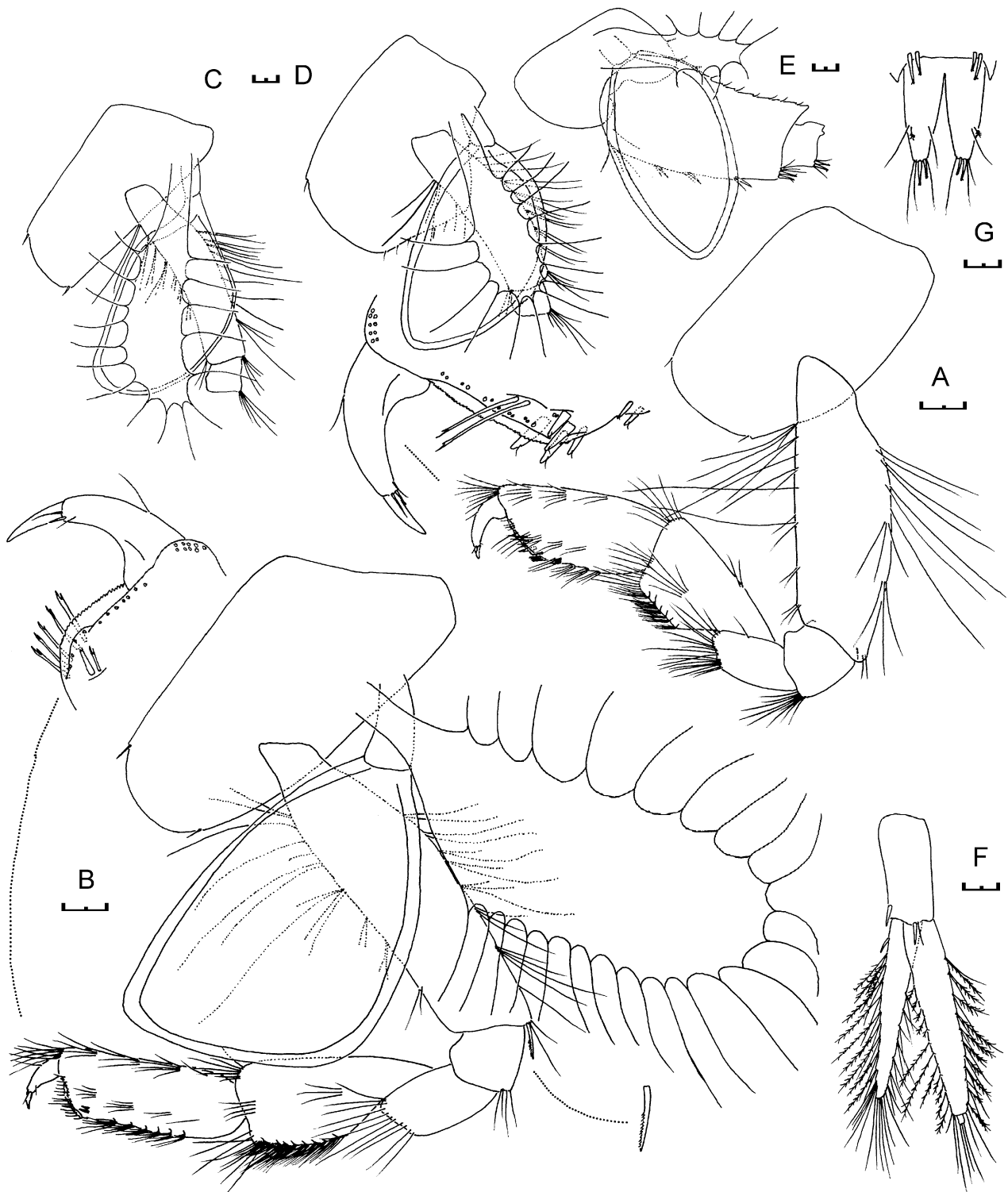


FIGURE 5. *Gammarus troglomorphus*, sp. n., female, 11.5 mm, paratype NC182: (A) gnathopod I; (B) gnathopod II; (C) pereopod III, part; (D) pereopod IV, part; (E) pereopod V, part; (F) uropod 3; (G) telson. Scale bars 0.2 mm.

Ecology and distribution. Suw Oyuk (Suuvoyuk) 37.596778, 66.405500, alt. 360 m near Garlyk (Karljuk), Lebap Province, is a collapse sinkhole, an opening into a drowm cave system. The lake on the sink's 'bottom' is in fact the upper layer of a deep system of karst phreatic waters. Some individuals of the troglobiotic fish *Triplophysa starostini* (Parin) (syn. *Noemacheilus s.*, *Paracobitis s.*, *Troglocobitis s.*) were obtained snorkeling. Some individuals of *Gammarus* were found pending on the net trap for catching fishes, left there overnight. Considering

the diver's (M. Pereladov) report, some specimens of the probable subterranean stenasellid isopod *Stenasellus asiaticus* Birstein et Starostin have been observed deeper. All other animals are represented by normally pigmented epigeal populations. In the shallows of the bottom lake there are some aquatic plants and filamentous algae, as well as epigeal aquatic fauna including a small population of the toad *Bufo* cf. *oblongus*. Gastropoda only represented by Lymnaeidae (cf. *Radix* sp.); Ostracoda (many), Cyclopoida (many), Cladocera, Coleoptera Dytiscidae, larvae of Diptera Chironomidae (many), Trichoptera, at least 2 species of Odonata flying (*Ischnura* cf. *elegans*, *Orthetrum* cf. *coerulescens*). However, gammarids have not been seen in this layer.

Remarks. *Gammarus troglomorphus*, sp. n. is a rather aberrant eyeless species with extremely elongated appendages and modified outer plate of maxilla I. By elongated appendages it resembles *Gammarus microps* Pinkster et Goedmakers, 1975 known from a cave in Morocco. By laterally compressed and elevated urosomites it resembles *Gammarus syriacus* Chevreux, 1895, *Gammarus laborifer* Karaman et Pinkster, 1977 and to several similar species known from the Middle East (Lebanon, Egypt, Syria and other countries) (see Zamanpoore *et al.* 2011). Its epimera II appear to be the most produced in *Gammarus*. The characteristics distinguishing a new species from the phylogenetically close *G. parvioculatus*, sp. n. are discussed below.

***Gammarus parvioculatus*, sp. n.**

Figures 1B, 6–8

Material examined. Holotype specimen NC183: male, 9.0 mm; spring-cave, 37.943889, 66.612500, 1100 m a.s.l., Khodzhapil (Hodžapil', Hojeypil), near Koyten, Köýtendag District, Lebap Province, Turkmenistan, leg. 25 May 2015 by B. Sket. Paratype NC184: female, 9.0 mm, oostegites developed, setose, bearing 6 medium-sized eggs; under submerged plants in limnocrone; same data as holotype.

Other specimens examined from the same locality (not included in the type series): NC185-NC188: 4 males (4x11.0 mm). Partially dissected, measured and deposited at the research collection of the Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani.

Diagnosis. Stout, medium sized *Gammarus* with slightly diminished eyes; all appendages comparatively short; antennae with setae shorter than article widths; maxilla I exterior lobe spines weakly to densely serrated; pereopods III–IV with densely setose articles 4–6 posteriorly; uropod III endopodite longer than half exopodite, all margins with long setae.

GenBank accession number: MG655629 for isolate 515GparviocTUM.

Etymology. Specific epithet '*parvioculatus*' refers to the reduced size of eyes (*parvus* - small in Latin).

Description. GENERAL BODY MORPHOLOGY (Figs 1B, 7D, H, I). *Body* stout. Genal plates short, rounded triangular, nearly symmetric up-down; eyes small, slightly shorter than antennal article 1 width. *Coxae I–IV* long (high), I widened towards its apex, IV lobate; apical margins slightly convex, I–II with ca. 5 distant, small setae, III–IV with setae only at angles. *Pleonites* with small setae along dorsal and lateral margins, epimeral plates with 4–5 small spines in their apical parts, *epimeron II* posteriorly ending rectangularly, *epimeron III* slightly acute. *Urosoma* without noticeable elevations, its median spines at the posterior margins, widely distant mutually, with some short setae among spines; formula for urosomites I–III is 1–1–1–1 // 2–1–1–2 // 2–2–2. *Telson* equally long as wide, deeply split, each lobe with 2 apical and 1 baso-marginal spine, moderately numerous apical and facial setae up to 4x as long as spines. ANTENNAE (Figs 1B, 6A, B). *Antenna I* 57% body length. Peduncle articles in relation 10:7:5; articles 1 and 3 with short apical setae, 2 also with a group in its middle; flagellum of 27 articles which are longer than wide, with row of short (ca. 30% of article lengths) setae along apical margins, including also single equally short aesthetascs. *Antenna II* ca. 50% previous antenna length, with length relations of 4:5; flagellum as 10:10:13; flagellum of 9 articles; articles 4–5 with ca. 10 groups of setae each (with stiff notched setae on inner face), their length approximately equal the width of articles; flagellum with tender tufts of setae on lateral margins and apices of articles. MOUTH PARTS (typical gammarid, Figs 6C–J). *Mandible* normal, the palp with ca. 15 differently long setae along the article 2; article 3 with 2 facial groups of 2–4 setae. *Maxilla I* asymmetric, palps only distally armed, left palp with ca. 10 simple setae, right with 5 teeth and 2 setae; outer lobe with ca. 12 serrated spines, inner ones with ca. 10, outer ones with 3–4 denticles. *Maxilla II* normal, the oblique row of setae very close to the inner margin. GNATHOPODS (Figs 7A, B). *Gnathopod I* moderately setose, article 5 triangular, with closely pressed posterior groups of setae and with one group of setae in the middle of the anterior

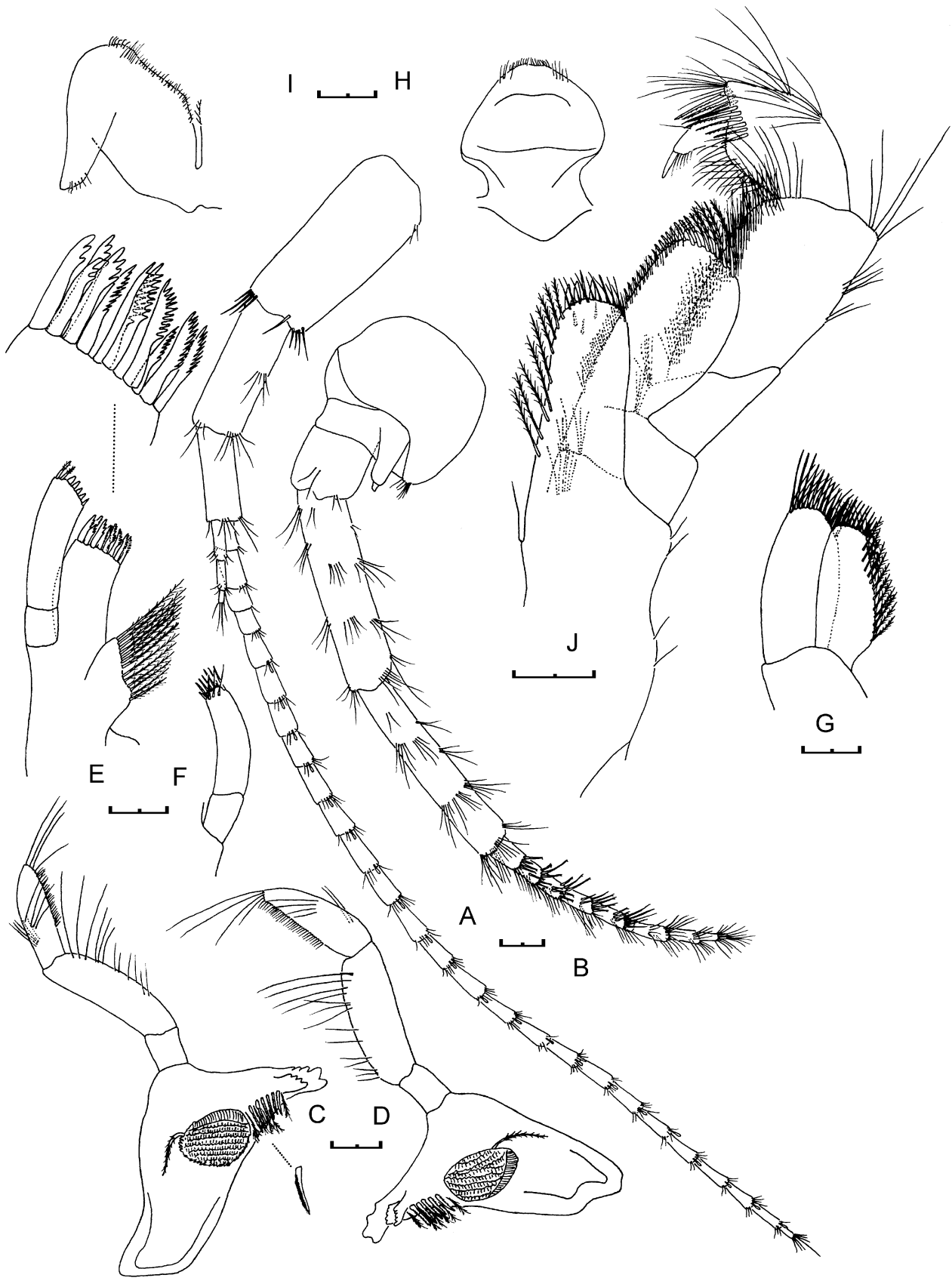


FIGURE 6. *Gammarus parvioculatus*, sp. n., male, 9.0 mm, holotype NC183: (A) antenna I; (B) antenna II; (C) mandible, left; (D) mandible, right; (E) maxilla I, right; (F) palp of maxilla I, left; (G) maxilla II; (H) upper lip; (I) lower lip, fragment; (J) maxilliped. Scale bars 0.2 mm.

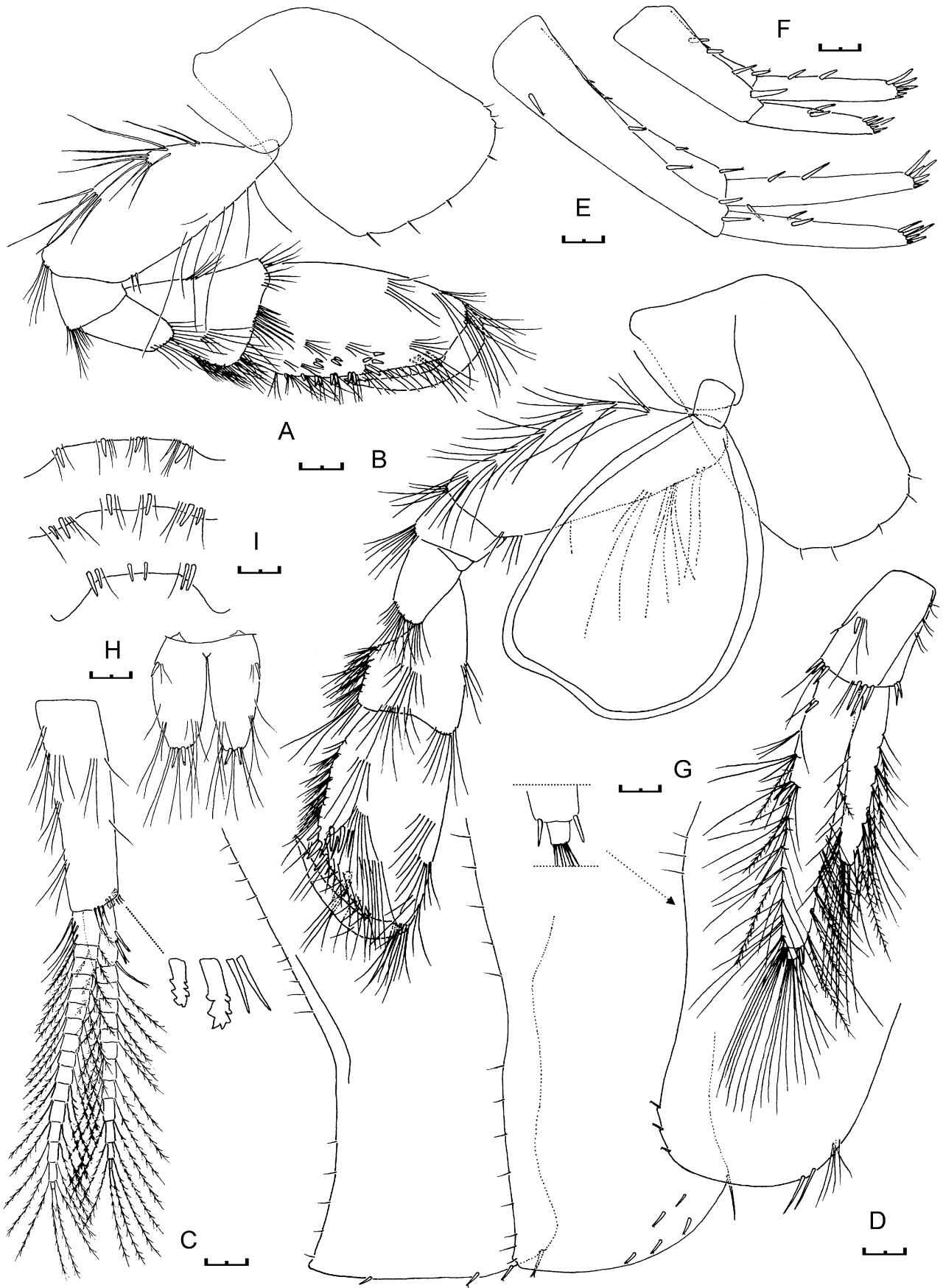


FIGURE 7. *Gammarus parvioculatus*, sp. n., male, 9.0 mm, holotype NC183: (A) gnathopod I; (B) gnathopod II; (C) pleopod I; (D) epimeral plates; (E) uropod I; (F) uropod II; (G) uropod III; (H) telson; (I) urosoma, dorsal view. Scale bars 0.2 mm.

border; article 6 with a very steep palmar margin, palmar angle not marked, with ca. 15 small spines in the area, no large spines present; with 5 facial groups of 2-6 moderately long setae. *Gnathopod II* article 5 longer, with 8 groups of setae along posterior margin. Spines in the palmar angle area longer, larger spine in middle of palmar border, ca. 5 facial groups of 5-7 very long setae. PEREOPODS (Figs 1B, 8A–E). *Pereopods III–IV* with (equally) dense brushes of long (for double article widths) setae along posterior margins of articles 4-6. *Pereopods V–VII* in length relation 100:116:112, VII 50% of body length. With basipodites rounded at angles, V with marked distoposterior angle, VII with slightly convex longitudinal margins, tapering distally, with 3 small spines and a tuft of setae along the anterior and over 15 small setae along posterior margin; articles 4-5 with 2 pairs of paired spines along margins; dactylus ca. 25% of article 6 long, with a short nail. PLEOPODS AND UROPODS (Figs 7C, E–G). *Pleopods* normal, peduncle with some groups of setae, retinacula of 2 hooked and 2-3 slender simple spines. *Uropods I–II* peduncles reaching approximately the end of urosoma, rami slightly beyond the end of uropod III peduncle; peduncles with ca. 4 spines along the edges, uropod I with a basofacial spine, with 1 or 2 single or paired spines along rami, their apical spines moderately long, 5-6 in number. *Uropod III* peduncle with a facial spine and some setae and ca. 10 spines on the apical border; endopodite 60% of exopodite length, both with moderately dense marginal brushes of moderately long with mix of simple and plumose setae.

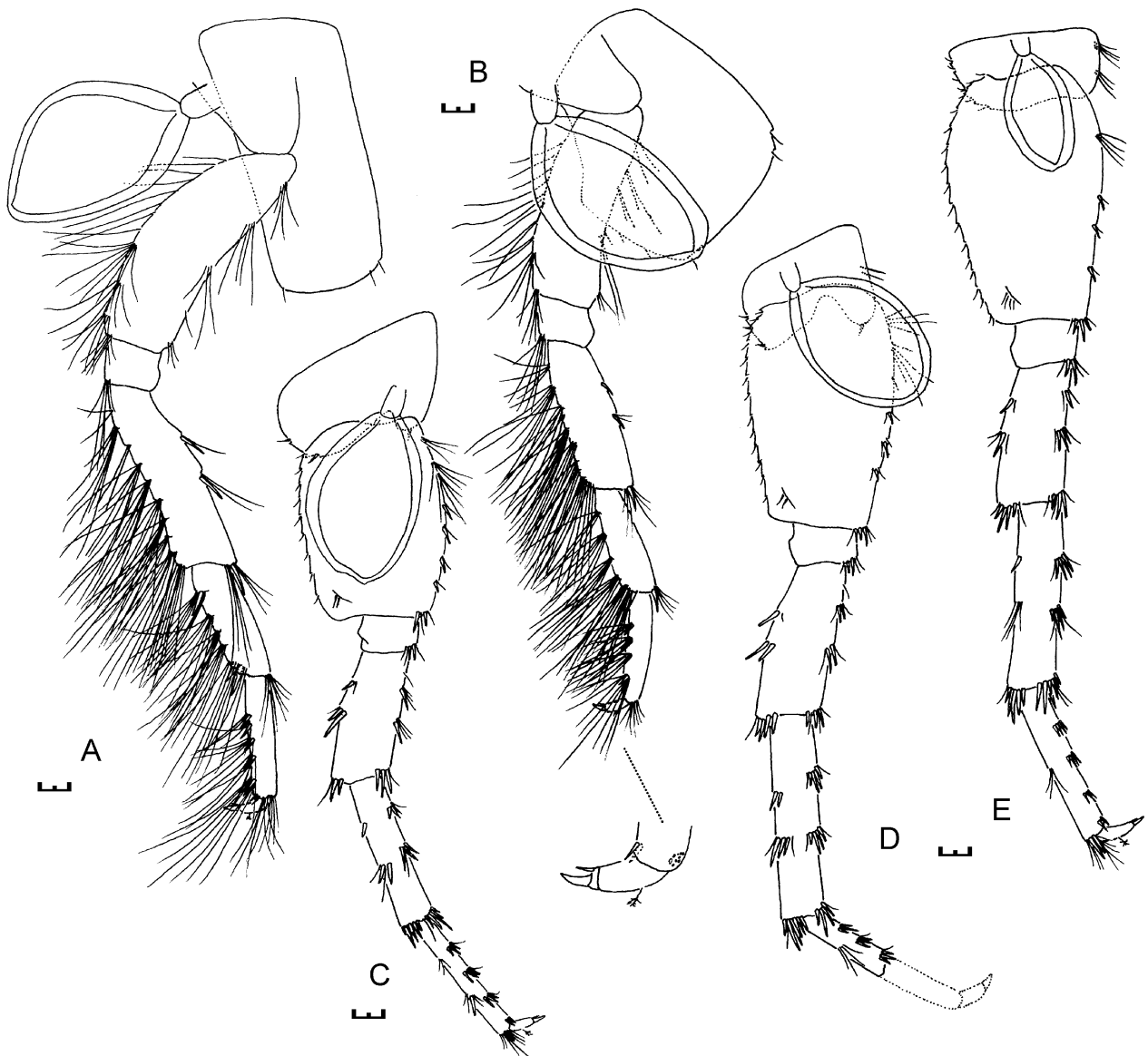


FIGURE 8. *Gammarus parvioculatus*, sp. n., male, 9.0 mm, holotype NC183: (A) pereopod III; (B) pereopod IV; (C) pereopod V; (D) pereopod VI; (E) pereopod VII. Scale bars 0.2 mm.

Female. Body 9.0 mm long. *Antenna I* with 19 articles. *Gnathopod II* propodus sub-rectangular. *Pereopods V* to *VII* without setae on the anterior margins. *Uropod III* in all characters similar as in male, just smaller and less richly setose.

Variability. In the subterranean brook, some specimens are pigmented, some without body pigmentation, but no difference in eye size.

Ecology and distribution. Ca. 10 individuals found where a hole of 2 m² opens into a narrow subterranean corridor with a shallow, weak (20 cm wide) stream. In this small illuminated part of the stream was found a diverse epigeal fauna: 'Hydracarina', Nematoda, Oligochaeta, larvae of Diptera Simuliidae (many), Chironomidae (many), Ephemeroptera (cf. *Baetis*, *Caenis*, Ecdyonuridae). Only one pigmented specimen obtained in a dense lump of submerse plants in a large limnocrene.

Remarks. Although *Gammarus parvioculatus*, **sp. n.** is also related to a subterranean habitat, it shows no troglomorphy except the slight eye diminution. Even in comparison to epigeal species it is very stout, with comparatively short appendages and with particularly richly setose pereopods III–IV. From *G. troglomorphus*, **sp. n.** it also differs by obtuse epimera and a smooth urosoma. *Gammarus parvioculatus*, **sp. n.** possesses an interesting feature of anterior margin of coxae VI and VII bearing groups of setae as in *Gammarus parthicus* Stock, Mirzajani, Vonk, Naderi et Kiabi, 1998 (Stock *et al.* 1998). We can not exclude that this species was reported by Martynov (1935) under the names *Gammarus turanus subnivalis* Martynov, 1935, *G. turanus karabasicus excisus* Martynov, 1935 and/or *G. turanus coxalis* Martynov, 1935 which are poorly identifiable cryophilic spring forms; but, *G. parvioculatus*, **sp. n.** was found pretty far from the Martynov's animals, and beside this it is a molecularly proven close relative of *G. troglomorphus*, **sp. n.**; its relation to the supposed *G. subaequalis* is much more distant. The pair *G. troglomorphus*, **sp. n.** and *G. parvioculatus*, **sp. n.** are phylogenetically clustered together (but poorly supported), along with *G. decorosus* Meng, Hou et Li, 2003 from Xinjiang. Although three Turkmen species are geographically very close, just some kilometers apart, they are not closely related. *Gammarus troglomorphus*, **sp. n.** and *G. parvioculatus*, **sp. n.** split from the proximal part of the aggregate clade. Both species are morphologically among the most distant pairs within the formal genus *Gammarus*.

***Gammarus cf. subaequalis*-Garlyk**

Figures 1C, 9–11

probable syn.: *Rivulogammarus subaequalis* Martynov 1935, p. 440, figs 30–35 (orig. descrip.), non *Gammarus* (*Rivulogammarus*) *syriacus subaequalis*: Birštejn 1948, p. 263, fig. 1.

Material examined. Turkmenistan: four specimens 16/3-DAS: 3 males, 9.5 mm, 2x11.5 mm, female, 8.5 mm, oostegites developed, setose, bearing 10 medium-sized eggs dissected on slides; small stream with rich immersed vegetation in Karabulak river basin, 37.589167, 66.340833, 324 m a.s.l., near Garlyk, Köýtendag District, Lebap Province, leg. 25 May 2015 by B. Sket.

Diagnosis. A moderately stout *Gammarus* with smooth body, eyes normal; epimera disto-posteriorly pointed; urosomites with paired dorsal spines, median groups I–II divided into 2 pairs of spines each; telson as wide as long, its lobes with 2–3 apical and 1 basofacial spines, setae moderately numerous on the face; both antennae with scarce and short setae; gnathopods richly setose, articles 4–6 of pereopods III–IV with dense brushes of long setae; basis of pereopod V distally wide, of VII broadly rounded; uropod III endopodite 86% of exopodite, all margins setose.

GenBank accession number: MG655630 for isolate 516GGarlykTUM.

Short description. GENERAL BODY MORPHOLOGY (Figs 1C, 11B, F, G). *Body* smooth. *Coxae I–IV* distally rounded with only few short marginal setae. *Epimera* disto-posteriorly acute, but not produced, coxae II–III with 2–3 spines along distal margin. *Urosomites* dorsally with slight elevations, spines at the posterior margin, spines with some setae mainly paired, median groups of I–II divided into two separate pairs; III with median group replaced by some setae. Formula for urosomites I–III is: 3–2–2–2 // 2–2–2–2 // 2–0–3. *Telson* as wide as long; lobes with 2–3 spines apically and 1 spine basofacially, with up to 15 setae, up to half longer than apical spines, grouped in apical and some facial groups. ANTENNAE (Figs 1C, 9A, B). *Antenna I* ca. 50% of body length, peduncle articles lengths 10:7:5, poorly setose with some distal short setae in the middle; flagellum of 28, accessory flagellum of 4 articles, flagellar setae up to half as long as articles. *Antenna II* 72% of antenna I length,

long articles and flagellum lengths 10:9:19; flagellum with 15 articles and with calceoli; poorly setose, setae as long as widths of bearing articles. MOUTH PARTS (typical gammarid, Figs 9C–J). *Mandibula* with ca. 10 setae on palp article 2; article 3 with twice 3 B setae and a group at outer margin. *Maxilla I* outer lobe with 11 spines, the inner half finely comb-shaped, outer with shorter and thicker denticles; palpus asymmetric, distally with 5 teeth and 2 setae, or with ca. 10 differently thick setae respectively. GNATHOPODS (Figs 10A, B). *Gnathopods* shaped and setose like in *G. parvioculatus*, sp. n. PEREOPODS (Figs 10C–G). *Pereopods III–IV* articles 4–5 with dense brushes of setae along posterior sides. *Pereopod V* base distally not markedly narrowed, with a large, but rounded rectangular disto-posterior lobe; anterior margin with ca. 10 spines. *Pereopod VII* ca. 52% of body length; base posteriorly convex, tapering distally, with many small setae, distoposterior corner rounded. PLEOPODS AND UROPODS (Figs 11A, C–E). *Pleopods* ordinary. *Uropods I–II* with 1–2 single or paired spines along branches, distal spines very short. *Uropod III* endopodite 86% of exopodite, all margins densely setose with plumose setae, except basally; exopodite article 2 well developed, twice as long as surrounding spines.

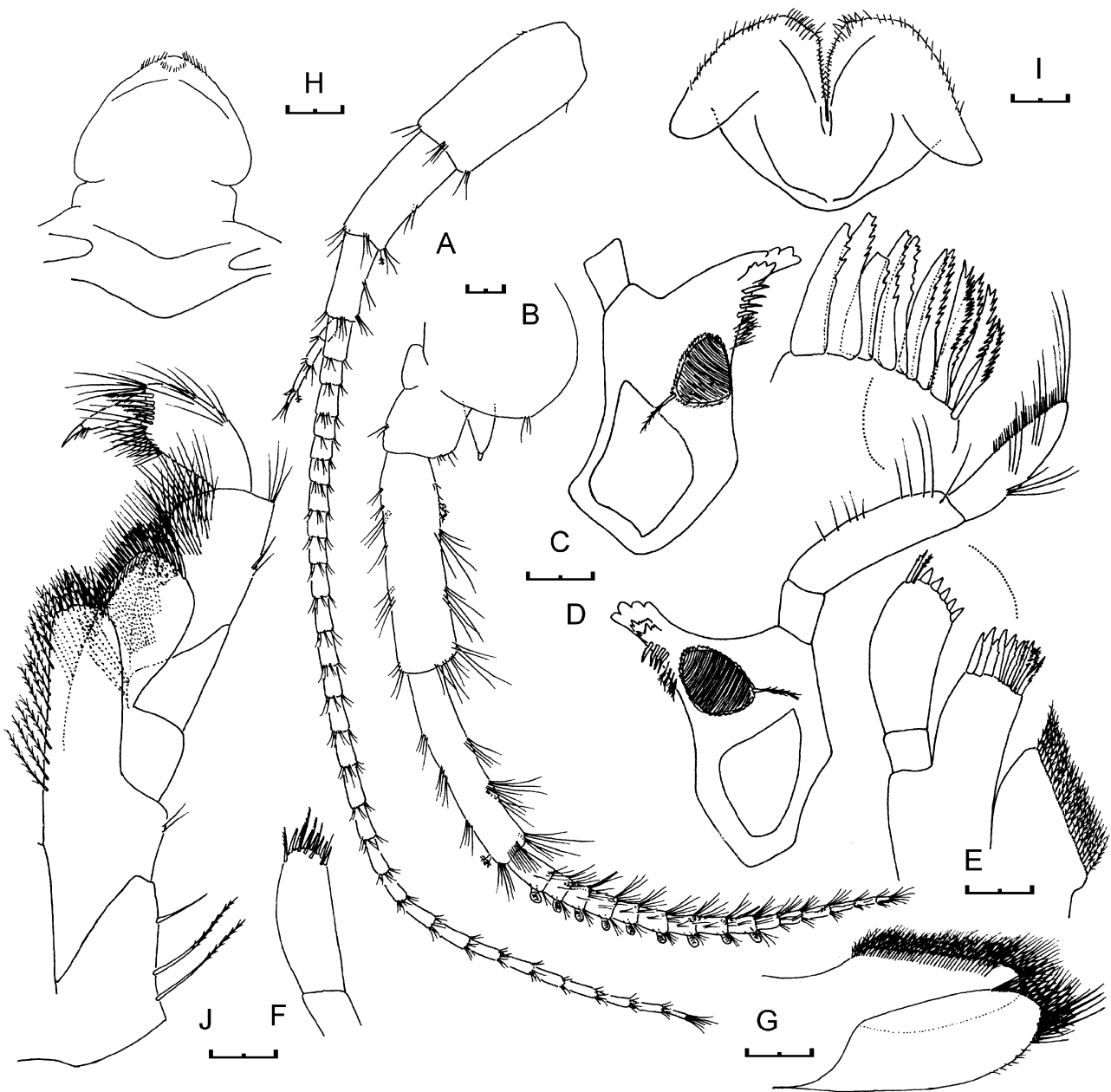


FIGURE 9. *Gammarus* cf. *subaequalis*-Garlyk, male, 11.5 mm, 16/3-DAS: (A) antenna I; (B) antenna II; (C) mandible, left; (D) mandible, right; (E) maxilla I, right; (F) palp of maxilla I, left; (G) maxilla II; (H) upper lip; (I) lower lip; (J) maxilliped. Scale bars 0.2 mm.

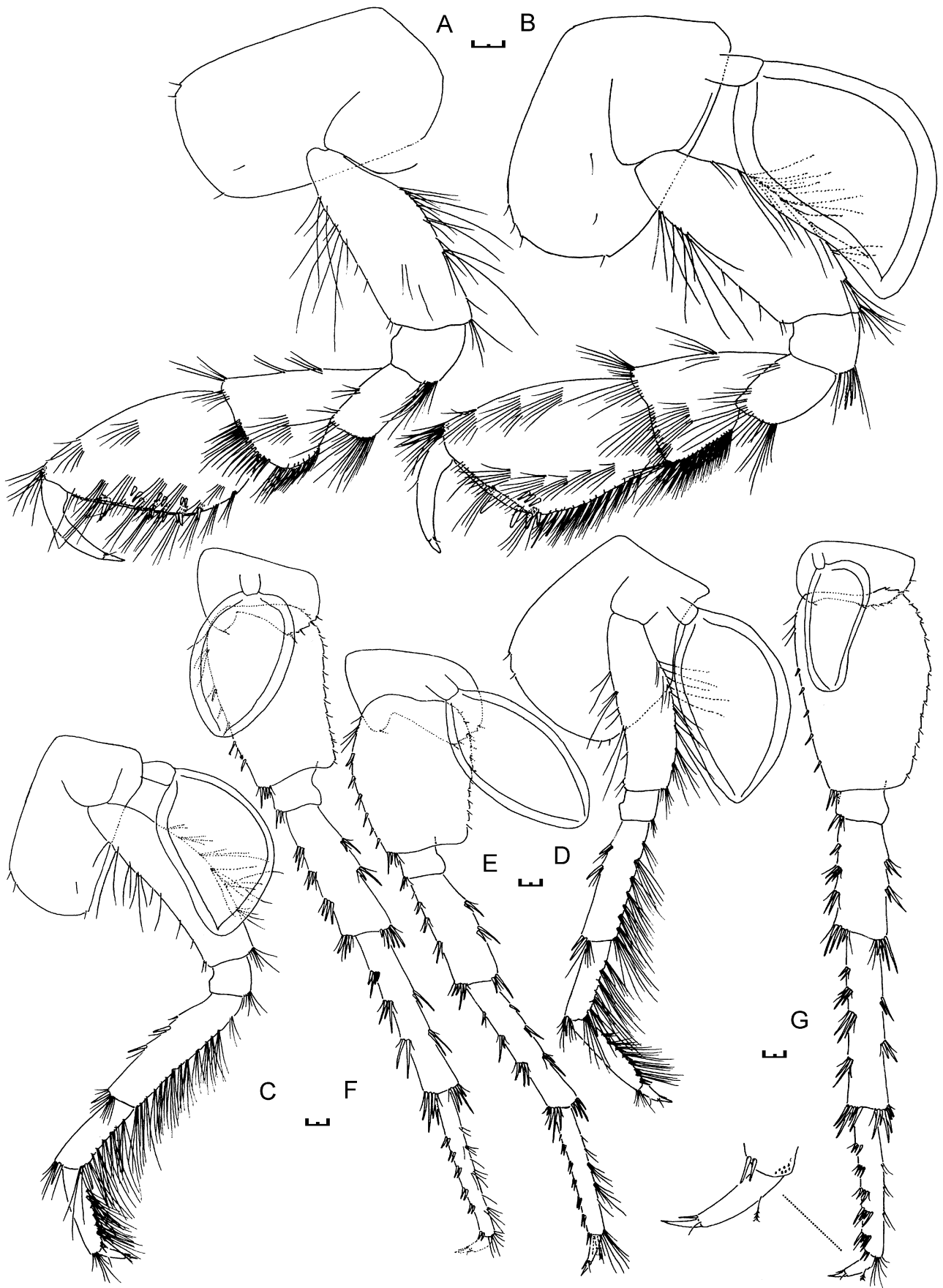


FIGURE 10. *Gammarus* cf. *subaequalis*-Garlyk, male, 11.5 mm, 16/3-DAS: (A) gnathopod I; (B) gnathopod II; (C) pereopod III; (D) pereopod IV; (E) pereopod V; (F) pereopod VI; (G) pereopod VII. Scale bars 0.2 mm.

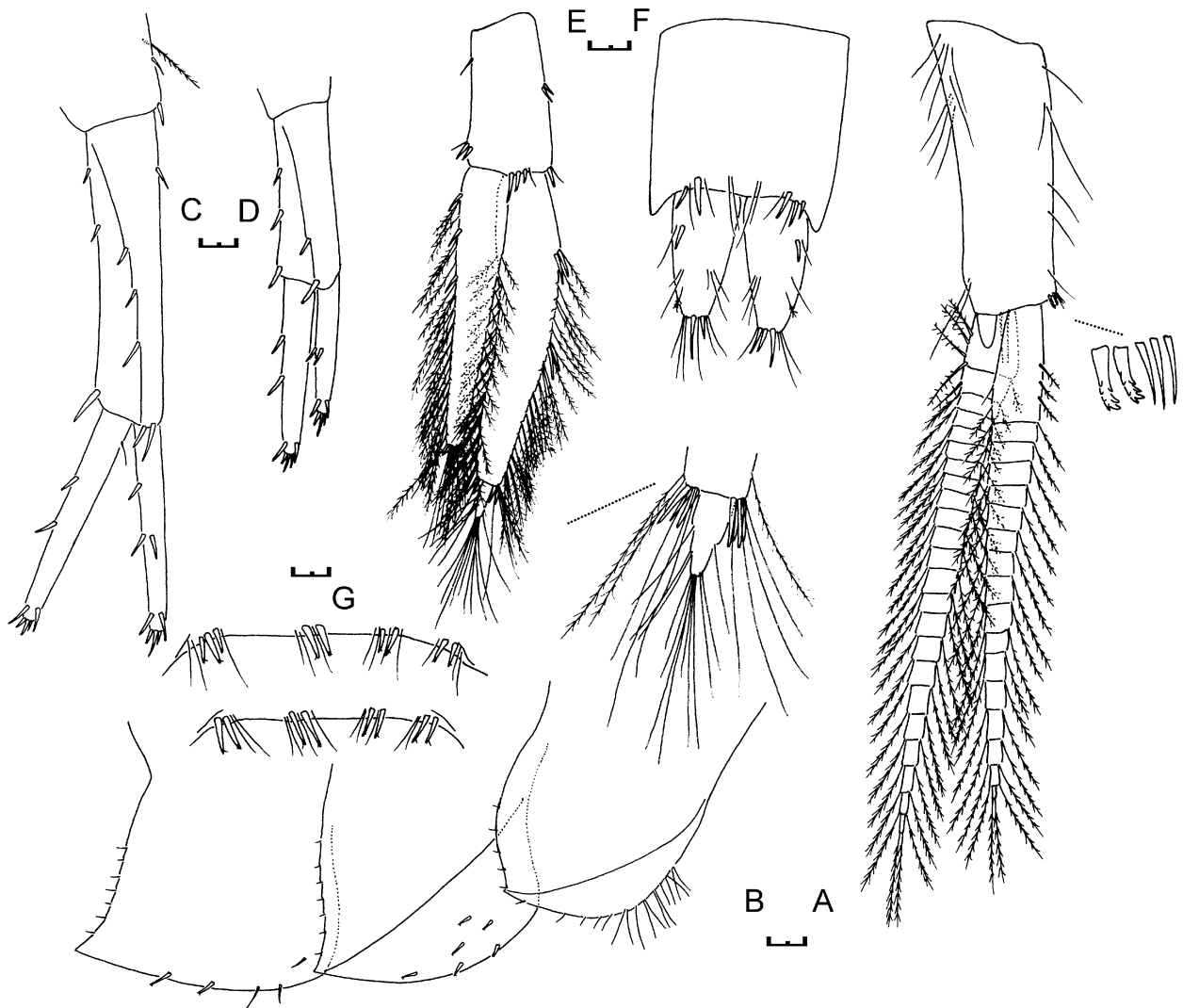


FIGURE 11. *Gammarus* cf. *subaequalis*-Garlyk, male, 11.5 mm, 16/3-DAS: (A) pleopod I; (B) epimeral plates; (C) uropod I; (D) uropod II; (E) uropod III; (F) telson; (G) urosoma, dorsal view. Scale bars 0.2 mm.

Female. Body 8.5 mm long. *Antenna I* with 24 articles. *Pereopods V* to *VII* without setae on the anterior margins. *Uropod III* in all characters similar as in male, just smaller and less richly setose.

Ecology and distribution. This population inhabits a small epigeic stream with rich vegetation in the village Garlyk, not close to any spring. A series of populations, very close to it molecularly, is distributed in the line from Garlyk in Turkmenistan till Ysyk Köl (Yssyk Kul) area in Kyrgyzstan (Sket *et al.* in prep.). They have not been morphologically studied. Although inhabiting the same area as both previously described species in the extreme East of Turkmenistan, it is only feebly related to them.

Remarks. *Gammarus* cf. *subaequalis*-Garlyk seems to represent the most widely spread epigeic taxon of *Gammarus* in Central Asia between E Turkmenistan and E Kyrgyzstan, it is morphologically similar to *G. subaequalis* Martynov, 1935 and *G. turanus* Martynov, 1935 and to some other taxa of Martynov (1935) as well as to *Gammarus lacustris* G.O. Sars, 1863. *Gammarus turanus* it resembles particularly in the shape of pereopod V base, but it is very different in telson shape and setation. In telson and in uropod III dimensions and setation, it is closer to *G. subaequalis*. Our taxon is very different from both in urosomal spines. *Gammarus lacustris* differs mainly in more acute epimera. They also resemble to some degree *Gammarus pseudosyriacus* Karaman et Pinkster, 1977 in which, however, the uropod III endopodite is shorter and urosome carination is much stronger. In the phylogram of the aggregate *lacustris* (Sket *et al.* in prep.) the entire group of populations is positioned in the terminal subclade *lacustris-A* which contains mainly Asiatic populations of the *G. lacustris* shape, but also the aberrant *Gammarus bergi* Karaman et Pinkster, 1977 and some North American *G. cf. lacustris* populations. The

type locality of the Martynov's *G. subaequalis* is a spring in Galkino near Shimkent, 150 km NE Tashkent; *G. turanus* at the spa in Chimgan. Both localities are less than 100 km apart and 400 to 500 km NE from Garlyk, but only ca. 200 km away from the line Garlyk—Ysyk K l, which is sparsely inhabited by populations of *Gammarus* cf. *subaequalis*-Garlyk.

Genus *Tadzocrangonyx* Karaman et Barnard, 1979

Tadzocrangonyx alaicus, sp. n.

Figures 1D, 12–15

Material examined. Holotype specimen NC189: female, 4.5 mm, oostegites weakly developed, non-setose; Kyzyl Bulak spring, 40.062972, 71.723139, 1155 m a.s.l., Kyzyl Bulak, Kadamjay District, Batken Region, Kyrgyzstan, leg. 10 June 2012 by B. Sket. Paratypes NC190-NC193: 3 females, 5.2 mm, ca. 5.0 mm, 4.0 mm, oostegites weakly developed, non-setose, 1 probable male, 4.2 mm; same data as holotype.

Other specimens examined from the same locality (not included in the type series): NC194-NC203: 1 female (4.2 mm, fragment), 3 (sex unknown) fragments, 6 juveniles 2.5-3.0 mm. Partially dissected, measured and deposited at the research collection of the Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani.

Diagnosis. Small, eyeless, pigmentless crangonyctid shaped amphipod without sternal gills; telson short and deeply split; mandibular palpus normally developed; coxal plates II–IV short (shallow) not longer than wide; propodus of gnathopods armed with 2 spines at defining angle; uropods I not reaching tips of II, uropod III endopodite scale-like, exopodite with well developed distal article.

GenBank accession number: MG655627 for isolate 373TadzocrKYR.

Etymology. Specific epithet '*alaicus*' for the Alai Mountains where the specimens were collected.

Description. GENERAL BODY MORPHOLOGY (Figs 1D, 12A, E, H, 15F). *Body* dorsally with few fine setae; pleon not armed dorsally; length 4.5 mm. *Head* as long as pereonites I and II combined, rostrum indistinct, eyes (eye pigmentation) absent. *Epimeral plates I–III* without post-ventral teeth, although plate II slightly acuminate, corners bearing minute seta or unarmed; epimera without ventral robust setae, posterior margins sinuous and with 1 seta or naked. *Urosomites I–III* without dorsal cuticular armaments; each armed with notched spines in the following manner: 1–1 // 1–1 // 1–1. *Telson*: shortened, half shorter than uropod III peduncle, length half its width; entirely cleft; apices with 6 short robust setae in a row and a pair of setules dorsolaterally. ANTENNAE (Figs 1D, 12A–D). *First antenna*: long, 0.7 body length, approximately 0.35 as long as second antenna; peduncular articles I–III with a length ratio of 1:0.6:0.5, articles 1 and 2 with a few sets of setae on medial and ventral margins, the third article bearing sparse setae; primary flagellum with 21 uniform, sparsely setulate articles, lanceolate aesthetascs present on articles 5–19; accessory flagellum 2-articulate, longer than accompanying primary flagellar article. *Second antenna*: length about 0.35 body, peduncle length 1.3 flagellum; peduncular articles 4 and 5 in length ratio 1:0.9, both setose with stiff notched setae along ventral and dorsal faces, article 4 bearing bundle of stiff simple setae on its ventro-distal corner; gland cone somewhat tapered; calceoli absent; flagellum with 12 weakly setate articles, 8 distal of them with single rod-like aesthetasc each. MOUTH PARTS (Figs 13A–I). *Upper lip* oblong, rounded, with minute setae at apex. Mandibles subequal, mandibular body small, slightly compressed. *Left mandible*: palp article 2 longer than article 3 (distal), with 3 inner marginal setae, article 3 weakly falcate, bearing 12 D-setae and 3 E-setae; incisor process with 7 teeth; lacinia mobilis with 6 teeth and 4 stiff plumose setae in a row. *Right mandible*: incisor process bearing 7 teeth; lacinia mobilis bifid with few setules and 3 stiff plumose setae in a row, molar process with grinding surface bearing long posterior plumose seta. *Lower lip*: outer lobes moderate, slightly angulated, densely setose with setules; mandibular process distinct (narrow); inner lobes present, vestigial. *Maxilla I*, palps a little asymmetrical: left *maxilla*: palp long and slender, article 1 half shorter than article 2 with 4 short spines and 2 simple robust setae on its apical and sub-apical margin; outer plate with 9 thick spines (2 bidentate, 7 multi-dentate); inner plate narrow, with 4 plumose apical setae; right *maxilla I*, palp article 2 with 5 robust setae (1 of them serrate) on apical margin. *Maxilla II* with both plates narrow, outer plate apical margin with 21 long simple setae in two rows; inner plate with oblique row of 7 plumose setae and bearing 25 long simple setae in two rows on apical margin. *Maxilliped*: inner plate oblong, narrow, with 3 forked subtle spines, 1 simple spine and 2 naked setae apically, 11 plumose setae on inner ventral face; outer plate long, sub-ovoid, with a row of 11 strong, knifelike spines and 3 pappose setae along outer margin, and 10 stiff setae

sub-marginally; maxilliped palp article 2 linear, with a rows of about 35 thin setae along inner ventral face and 1 elongate apicolateral seta; palp article 3 narrow, with set of 4 long setae on outer margin, 4 setae on inner margin, medioventral area with a row of long simple setae (2 of them strong, serrated); palp article 4 (distal), 0.3 shorter than palp article 3, nail slender, bearing 6 setae at its base. *Lateralia* with 12 strong, simple spines and a row of long setae. COXAL PLATES, GILLS AND OOSTEGITES (Figs 1D, 14A, B, 15A–E). *Coxal plates I–IV* of dissimilar shape, roughly square or rectangular, with a sparse row of short setae along ventral margin of each; coxal plates V and VI with distinct anterior lobes, posterior margin slightly notched bearing 1 seta; coxal plate VII smallest, semilunar, with 1 seta on posterior margin; each plate II–VI bearing single, sac-like *coxal gill* with long stalk. *Sternal gills* absent. *Oostegites II–V* not well developed, oblong, narrow (not gammarid). GNATHOPODS (Figs 14A, B). *First gnathopod*: basis with 1 long and 4 short setae on anterior and 3 long setae on posterior margins; carpus stout, posterior margin with 2 setae and posterior angle bearing 1 seta, 2 groups of stiff setae on ventral margin, a row of stiff setae on inner face; propodus sub-trapezoidal, longer than wide, bearing 3 long setae on anterior margin, a group of 7 setae on antero-distal corner, 3 groups of stiff setae on inner face and 3 groups of setae along posterior margin, palm as long as posterior margin, beveled, straight with cutting margin smooth, palmar margin with 10 short setae along outer and inner faces, palmar angle defined and armed with 2 distally-notched spines accompanied with a group of long setae on inner face; dactylus crescent-shaped, nail long, 0.37 of total length of dactylus, 1 seta along anterior margin, inner margin smooth, with a group of 3 minute setules at hinge. *Second gnathopod* generally similar to gnathopod I, but a little larger; carpus feeble, with 4 groups of stiff setae on ventral margin; propodus and dactylus sub-similar to that of gnathopod I. PEREOPODS (Figs 1D, 15A–E): *pereopods III* and *IV* subequal in length, somewhat longer than the gnathopod II, article IV bearing short setae posteriorly, articles V and VI of third leg bearing 1-1-1 and 2-2-2-1 posterior spines correspondingly, and of the fourth leg 1-1-1 and 1-2-2-1; *pereopods V–VII* similar, second articles slightly expanded posteriorly, posterior margin serrate with short marginal setae, posterior margins of propodi armed with notched spines except articles VI bearing long setae, dactyli III and IV with single facial pennate setules, dactyli V–VII with additional facial setules. PLEOPODS AND UROPODS (Figs 12E–I, 15G–I): *pleopods* each with two retinacula; peduncular articles naked except for 3 long stiff medial setae on the third; rami of 8-7, 8-7, 7-6 articles of outer and inner respectively. *Third uropod* extending well beyond uropods I and II in the intact body; uropod lengths relative to uropod I; uropod II 0.8, uropod III 1.5; *uropod I* peduncle length 1.4 inner and 1.6 outer rami, with 1 strong basofacial spine, lateral margin with a row of 3 notched dorsal spines, medial margin bearing 2 strong notched spines; rami of unequal length, inner ramus with 2 rows of lateral spines, and 4 apical notched spines; *uropod II* peduncle 0.2 as long as inner ramus, with 2 short dorsolateral spines including 1 apical spine, outer ramus slightly shorter than inner, inner ramus with 3 mediolateral spines, both rami with 4 terminal notched spines; *uropod III* parviramous, peduncle as long as urosomite III, 0.3 length of outer ramus, bearing 3 facial and 5 ventrodistal notched spines, outer ramus two-articulate, proximal article with transverse row of spines arranged medially 3-3-3, laterally naked, with 2 groups of 6-7 terminal spines, distal article short, approximately 0.38 proximal, bearing 2 spines medially and 2 spines accompanied with fine setules apically, inner ramus vestigial, short, 0.16 outer, with 1 apical spine and 1 seta only.

Sexual dimorphism. One probably male specimen with body length 4.2 mm is similar to female but with a smaller body size and slightly differing in morphology of gnathopods (see Figs 14C, D).

Variability. The examined specimens have an insignificant variation in the shape of epimeral plates and armoring of uropod 3.

Ecology and distribution. *Tadzocrangonyx alaicus*, **sp. n.** was found only in the Pamir-Alay mountain system, at elevation 1155 m a.s.l. of the northern foothills of the Alai Range in a karst spring located in the Shakhimardan river basin.

Remarks. According to molecular analysis this amphipod belongs to Gammaridae, as the most basal branch of the *Sarothrogammarus* group of genera (Sket & Hou, 2018). The *Sarothrogammarus* group has a disjunct distribution between Pamir Plateau freshwaters and Mediterranean shores; while the genus *Tadzocrangonyx* is limited to Central Asia. These distribution patterns might be driven by the Tethyan retreat (Hou et al., 2014). Although of a crangonyctid shape, it differs from crangonyctids by the absence of sternal gills as well as by a deeply split, non-crangonyctid telson. Since we have no molecular data about both previously described *Tadzocrangonyx* species, the type *T. schizurus* (Birštein, 1948) and *T. setiferus* (Birstein et Ljovuschkin, 1972), our taxonomic decision is supported by geographical position between both as well as by morphological similarity of three species.

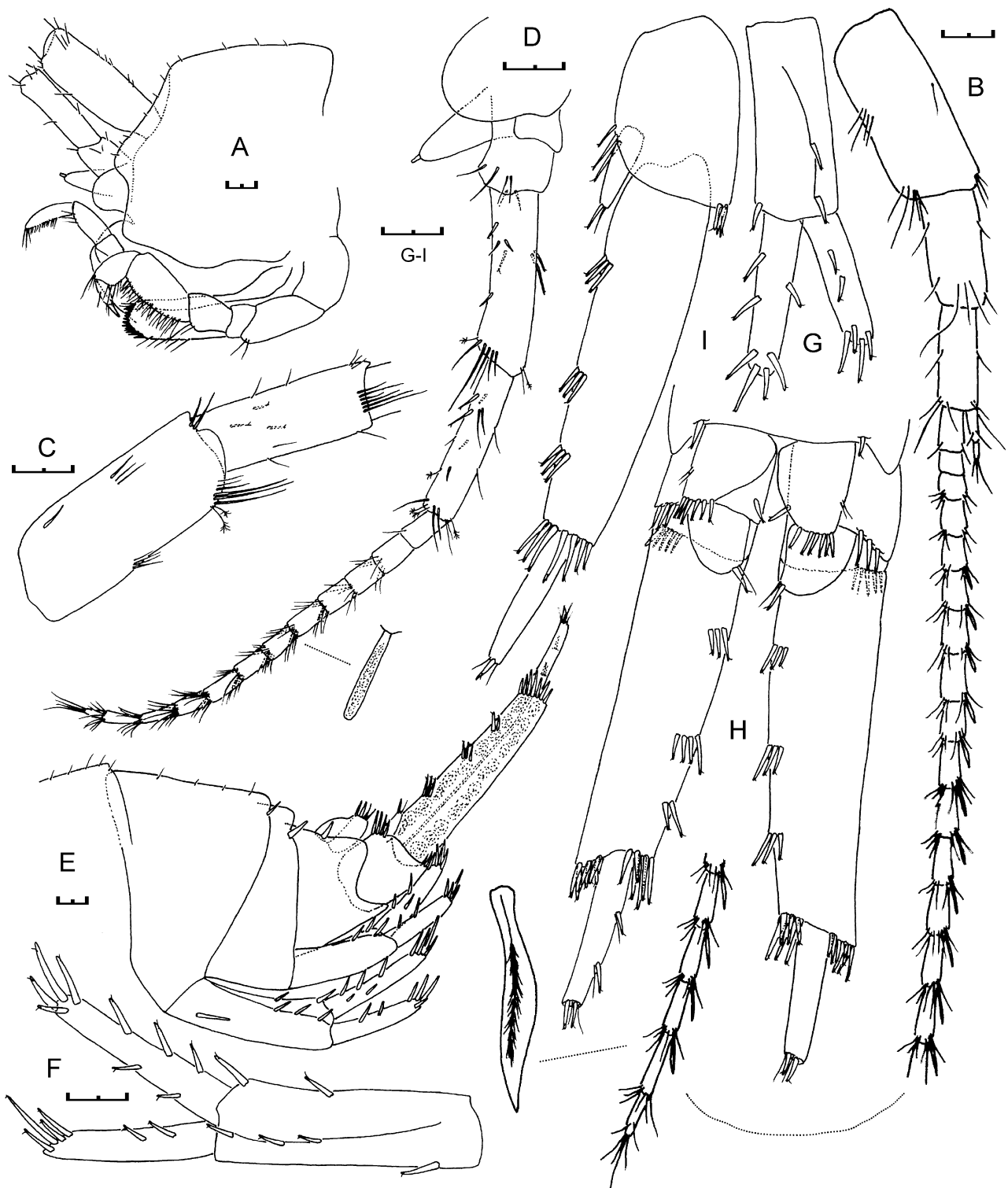


FIGURE 12. *Tadzocrangonyx alaicus*, sp. n., female, 4.5 mm, holotype NC189: (A) head; (C) antenna I, part; (D) antenna II; (E) urosome; (F) uropod I; (G) uropod II; (H) uropod III and telson, dorsal view; (I) uropod III, lateral view. Female, 5.0 mm, paratype NC190: (B) antenna I. Scale bars 0.2 mm.

The most disturbing character is a well developed terminal article of the uropod III exopodite, which is missing at both previous species. However, this is not a phylogenetically stable character. In the related genus

Sarothrogammarus, this article may be twice the length of surrounding spines in Atlantic and Mediterranean relatives (Stock 1971), or more than half shorter and not thicker than surrounding spines (in *S. ruffoi* Karaman, 1971), or even 'not visible (reduced)' (in *S. asiaticus* Martynov, 1935). In the less related genus *Niphargus* Schiödte (fam. Niphargidae) this article may be of the same length as the proximal article, or much shorter, or even absent (in *N. buturovici* S. Karaman, 1958). It is absent also in *Haploginglymus* spp. which appeared to be molecularly nested within *Niphargus* (see also Moškrič, 2016). Thus, the difference in the uropod III does not prevent the new taxon of being a member of the same phylogenetic branch, of the *Sarothrogammarus* group and of the genus *Tadzocrangonyx*.

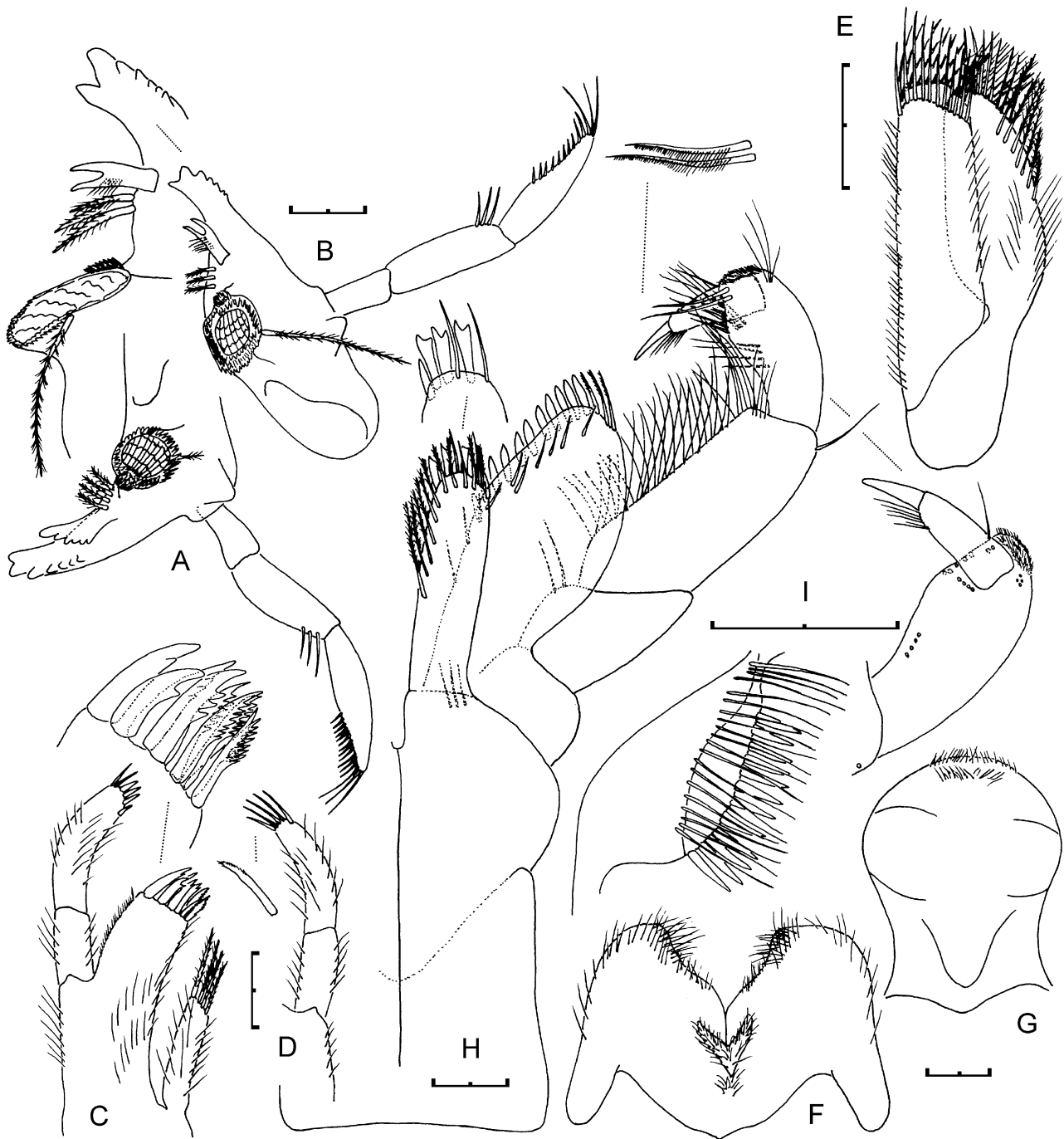


FIGURE 13. *Tadzocrangonyx alaicus*, sp. n., female, 4.5 mm, holotype NC189: (A) mandible, left; (B) mandible, right; (C) maxilla I, left; (D) palp of maxilla I, right; (E) maxilla II; (F) lower lip; (G) upper lip; (H) maxilliped; (I) lateralia. Scale bars 0.2 mm.

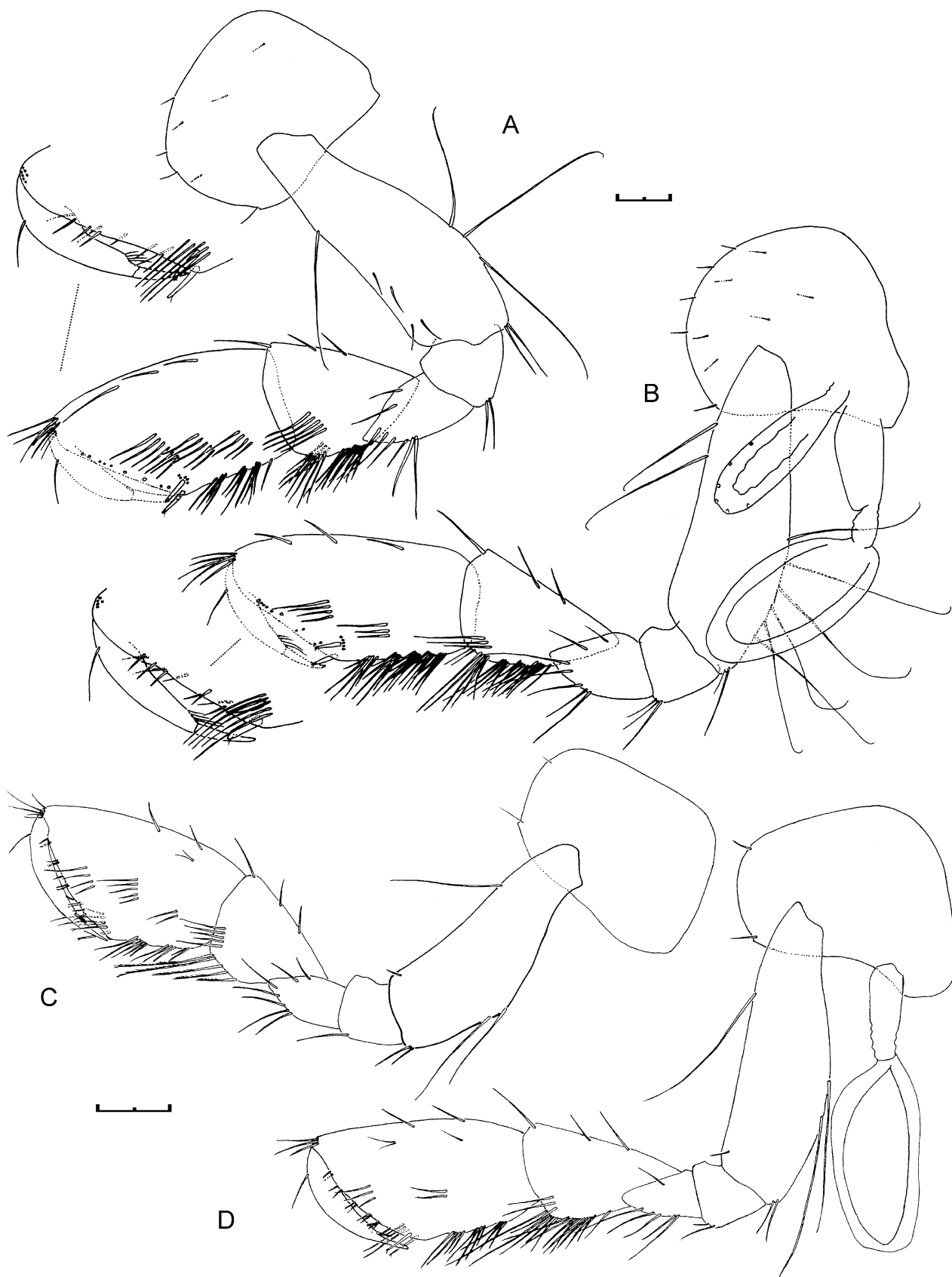


FIGURE 14. *Tadzocrangonyx alaicus*, **sp. n.**, female, 4.5 mm, holotype NC189: (A) gnathopod I; (B) gnathopod II. Male (?), 4.2 mm, paratype NC191: (C) gnathopod I; (D) gnathopod II. Scale bars 0.2 mm.

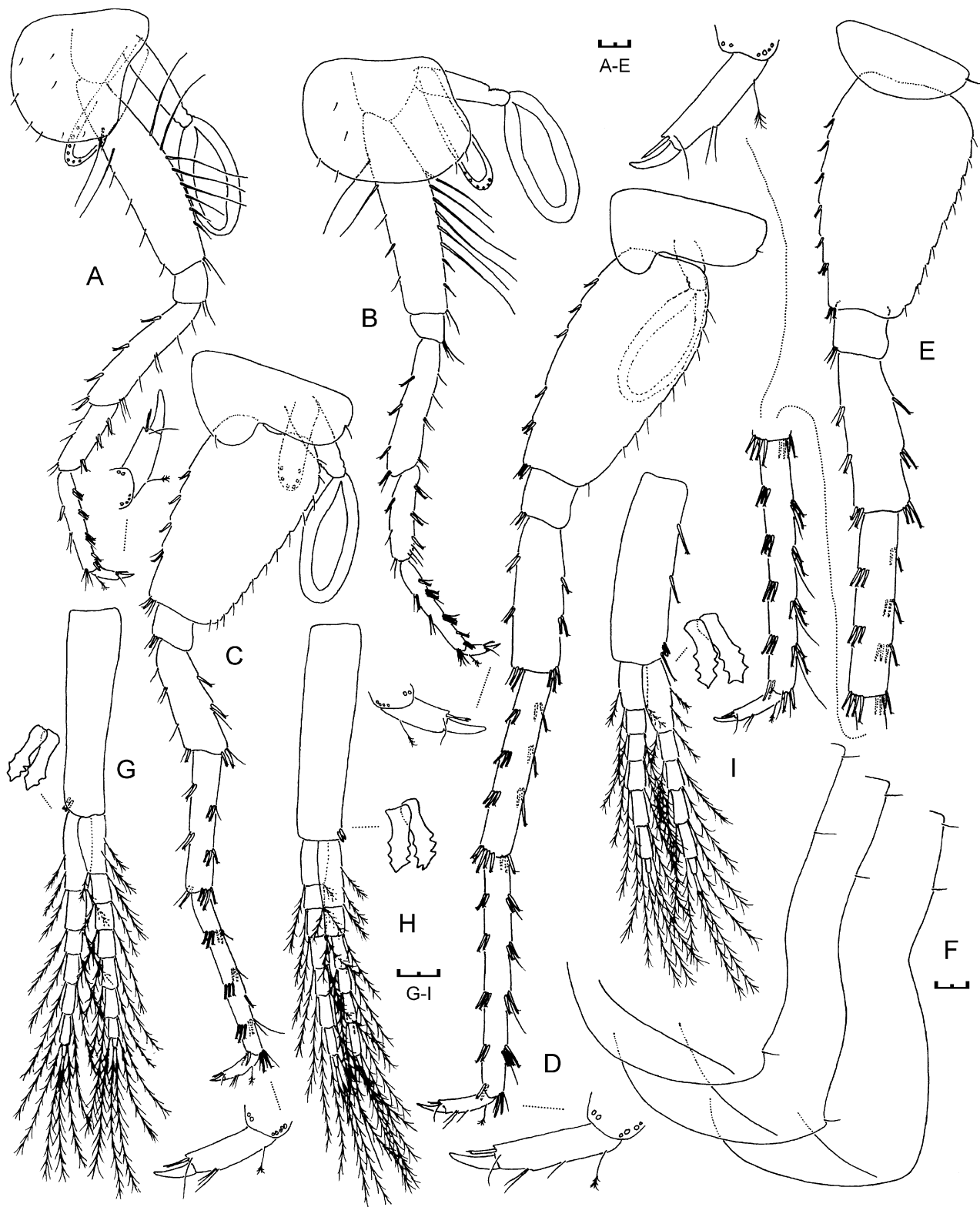


FIGURE 15. *Tadzocrangonyx alaicus*, sp. n., female, 4.5 mm, holotype NC189: (A) pereopod III; (B) pereopod IV; (C) pereopod V; (D) pereopod VI; (E) pereopod VII; (F) epimeral plates; (G) pleopod I; (H) pleopod II; (I) pleopod III. Scale bars 0.2 mm.

The systematics of the Central Asian sarothrogammarids, *Sarothrogammarus*, *Comatogammarus*, *Barnardiorum* and *Tadzocrangonyx* is rather poorly developed and their taxonomic relationship is controversial. Nevertheless, in the course of the comparative morphological analysis we decided that the suite of morphological

characters of the new species most resembles *Tadzocrangonyx* (see Karaman & Barnard 1979). Two previously described species of the genus *Tadzocrangonyx* known from the Central Asia are rather different from each other, essentially differing primarily in the structure of the uropod III. Both species significantly differ by armature of both gnathopods and by a special shape of telson in *T. alaicus*, **sp. n.** (see Table 1). Maxilla II is also very different with a very narrow inner plate. However, for a number of significant features we consider the new species clearly relates to the genus *Tadzocrangonyx*: i.e., shortened coxal plates I–IV, sub-symmetrical palps of maxilla I, structure of gnathopods (palm not oblique), unmodified pereopods III and IV (see also Stock 1971). *Tadzocrangonyx alaicus*, **sp. n.** is significantly different from the known species of *Tadzocrangonyx* and other sarothrogammarids by a quite unique structure of uropod III with the relatively well developed terminal segment of the exopodite. We may suppose that *Tadzocrangonyx* represents a stygobiotic relative of a much diversified *Sarothrogammarus*-group in the region.

TABLE 1. Main diagnostic differences between *Tadzocrangonyx* species.

	<i>T. schizurus</i> (probably ♂, 4.2 mm)	<i>T. setiferus</i> (♀, 9.0 mm)	<i>T. alaicus</i> , sp. n. (♀, 4.5 mm)
Head, interantennal lobe	broad	- ? -	narrow
AII, flagellar articles	6	8	12
Md, palp article III	with A-setae	without A-setae	without A-setae
MxI, inner plate with	8 setae	9 setae	4 setae
MxI, outer plate with	8 spines	10 spines	9 spines
MxI, left palp	broad	narrow	narrow
MxII, oblique row of inner plate with	7 setae	11 setae	7 setae
Ll, inner lobes	well-developed	absent	vestigial
Mxp, inner plate with	3 spines	3 spines	3+1 spines
GI, defining angle with	3 notched spines	6 notched spines	2 notched spines
GII, defining angle with	3 notched spines	6 notched spines	2 notched spines
Coxal plate VII, anterior lobe	?present	?present	absent
Epl-III, armament of ventral margin	I(?), II(2), III(2)	I(?), II(2), III(2)	I(0), II(0), III(0)
Epl-III, posterior corners	acuminate	roundish	predominantly roundish
Pl I-II, inner ramus	reduced	normal	normal
Coxal gill VII	present	absent	absent
UpI, basofacial spine	absent	absent	present
UpIII, outer ramus	1-segmented	1-segmented	2-segmented
Telson, lobes	narrow	narrow	broad
References	Birštejn (1948)	Birštejn & Levuškin (1972)	present study

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