

Research article

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A new genus and two new species of cavernicolous amphipods (Crustacea: Typhlogammaridae) from the Western Caucasus

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Abstract. This study deals with the biodiversity and distribution of cavernicolous Amphipoda in caves of the Arabika massif (Western Caucasus). The Sarma, Trojka and Orlinoe Gnezdo caves were explored during speleological expeditions over the years 2011–12. Two new species of Amphipoda were found: a sub-surface dweller *Zenkevitchia sandroruffoi* sp. nov. is reported from the Sarma, Trojka and Orlinoe Gnezdo caves at depths from -30 m to -350 m; the second one, a deep dweller *Adaugammarus pilosus* gen. et sp. nov. is reported from the Sarma Cave at depths of -1270 to -1700 m. *Adaugammarus* gen. nov. shares similarities with *Typhlogammarus* Schäferna, 1907 and *Zenkevitchia* Birstein, 1940. The species *Anopogammarus birsteini* Derzhavin, 1945 is also re-described herein based on new samples that suggest close affinity of this species with the family Gammaridae. The original taxonomic combination is resurrected for *Zenkevitchia revazi* Birstein & Ljovuschkin, 1970, comb. resurrect. (from *Anopogammarus* Derzhavin, 1945). To accommodate morphologically different species in the genus *Zenkevitchia*, two new groups are proposed. These are the *admirabilis*-group (*Z. admirabilis* Birstein, 1940 and *Z. yakovi* Sidorov, 2015) and the *sandroruffoi*-group (*Z. sandroruffoi* sp. nov. and *Z. revazi*). An updated molecular (mt-*cox1*) phylogeny, an identification key to the genera and a distribution map for the typhlogammarid amphipod species of Transcaucasia are provided.

Keywords. Gammaroidea, mtDNA, phylogeny, Sarma Cave, subterranean species.

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Introduction

The Arabika karst massif is one of the largest and highest in the limestone band of the Western Caucasus. It is bounded by the canyons of the rivers Kutu-Sara, Gega and Bzyb on the North and East, by the Black Sea coast on the Southwest and by the valleys of the Khashupse and Tsandrypsh rivers in the West. The following separation and nomenclature for the speleological areas of the Arabika massif is adopted: the Ortobalagan trough, Gel'geluk trough, Treugol'nik caving district (Zont-Utug-Khyrka), Minskaja Valley trough and the Dzou tract.

Since Birstein and co-authors (Birstein 1940; Birstein & Lopaschov 1940) presented their first studies on the biodiversity of subterranean animals in Transcaucasia, both significant speleological discoveries were made and taxonomic views changed considerably. Dozens of new caves have been explored (Dublyansky *et al.* 1987) and several new taxa have been discovered (Birstein & Ljovuschkin 1967). The contemporary period is marked by several publications on the cavernicolous fauna of the region (Marin & Sokolova 2014; Vinarski *et al.* 2014; Sidorov *et al.* 2015), including biospeleological studies on caves located in the Arabika massif (Jordana *et al.* 2012; Sendra & Reboleira 2012; Sidorov *et al.* 2014). However, the invertebrate troglofauna of the Western Caucasus and surrounding areas is still poorly known (Barjadze *et al.* 2015).

The family Typhlogammaridae was proposed by Bousfield (1978) and consists of five genera: *Typhlogammarus* Schäferna, 1907; *Metohia* Absolon, 1927; *Zenkevitchia* Birstein, 1940; *Anopogammarus* Derzhavin, 1945 and *Accubogammarus* G. Karaman, 1974 (Schäferna 1907; Absolon 1927;

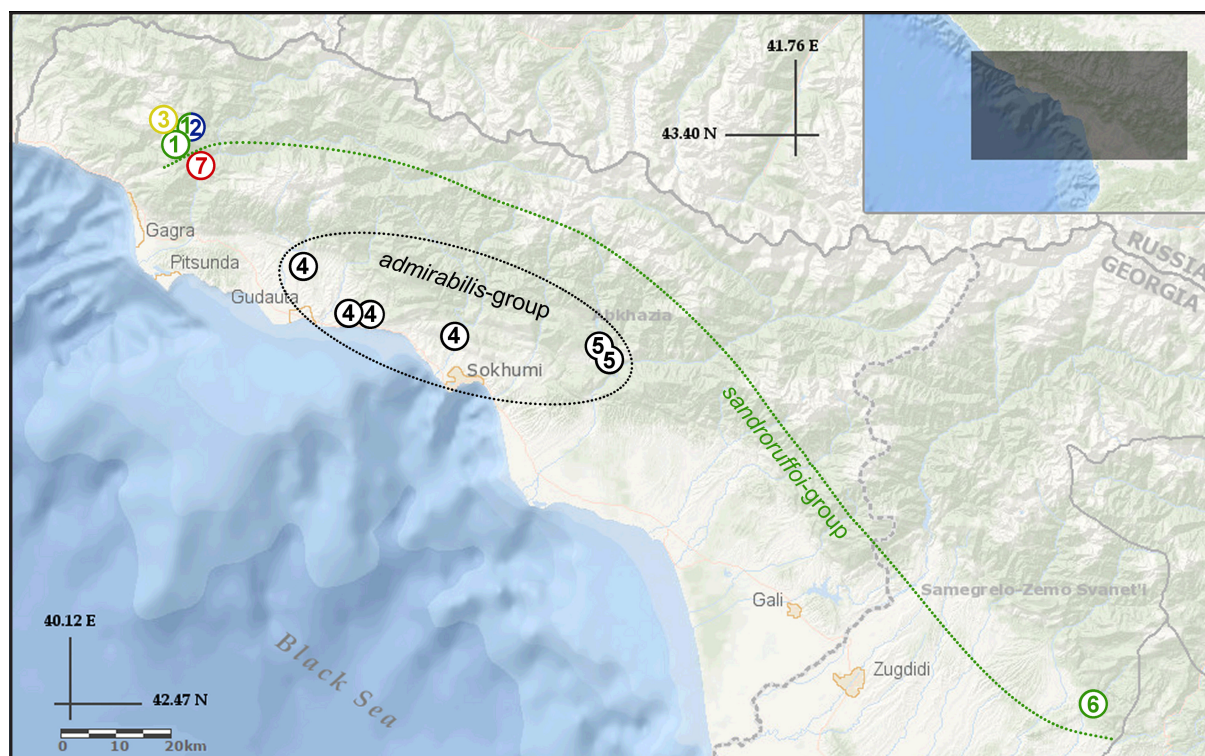


Fig. 1. Distribution map of Typhlogammaridae species and *Anopogammarus* in the Transcaucasia. 1. *Zenkevitchia sandroruffoi* sp. nov. 2. *Adaugammarus pilosus* gen. et sp. nov. 3. *Zenkevitchia* sp. *sensu* Jaume in Sendra & Reboleira (2012). 4. *Zenkevitchia admirabilis* (complex of species). 5. *Zenkevitchia yakovi* Sidorov, 2015. 6. *Zenkevitchia revazi* Birstein & Ljovuschkin, 1970, comb. resurr. 7. *Anopogammarus birsteini* Derzhavin, 1945.

Birstein 1940; Derzhavin 1945; Karaman 1974). The typhlogammarids mostly inhabit subterranean waters in caves and are sometimes observed in the karstic springs of the Balkan-Transcaucasian region. An interesting feature of this group of invertebrates is their ability to move across the stone surface within a thin film of water, the so-called “cave hygropetric habitat” (Sket 2004).

In this paper, we present results of a biospeleological survey from the most studied caving area, Treugol'nik, with about 30 known caves including one of the world's deepest caves, the Sarma Cave. The Sarma, Trojka and Orlinoe Gnezdo caves were studied and among other things (Sidorov *et al.* 2014), amphipods of the Typhlogammaridae family were collected there. The DNA barcode region of the mitochondrial *cytochrome c oxidase* subunit 1 (COI) gene sequence was used to verify the distinction of described species, along with comparative morphological analyses.

Material and methods

Specimen collection

The samples of blind, unpigmented aquatic amphipods were collected in three limestone caves; the meters refer to the explored cave depth: Sarma (-1830 m), Trojka (-257 m), and Orlinoe Gnezdo (-75 m) in the Arabika massif of Abkhazia (Fig. 1, Table 1). Additionally, samples containing specimens of *Anopogammarus birsteini* Derzhavin, 1945 were collected at the type locality near Goluboe Lake in the Gagra District of Abkhazia. Specimens were preserved in 96% ethanol at each field site. The geographical map showing the sampling sites and distribution pattern of the Typhlogammaridae species in the Western Caucasus was constructed with GMT 4.5.6.-1. GIS software (Fig. 1).

Morphology and taxonomic terms

The body length of the amphipods was recorded by holding the specimen straight and measuring the distance along the dorsal side of the body from the base of the first antenna to the base of the telson, using a micrometer eye piece in a Lomo MBS-9 dissecting microscope. Appendages were drawn with a Carl Zeiss NU-2 compound microscope equipped with a drawing device as described in Gorodkov (1961). Heavily calcified specimens of crustaceans were placed in 4% lactic acid and then washed and boiled in clean water to remove air bubbles within the segments. Permanent preparations were made using a methylene blue staining solution, and polyvinyl lactophenol (PVL) was used as the mounting medium. The descriptive terminology follows the classification system in the original conventional sense and does not agree with the homology concepts proposed by Watling (1989). To make the nomenclature more stable, we use the term “spine” for robust setae and the term “seta” for slender, usually flexible structures. The term “palmar angle” of the gnathopod propodi refers to the angle formed at the end of the palm and beginning of the posterior margin or at the point where the tip of the dactylus closes on the propodus (Birstein 1941). The fore-gut lateralia comprise a potentially useful morphological character in the phylogenetic analysis (Coleman 1991). The nomenclature for setal patterns on article 3 of the mandibular palp follows the practice of Karaman (1970) and Stock (1974). The descriptions are based on the type series and all material examined is deposited in the Zoological Museum of the Far East Federal University, Vladivostok (FEFU; the holotypes are kept there) or in the research collection of D.A. Sidorov at the Institute of Biology and Soil Science, Vladivostok (IBSS).

DNA extraction, amplification, sequencing and analysis

Total DNA was extracted from the muscle tissue with a DNeasy Blood & Tissue kit (QIAGEN GmbH, Hilden, Germany) according to the manufacturer's protocol. The COI gene fragment was amplified using the universal primers HCO2198 and LCO1490 (Folmer *et al.* 1994). The annealing temperature was set at 40°C for 20 s. The PCR products were sequenced directly using the same primers and a BigDye terminator v. 3.1 sequencing kit (Applied Biosystems, USA). Sequences were analyzed on an ABI 3130 genetic analyzer (Applied Biosystems, USA) and assembled with the Staden Package v. 1.4

Table 1. List of the specimens, sampling sites and accession numbers of the sequences included in this study. References are given for sequences obtained from GenBank.

Specimen	Locality	GenBank acc. no. COI	Reference/ or year of sampling
<i>Adaugammarus pilosus</i> SC1270m1	Georgia, Abkhazia: Sarma Cave, -1270 m	KT427516	This study (2011)
<i>Adaugammarus pilosus</i> SC1270m2	Georgia, Abkhazia: Sarma Cave, -1270 m	KT427517	This study (2011)
<i>Adaugammarus pilosus</i> SC1270m3	Georgia, Abkhazia: Sarma Cave, -1270 m	KT427518	This study (2011)
<i>Adaugammarus pilosus</i> SC1700m	Georgia, Abkhazia: Sarma Cave, -1700 m	KT427519	This study (2011)
<i>Zenkevitchia sandroruffoi</i> SC230m	Georgia, Abkhazia: Sarma Cave, -230 m	KT427520	This study (2012)
<i>Zenkevitchia sandroruffoi</i> SC350m	Georgia, Abkhazia: Sarma Cave, -350 m	KT427521	This study (2012)
<i>Zenkevitchia sandroruffoi</i> TC	Georgia, Abkhazia: Trojka Cave, -30 m	KT427522	This study (2012)
<i>Zenkevitchia sandroruffoi</i> OG1	Georgia, Abkhazia: Orlineo Gnezdo Cave, -75 m	KT427523	This study (2011)
<i>Zenkevitchia sandroruffoi</i> OG2	Georgia, Abkhazia: Orlineo Gnezdo Cave, -75 m	KT427524	This study (2011)
<i>Zenkevitchia sandroruffoi</i> OG3	Georgia, Abkhazia: Orlineo Gnezdo Cave, -75 m	KT427525	This study (2011)
From GenBank			
<i>Accubogammarus</i> sp. SLOCHN114	Montenegro: Grahovo, Vojvode Dakovića cave	KF478592	Hou <i>et al.</i> 2014
<i>Anopogammarus revazi</i> SLOCHN245	Georgia: Martvili, Motena cave	KF478522	Hou <i>et al.</i> 2014
<i>Metohia carinata</i> SLOCHN019	Montenegro: Rijeka Crnojevića, Obodska cave	KF478584	Hou <i>et al.</i> 2014
<i>Metohia carinata</i> SLOCHN025	Bosnia-Herzegovina: Čičevo, Velja gora, Šumet cave	KF478585	Hou <i>et al.</i> 2014
<i>Typhlogammarus mrazeki</i> SLOCHN020	Bosnia-Herzegovina: Popovo polje, Zavala, Vjetrenica cave	KF478586	Hou <i>et al.</i> 2014
<i>Typhlogammarus mrazeki</i> SLOCHN113	Montenegro: Cetinje, Lipska cave	KF478590	Hou <i>et al.</i> 2014
<i>Typhlogammarus</i> sp. SLOCHN252	Croatia: Zrmanja, Krupa cave	KF478591	Hou <i>et al.</i> 2014
<i>Zenkevitchia admirabilis</i> SLOCHN199	Georgia, Abkhazia: Suhumi, Verhnie Pešeri, Verhne-esherskaja (=Sobachya) cave, approx. 43°0658 N, 40°9922 E	KF478600	Hou <i>et al.</i> 2014
<i>Zenkevitchia admirabilis</i> SLOCHN200	Georgia, Abkhazia: Gudauta, Lihni, Tarkili (=Tarkiladze) cave, 43.19441 N, 40.65165 E	KF478599	Hou <i>et al.</i> 2014
<i>Zenkevitchia yakovi</i> T	Georgia, Abkhazia: “Istočnik Tcebel’da” cave, 43°0262 N 41°2830 E	KP844572	Sidorov <i>et al.</i> 2015
<i>Zenkevitchia yakovi</i> S1	Georgia, Abkhazia: Sredne-Shakuranskaya cave, 43°0297 N 41°3331 E	KP844573	Sidorov <i>et al.</i> 2015
<i>Zenkevitchia yakovi</i> S2	Georgia, Abkhazia: Sredne-Shakuranskaya cave, 43°0297 N 41°3331 E	KP844574	Sidorov <i>et al.</i> 2015

(Bonfield *et al.* 1995). The Akaike information criterion (AIC2) in ModelGenerator 0.85 (Keane *et al.* 2006) was used to select the model of sequence evolution best fitting our data set (HKY+G+I). The data set was analyzed using the maximum-likelihood (ML) algorithm in Mega 6.0 (Tamura *et al.* 2013), and pairwise sequence divergence was estimated using the same environment. A standard BioNJ initial tree was obtained automatically by applying the Nearest-Neighbor-Interchange (NNI) for tree inference. To assess support for clades 1,000 bootstrap replicates (Felsenstein 1985) were performed.

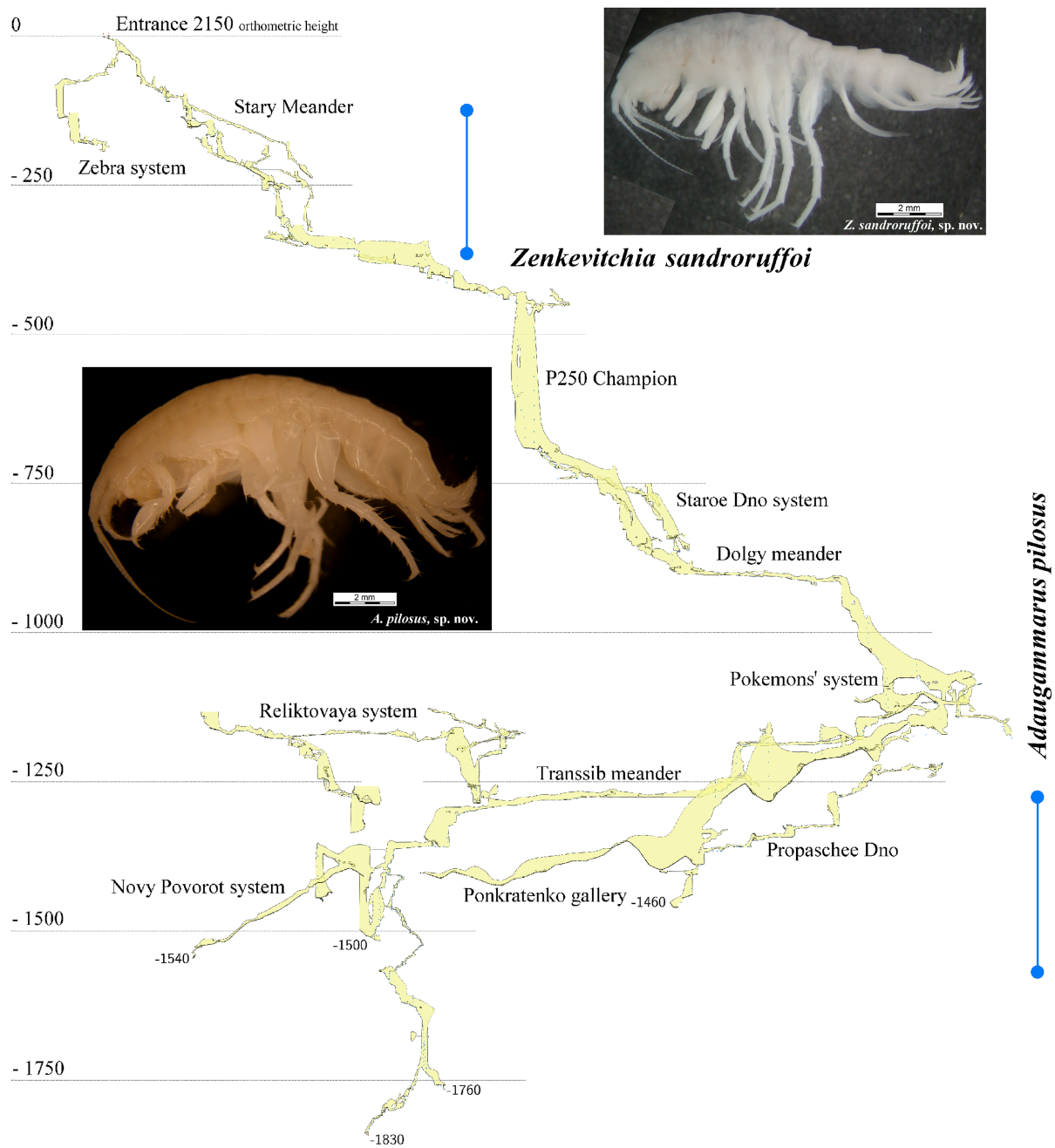


Fig. 2. Vertical distribution of amphipod species in the Sarma Cave. Map adapted from Sidorov *et al.* (2014), compiled by V.V. Sukhachev.

Results

Order Amphipoda Latreille, 1818
Family Gammaridae Leach, 1814
Genus *Anopogammarus* Derzhavin, 1945

Anopogammarus birsteini Derzhavin, 1945
Figs 4A–E, 5–6

Anopogammarus birsteini Derzhavin, 1945: 34, pl. 2.

Anopogammarus birsteini – Birstein & Ljovuschkin 1967: 1512; 1970: 1478, figs 4–6. — Stock 1973: 339. — Bousfield 1977: 291. — Karaman & Barnard 1979: 142. — Barnard & Karaman 1980: 8. — Barnard & Barnard 1983: 502. — Ruffo 1995: 450. — Karaman & Ruffo 1995: 159, 160.

Material examined

GEORGIA: 1 ♀, 1 ♂, Western Caucasus, Gagra District, near Goluboe Lake (43°35'08" N, 40°41'19" E). Specimens, completely dissected and mounted on a single slide per number: ♀ (oostegites initial, non-setose) 9.0 mm, ♂ 8.5 mm, 15 Jun. 2015, 133 m a.s.l., springs, coll. D.M. Palatov (X44039/Cr-1645-46-FEFU).

Additional material examined

GEORGIA: 5 ♀♀ (6.0 mm, 3x7.0 mm, 7.5 mm; oostegites initial, non-setose), 5 ♂♂ (3x6.0 mm, 7.5 mm, 9.0 mm), 3 juv., specimens measured, partially dissected and stored in different vials (1-12/1sd-IBSS), same data as above.

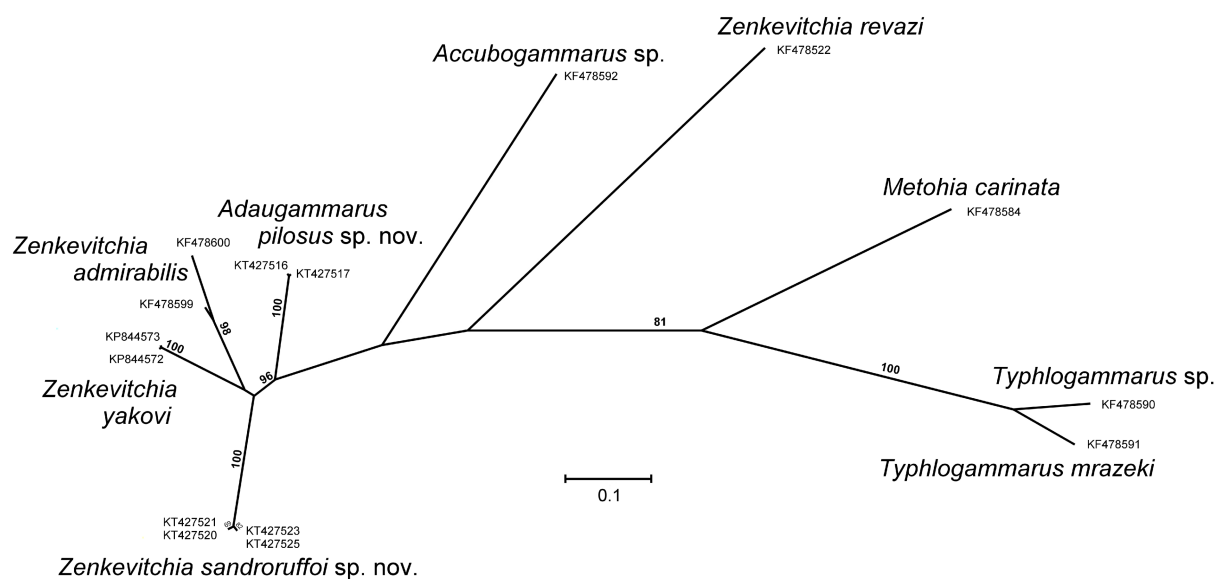


Fig. 3. Unrooted ML-tree with bootstrap support values based on the mt-*coxI* sequences (values less than 50% not shown). Specimen labels refer to information given in Table S1. Scale bar indicates the number of substitutions per site.

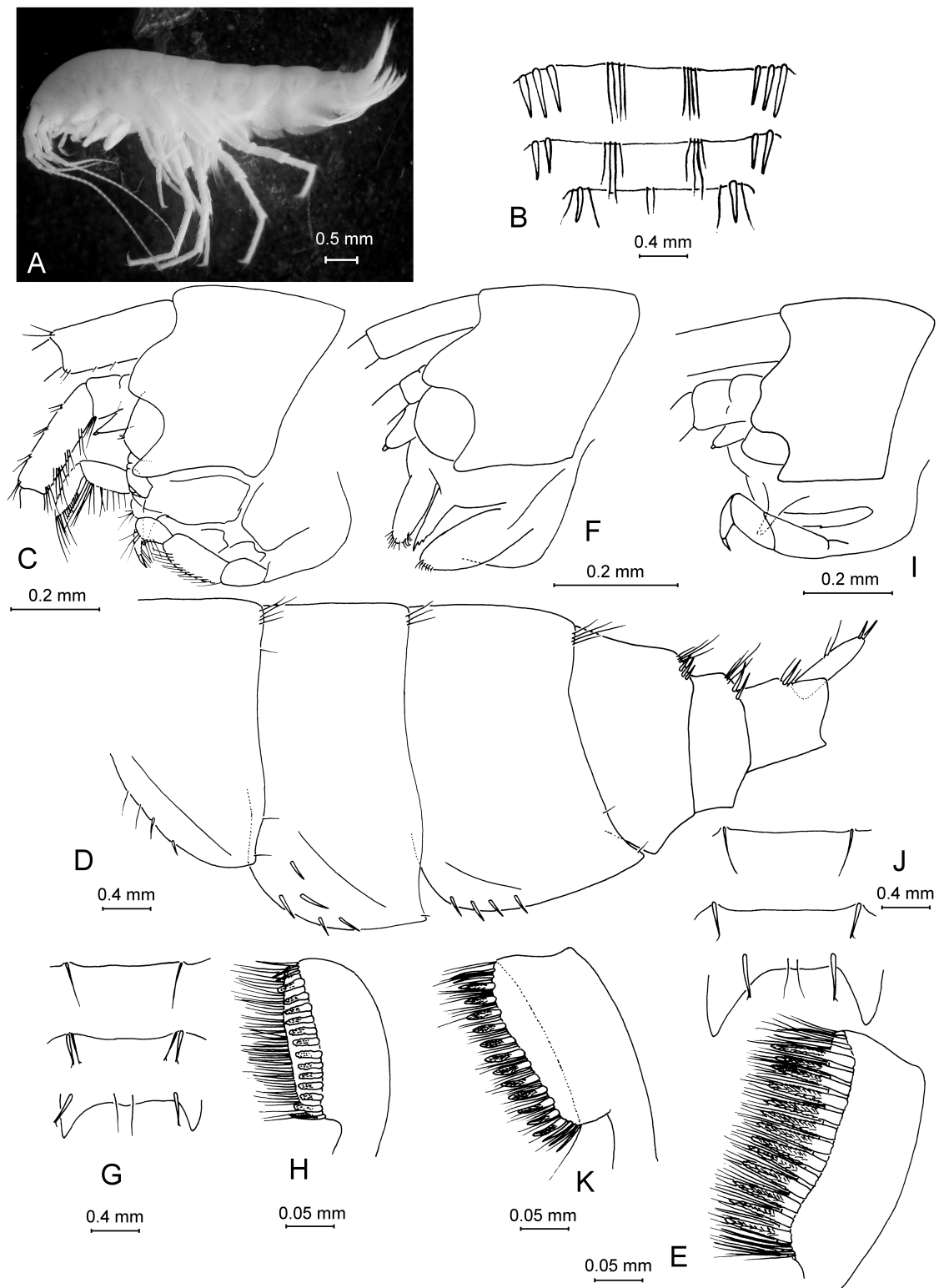


Fig. 4. — **A–D.** *Anopogammarus birsteini* Derzhavin, 1945. ♀, 9.0 mm, X44039/Cr-1645-FEFU: **A.** Habitus from left side. **B.** Urosome. **C.** Head. **D.** Metasomal and urosomal segments with telson. — **E–G.** *Zenkevitchia sandroruffoi* sp. nov. Paratype, ♀, 6.3 mm, X44045/Cr-1651-FEFU. **E.** Lateralia. **F.** Head. **G.** Urosome. — **H–K.** *Adaugammarus pilosus* sp. nov. Holotype, ♀, 13.5 mm, X44046/Cr-1652-FEFU. **H.** Lateralia. **I.** Head. **J.** Urosome. **K.** Lateralia.

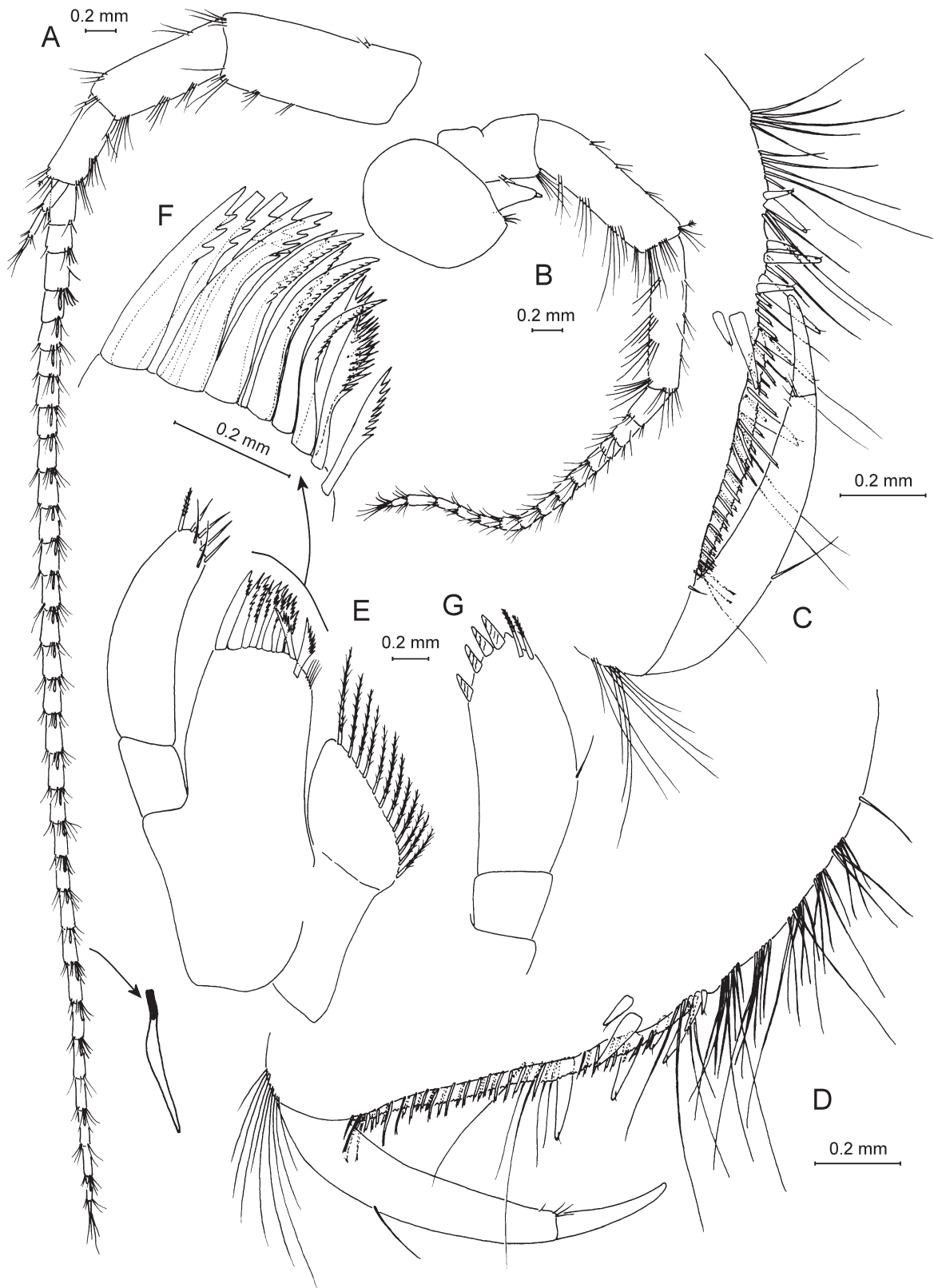


Fig. 5. *Anopogammarus birsteini* Derzhavin, 1945. ♀, 9.0 mm, X44039/Cr-1645-FEFU. A. Antenna 1. B. Antenna 2. C–D. Palmar margins of gnathopods 1 and 2 propodi. E. Maxilla 1. F. Outer plate of maxilla 1. G. Palp of right maxilla 1.

Remark

Although *A. birsteini* was described by Derzhavin (1945) based on an 8.0 mm female and was subsequently redescribed in detail (Birstein & Ljovuschkin 1970) based on both sexes, we further introduce an amended diagnostic description to emphasize some important characters.

Diagnostic description

SIZE. Female body length 9.0 mm and male, body length 8.5 mm (X44039/Cr-1645-46-FEFU). Robust, large-sized species of gammarid-like habitus (sexual dimorphism weakly pronounced, i.e., females larger than males). Coxal gills 2–7 stalked, triangular or sacciforme, largest on gnathopod 2, successively smaller on pereopods 3 to 7, gill 7 the smallest. Body length 6.0–17.0 mm (♀), 6.0–14.0 mm (♂).

GENERAL BODY MORPHOLOGY (Figs 4A–D, 6G). Body smooth, lacking dorsal cuticular elements. Head as long as first pereon segment; rostrum absent; inferior antennal sinus shallow, sub-rounded. Eyes absent. Pleosomites and urosomites on dorsal surface with lateral groups of spines and setae; medial elements absent. Dorsal surface of urosomites 1–3 armed with robust spines in the following manner: 1 (3-0-0-3), 2 (2-0-0-2), 3 (1-0-1). Epimeral plate 1: postero-ventral corner prominent; posterior and ventral margins convex; 2 stiff setae along ventral margin, 2 setae along posterior margin. Epimeral plate 2: postero-ventral corner acuminate; posterior and ventral margins convex; 5 stiff setae in two rows along ventral margin, 1 seta along posterior margin at corner. Epimeral plate 3: postero-ventral corner

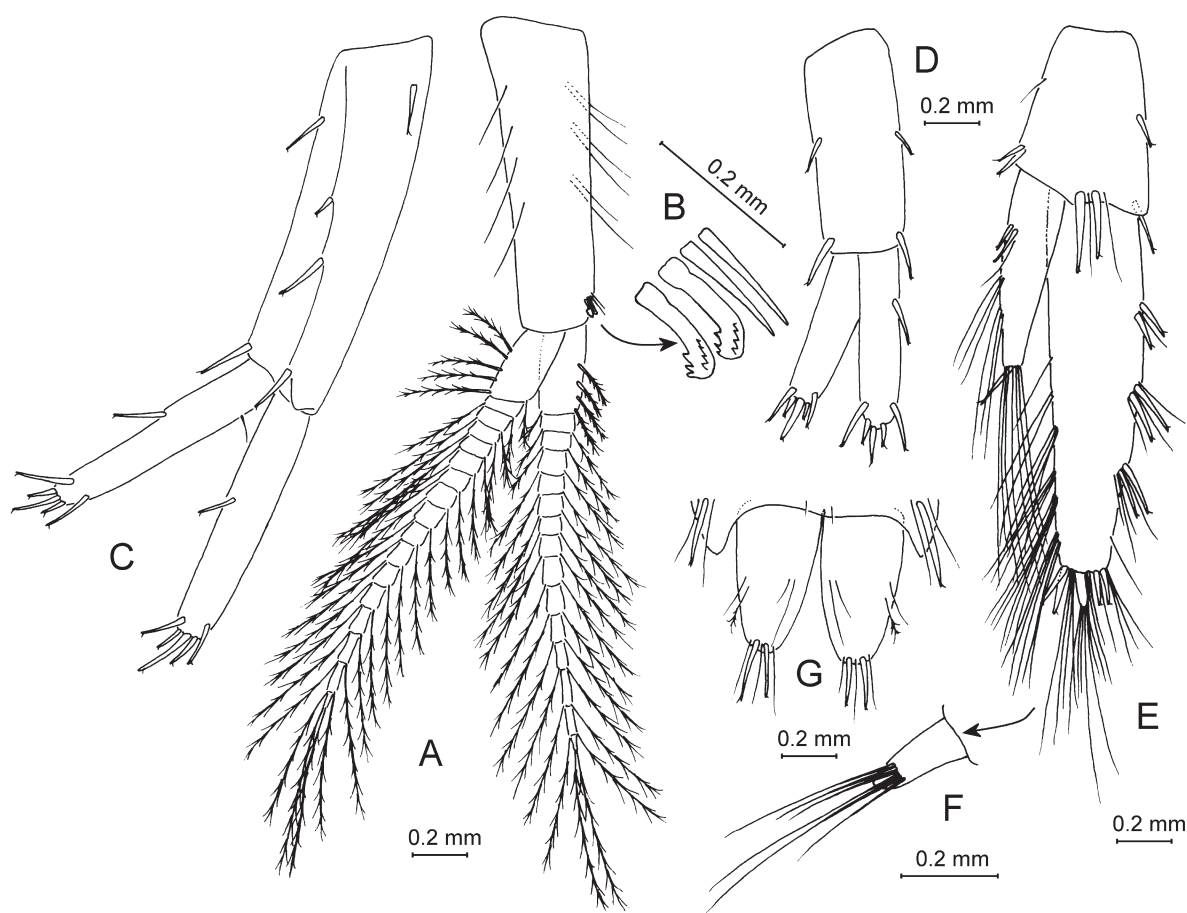


Fig. 6. *Anopogammarus birsteini* Derzhavin, 1945. ♀, 9.0 mm, X44039/Cr-1645-FEFU. A. Pleopod 2. B. Coupling setae of pleopod 2. C. Uropod 1. D. Uropod 2. E–F. Uropod 3. G. Telson.

acuminate; posterior margin concave; ventral margin convex; 4 stiff seta along ventral margin, 2 setae along posterior margin. Telson as long as broad; cleft entirely; 2 or 3 apical spines per lobe present, these are $0.2\times$ telson length, each accompanied by setae. Antennae (Figs 4A, 5A–B). Antenna 1 $0.65\times$ of body length; main flagellum with up to 30–32 articles; almost all flagellar articles bearing small aesthetascs accompanied by 2–8 short setae; peduncular articles in ratio 1:0.7:0.4; proximal article of peduncle with 3 sets of short setae along ventral margin; accessory flagellum 3- or 4-articulated. Length ratio of antenna 1 to antenna 2 is 1:0.5; flagellum of antenna 2 with 11–15 articles, each article densely setose; length ratio of peduncle articles 4 and 5 is 1:0.9; flagellum as long as peduncle (articles 4+5); peduncular articles 4 and 5 with sets of long stiff setae along ventral margin; gland cone short.

MOUTH PARTS (typical gammarid, Figs 5E–G). Maxilla 1 palp longer than outer plate, distal article with 5 apical and 2 sub-apical setae (both palps asymmetric, right palp broader, with 4–5 strong spines and 2 plumose setae on apex and 1–2 setae on outer margin); outer plate with 12–14 spines (5 poorly toothed and 9 multi-toothed); inner plate trapezoidal, with 12 plumose setae. Foregut lateralialia with 13 strong pectinate spines and densely setose row of stiff setae.

GNATHOPODS 1–2 (Fig. 5C–D). Gnathopod 1: propodus almond-shaped, palm convex, with cutting margin acanthaceous and $2\times$ longer than posterior margin; along posterior margin two sets of simple setae; antero-distal group of anterior margin with 10 setae; palmar margin with short, notched setae along outer and inner faces, palmar angle undefined, a group of 10 distally-notched strong spines on both faces (with 2 strong mid-palmar spines in the place where tip of nail close); nail long, $0.25\times$ total length of dactylus, 1 seta along anterior margin, with 4 setules at hinge. Gnathopod 2: propodus small (compared to the body) and slightly larger than propodus of gnathopod 1; propodus almond-shaped, palm convex, with cutting margin acanthaceous and as long as posterior margin; posterior margin with 6 sets of stiff setae; antero-distal group of anterior margin with 10 setae; palmar margin with short, notched setae along outer and inner faces, palmar angle undefined, a group of 8 distally-notched strong spines on both faces (with 2 strong mid-palmar spines in the place where tip of nail close); dactylus similar to that of gnathopod 1.

PLEOPODS (Fig. 6A–B). Pleopods 1–3 sub-equal, each with 2 coupling setae (retinacula) accompanied by 1–3 stiff setae; peduncular articles fringed with long, thin setae; proximal article of inner rami fringed with 4 setae. Pleopods 1–3 rami with 15–19 articles each.

UROPODS (Figs 4A, 6C–F). Uropod 1 protopodite with 1 basofacial spine, 3 dorso-lateral spines and 2 dorso-medial spines; exopodite as long as endopodite; rami straight, with single spines along outer margins; both with 5 spines apically and sub-apically (two of them strong). Uropod 2 endopodite slightly shorter than exopodite. Uropod 3 protopodite with 3 groups of spines on apex; endopodite as long as protopodite, with 1 spine and 7 long setae apically; exopodite 2-articulated, about $2.2\times$ longer than protopodite, with 3 groups of lateral spines, 6 groups of long simple setae along inner margin; proximal article with 4 spines and about 10 long setae on apex, terminal article short, $0.09\times$ as long as proximal article, with 6 long simple setae sub-apically.

Discussion of affinities

Describing the monotypic genus *Anopogammarus* Derzhavin (1945) noted a lack of eyes in *A. birsteini* as the only difference from the genus *Gammarus* and considered this feature characteristic. Later, Birstein & Ljovuschkin (1970) re-described *Anopogammarus birsteini* in detail and considered this species, along with *Metohia carinata* Absolon, 1927, as derived from *Gammarus*, implying a subgeneric status for the genera *Anopogammarus* and *Metohia*. However, according to their view, *Zenkevitchia revazi* occupies an intermediate position between the specialized *Zenkevitchia admirabilis* and *Gammarus* (Stock 1973). Subsequently, Karaman & Barnard (1979) transferred *Z. revazi* to *Anopogammarus*, based on the non-moplake structure of maxilla 1 and reduced palps in the former species. Later, the same authors

(Barnard & Karaman 1980) again confirmed that *Anopogammarus*, along with the rest of the taxa placed in the Family group 2 (*Typhlogammarus* group, hypogean large gammarids) *sensu* Bousfield (1977), has no strong distinction from the *Gammarus-Echinogammarus* group (see Barnard & Karaman 1980: 7–9). Ruffo (1995) and Karaman & Ruffo (1995), describing two genera of cavernicolous amphipods (*Albanogammarus* and *Sinogammarus* from Albania and Southwest China, respectively), discussed the position of the new taxa in depth and hypothesized an obvious affinity with *Anopogammarus*.

The revision of the group cannot be considered as completed, because the genus *Anopogammarus* is heterogeneous and needs to be split. We propose transferring *Anopogammarus revazi* to the genus *Zenkevitchia* (*Zenkevitchia revazi* Birstein & Ljovuschkin, 1970, comb. *resurr.*) and to the newly proposed group (*sandroruffoi*-group). The monotypic genus *Anopogammarus* based on *Anopogammarus birsteini* Derzhavin, 1945, however, should be considered a component of the family Gammaridae. As the above-mentioned authors, we believe that the monotypic genus *Anopogammarus* has an affinity to *Albanogammarus* and *Sinogammarus*. This assumption is based on the following shared features: the structure of the anterior margin of the cephalon (lateral interantennal lobes slightly subquadrate); powerful dorsal armament of urosomal segments; antenna 1 with small aesthetascs in males (? lacking in *Albanogammarus*); calceoli on antenna 2 absent; article 1 of antenna 2 being rather large, bearing short setae, and antennal gland cone short; structure of maxilla 1 (outer plate with multi-toothed non-falcate spines and palps clearly asymmetric); uropod 3 long and with 2-articulated outer ramus.

Family Typhlogammaridae Bousfield, 1978
Genus *Zenkevitchia* Birstein, 1940

Zenkevitchia Birstein, 1940: 51, fig. 4.

Zenkevitchia — Birstein 1941: 260, figs 1–3; 1950: 356. — Derzhavin 1945: 34. — Birstein & Ljovuschkin 1970: 1472, fig. 1. — Bousfield 1977: 291. — Barnard & Barnard 1983: 507.

sandroruffoi-group

Remarks

Although, as described below, *Zenkevitchia sandroruffoi* sp. nov. differs from other species of *Zenkevitchia* (*Z. admirabilis*, *Z. yakovi*) in the non-filtrative maxilla 1, we decided that it, along with *Z. revazi*, differs sufficiently to warrant recognition as a new species group within the genus *Zenkevitchia*, which we here designate as the *sandroruffoi*-group. The *sandroruffoi*-group (*Z. sandroruffoi* sp. nov. and *Z. revazi* Birstein & Ljovuschkin, 1970) is phenotypically more distant from the type species of the genus *Zenkevitchia*, bearing only up to 22 multi-toothed spines (non-falcate in shape). In some sense, the group occupies an intermediate position between *Zenkevitchia* (*admirabilis*-group) and other species of the Typhlogammaridae (cf. *Accubogammarus*), although, in our opinion, it is closer to the former. The indicators for affinity to *Zenkevitchia* are: interantennal cephalic lobes sub-acute, urosomal segments weakly armed, shortened antenna 1, antennal gland cone of antenna 2 long, reduced and sub-symmetrical palps of maxilla 1, structure and armament of gnathopods (both appendages with well-defined palmar angle).

Despite these points of similarity, *Z. revazi* needs re-description because some features, such as sexual dimorphism, were not described properly, although important characters that clearly differentiate both species (characteristics of *Z. sandroruffoi* sp. nov. in parentheses in the following list) are evident. These are: outer plate of maxilla 1 with 11 spines (22 spines), palps of maxilla 1 asymmetric, reduced (sub-symmetric, cf. *Typhlogammarus m. mrazeki* Schäferna, 1907 and *T. m. heteropalpus* Karaman, 1972; Karaman 1972, 1988) body of mandibles compacted (elongated), bases of pereopods 5–7 without

lobes (with extraordinary roundish postero-proximal lobes), uropod 3 well-developed, setose with plumose setae (reduced, weakly setose). *Zenkevitchia revazi* reveals a number of features in common with *Accubogammarus* and the minor differences between these taxa (Karaman 1973, 1974, 1988) are mainly related to the structure of uropod 3.

Zenkevitchia sandroruffoi sp. nov.

[urn:lsid:zoobank.org:act:707E6585-8A2E-47BA-802A-8349FAA1AAA2](https://doi.org/10.2307/2386585)

Figs 2, 4F–H, 7–11

Diagnosis (both sexes)

Robust, middle-sized species of gammarid-like habitus (sexual dimorphism weakly pronounced, i.e., males usually larger than females, antenna 2 and both gnathopods sexually dimorphic). Antenna 1 short, reaching 40% length of body; antenna 2 short, reaching about 60% length of antenna 1, gland cone long, reaching half of peduncle of segment 4. Maxilla 1 inner plate triangular, with 16 plumose setae, outer plate of non-filtration type (?scraper type), with 22 multi-toothed, comb-like spines; palps symmetrical and reduced. Mandibular palp article 3 with 1 A group of 2 setae, 2 B setae, 13 D setae and 4 E setae. Gnathopods 1–2 small, with propodus not larger than corresponding coxa; palmar angles of both gnathopods defined, with a group of notched, strong corner spines; dactyli with 1 seta each along outer margin, nails long. Pereopods 5–7 bases with distinct postero-proximal lobes; inner margin of dactyli of pereopods 3–7 with 1 stiff, notched seta. Urosomites with dorsolateral groups of spines. Pleopods 1–3 with 2 coupling setae (retinacula), each accompanied with 1 seta (2+1). Uropod 1 rami sub-equal, outer ramus scarcely shorter than inner ramus. Uropod 3 short, 0.3× shorter than uropod 2, endopodite small, 0.6× shorter than exopodite. Telson with 1 or 2 distal spines per lobe. Coxal gills 2–7 stalked, triangular or sacciforme, largest on gnathopod 2, successively smaller on pereopods 3 to 7, gill 7 the smallest. Body length 6.0–8.3 mm (♀), 8.0–12.5 (♂).

Etymology

This species is named in honor of Professor Sandro Ruffo (Museo Civico di Storia Naturale, Verona) for his outstanding contribution in the field of Amphipoda systematics.

Material examined

Holotype

GEORGIA: sequenced ♂, 8.0 mm, Sarma Cave (43°41'58" N, 40°36'33" E, approx.), 2346 m a.s.l., Muzykalnyj meander (sampling depth -350 m), Arabika massif, Gagra District, Western Caucasus, 25 Aug. 2012, coll. E.E. Golubnichaya (X44041/Cr-1647-FEFU).

Paratypes

GEORGIA: ♂, 10.5 mm, ♀ (oostegites developed, weakly setose), 8.3 mm, Sarma Cave (sampling depth -230 m), 28 Aug. 2012, coll. E.E. Golubnichaya (X44042/Cr-1648-51-FEFU); ♂, 12.5 mm, Trojka Cave (43°39'33" N, 40°36'25" E, approx.), 2333 m a.s.l., ~2-3 km SW of Sarma Cave (sampling depth -30 m), 27 Aug. 2012, coll. E.E. Golubnichaya; ♀ (oostegites developed, weakly setose), 6.3 mm, Orlineo Gnezdo Cave, (43°38'55" N, 40°36'37" E, approx.), 2126 m a.s.l., ~10 km SW of Sarma Cave (sampling depth -75 m), 15 Sep. 2011, coll. L.T. Kharlamova.

Additional material

GEORGIA: specimens measured, partially dissected and stored in different vials (1-11/2sd-IBSS): 2 ♀♀ with developed oostegites, weakly setose, 7.0 mm, 8.0 mm, Sarma Cave, Muzykalnyj meander (sampling depth -350 m), 25 Aug. 2012, coll. E.E. Golubnichaya; 2 ♀♀ with developed oostegites, weakly setose, 6.0 mm, 7.0 mm, Orlineo Gnezdo Cave, (sampling depth -75 m), 27 Aug. 2012, coll. E.E. Golubnichaya.

Differential diagnosis

Zenkevitchia sandroruffoi sp. nov. can easily be distinguished from the other cavernicolous typhlogammarids by the discriminative humps on its pleonal segments. See ‘Remarks’ section under *sandroruffoi*-group as well as the key below.

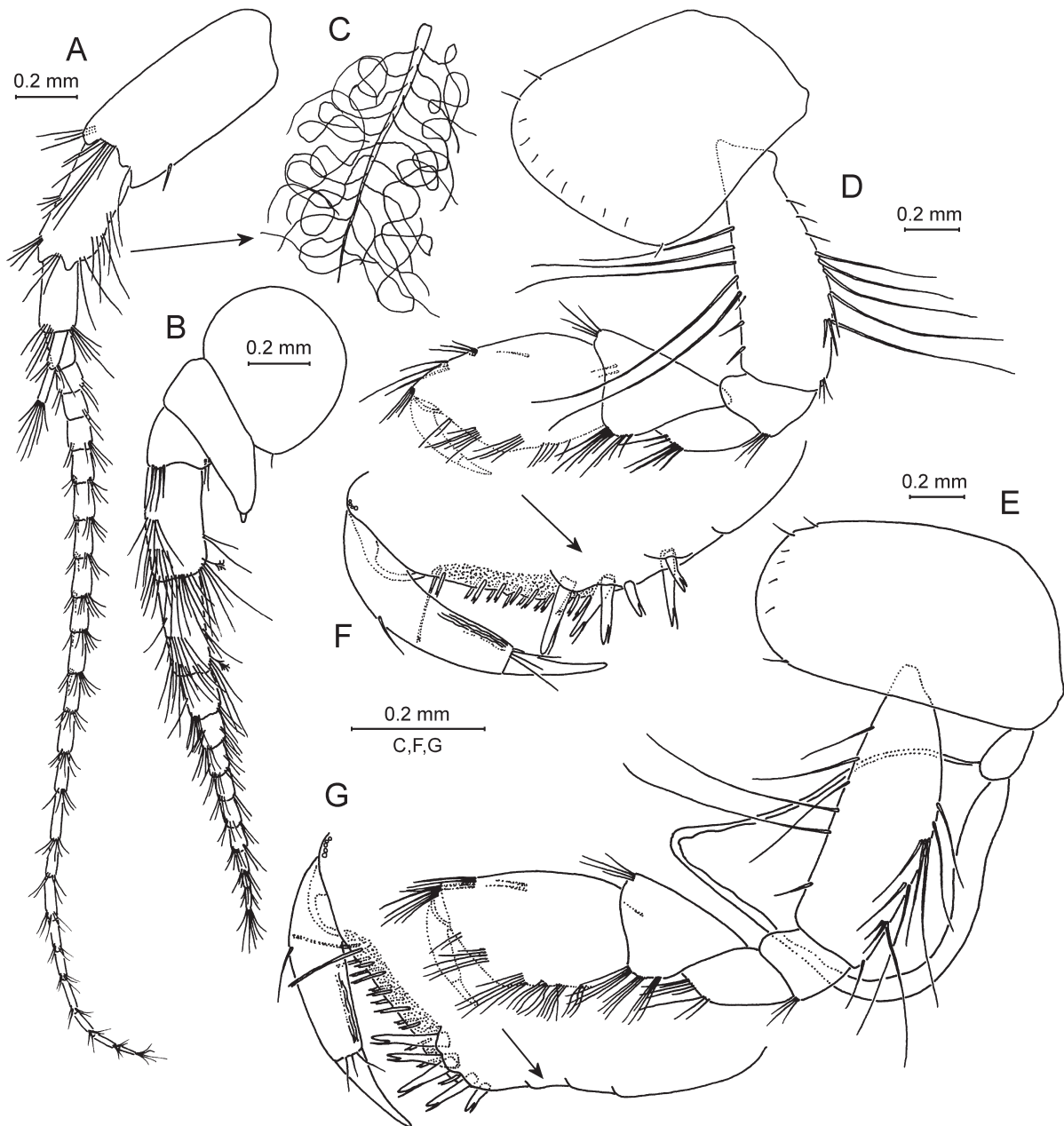


Fig. 7. *Zenkevitchia sandroruffoi* sp. nov. Holotype, ♂, 8.0 mm, X44041/Cr-1647-FEFU. **A.** Antenna 1. **B.** Antenna 2. **C.** Barbate seta with attached filamentous algae. **D.** Gnathopod 1. **E.** Gnathopod 2. **F–G.** Palmar margins of gnathopods 1 and 2 propodi.

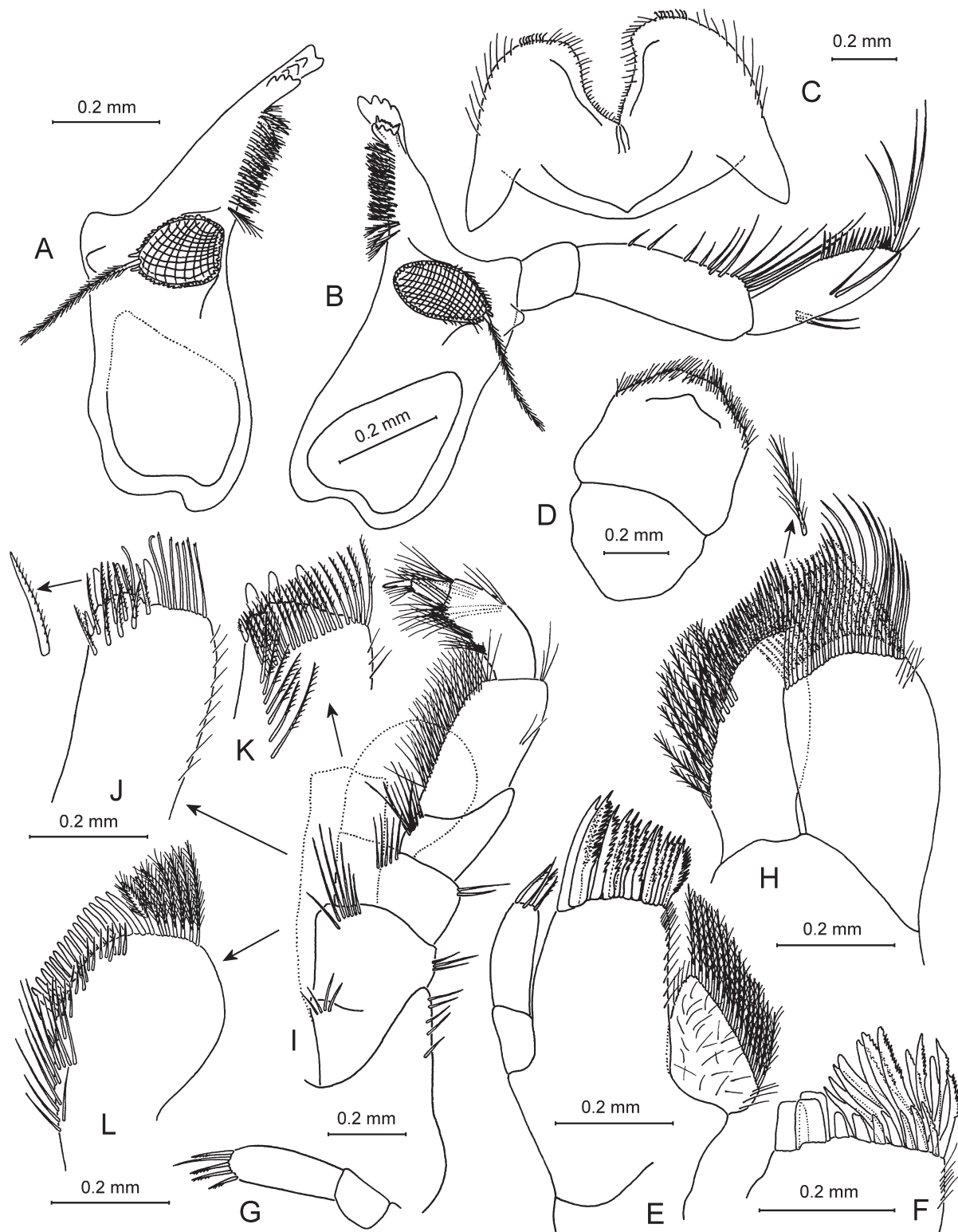


Fig. 8. *Zenkevitchia sandroruffoi* sp. nov. — A–E, G–K. Holotype, ♂, 8.0 mm, X44041/Cr-1647-FEFU. A. Left mandible. B. Right mandible. C. Lower lip. D. Upper lip. E. Maxilla 1. G. Palp of right maxilla 1. H. Maxilla 2. I. Maxilliped. J. Inner plate of maxilliped, inner face. K. Inner plate of maxilliped, outer face. — F, L. Paratype, ♀, 8.3 mm, X44043/Cr-1649-FEFU. F. Outer plate of maxilla 1. L. Outer plate of maxilliped.

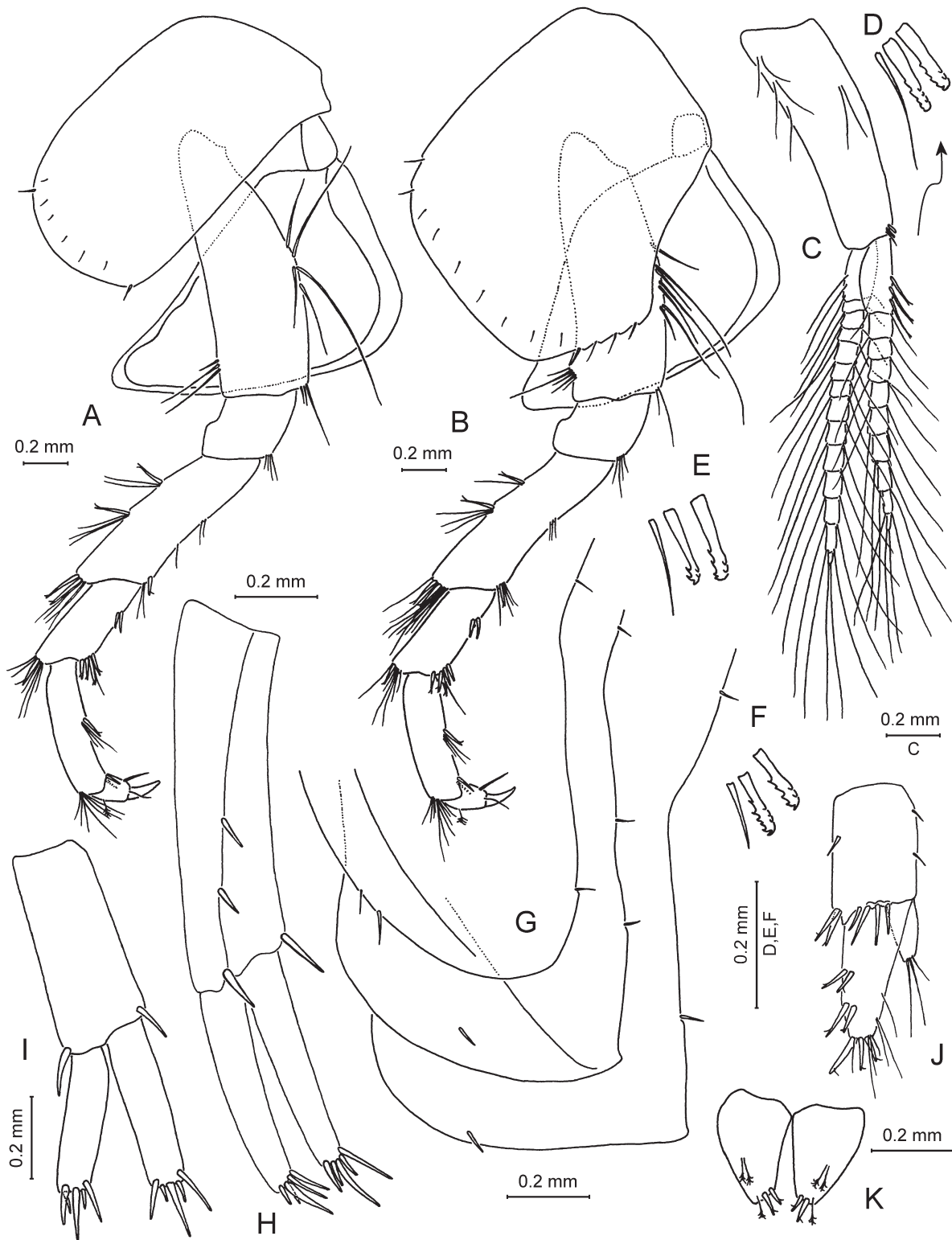


Fig. 9. *Zenkevitchia sandroruffoi* sp. nov. Holotype, ♂, 8.0 mm, X44041/Cr-1647-FEFU. **A.** Pereopod 3. **B.** Pereopod 4. **C.** Pleopod 1. **D–F.** Coupling setae of pleopods 1–3. **G.** Epimeral plates 1–3. **H.** Uropod 1. **I.** Uropod 2. **J.** Uropod 3. **K.** Telson.

Description

Male (holotype)

BODY LENGTH. 8.0 mm.

GENERAL BODY MORPHOLOGY (Fig. 9G, K). Body smooth, with median and lateral, sparse, single setae, lacking dorsal cuticular elements but with distinct humps on pleonal segments. Head as long as first pereon segment; rostrum absent; inferior antennal sinus deep, rounded. Eyes absent. Urosomites 1–3 on dorsal surface with lateral spines and setae; armed with notched spines in the following manner: 1 (0-0), 2 (2-2), 3 (1-0-1). Epimeral plate 1: postero-ventral corner beveled; posterior and ventral margins convex; 2 stiff setae along ventral margin, 1 seta along posterior margin. Epimeral plate 2: postero-ventral corner acuminate; posterior margin convex; ventral margin convex; 1 stiff seta along ventral margin, 2 setae along posterior margin. Epimeral plate 3: postero-ventral corner acuminate; posterior margin straight; ventral margin straight; 1 stiff seta along ventral margin, 1 seta along posterior margin. Telson: width:length ratio is 1:0.6; cleft entirely; 2 apical spines per lobe present, 0.3–0.4× telson length, each accompanied by 1 or 2 plumose setae.

ANTENNAE (Figs 2, 7A–B). Antenna 1 0.38× of body length; main flagellum with up to 23 articles; each article with 5–9 short setae; peduncular articles in ratio 1:0.7:0.4; proximal article of peduncle distally with 1 medial set of long setae; accessory flagellum 3-articulated. Length ratio of antenna 1 to antenna 2 is 1:0.6; flagellum of antenna 2 with 10 articles, each article densely setose; length ratio of peduncle articles 4 and 5 is 1:0.8; flagellum 0.4× longer than peduncle (articles 4+5); peduncular articles 4 and 5 with sets of long, stiff setae on lateral and medial faces; gland cone long, reaching half of peduncle of segment 4.

MOUTH PARTS. Typical gammarid, except for unusual maxilla 1 (Figs 4H, 8A–E, G–L). Labrum rounded, clypeus unfused, longer than broad. Inner lobes of labium absent, outer lobes broad with stiff curved setae marginally, mandibular process distinct (narrow). Left mandible: incisor with 5 teeth, lacinia mobilis with 4 teeth; between lacinia and molar a row of 14 serrate spines. Right mandible: incisor process with 4 teeth, lacinia mobilis bifurcate, with several small denticles, between lacinia and molar a row of 12 serrate spines; triturative molar process with long lanose seta. Mandibular palp article 2 slightly longer than article 3 (distal); proximal palp article without setae; second article with 12 setae; distal article narrowed, with 1 A group of 2 setae, 2 B setae, 13 D setae and 4 E setae. Maxilla 1 palp reduced, distal article with 4 or 5 apical setae (both palps sub-symmetrical); outer plate with 22 multi-toothed spines; inner plate triangular, with 16 plumose setae. Maxilla 2 inner plate smaller than outer one with, oblique row of 11 plumose setae; both of them apically with numerous setae in two rows. Maxilliped palp article 2 narrow, with about 55 setae along inner margin; article 3 narrow, with 2 dense sets of setae on inner face; article 4 (distal) with dorsal seta, bearing 5 setae at the nail base, nail shorter than pedestal; outer plate with 15 flattened naked spines and 7 long plumose setae on apex (3 of them flattened); inner plate with 3 strong spines (1 supplemental spine on medial face) and 8 stiff, naked setae on apex, 27 plumose setae on ventral face, 10 stiff denticulate setae in 2 rows on dorsal face. Foregut lateralialia with 15 strong pectinate spines, with densely setose row of stiff setae.

COXAL PLATES, GILLS (Figs 7D–E, 9A–B, 10A–C). Coxal plate 1 of rectangular shape, antero-ventral margin extended, with 3 setae. Coxal plate 2 of rectangular shape, antero-ventral margin narrowed, with 3 setae. Coxal plate 3 width:depth is 0.5:1, along antero-ventral margin with 2 setae. Coxal plate 4 of sub-quadrate shape, width:depth is 0.9:1; posteriorly with prominent excavation, along ventral margin 6 setae. Coxal plates 5–7 progressively smaller towards the posterior. Coxal plates 5–6: only anterior lobe well-developed; posterior margin pointed with 2 setae. Coxal plate 7 sub-triangular, anterior part beveled, along posterior margin with 3 setae in shallow serration. Coxal gills 2–7 stalked, large but progressively smaller towards the posterior; gills 2–4 triangular, gills 5–7 saccular or irregularly ovoid.

GNATHOPODS 1–2 (Figs 7D–G). Gnathopod 1: ischium with postero-distal set of 6 short setae. Carpus $0.4\times$ length of basis and $0.56\times$ length of propodus; anterior margin of carpus with 1 group of setae; carpus posteriorly with 2 sets of lateral setae. Propodus sub-rectangular, palm straight, with cutting margin smooth and shorter than posterior margin; along posterior margin 5 simple setae with 1 pair of notched spines; anterior margin with 2 sets of setae, antero-distal group with 4 setae; palmar margin with short, notched setae along outer and inner faces, palmar angle with a group of 4 distally-notched, strong

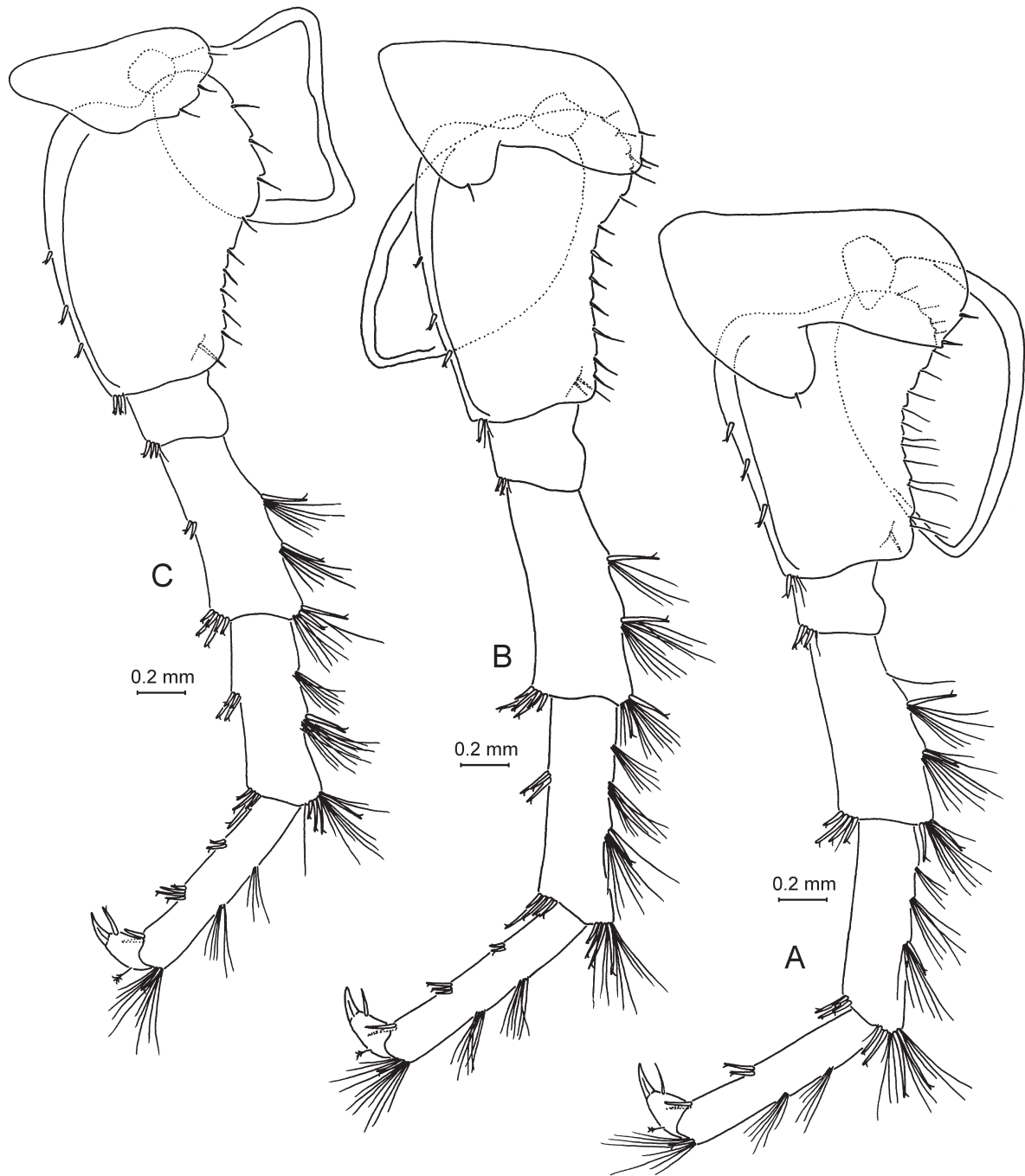


Fig. 10. *Zenkevitchia sandroruffoi* sp. nov. Holotype, ♂, 8.0 mm, X44041/Cr-1647-FEFU. A. Pereopod 5. B. Pereopod 6. C. Pereopod 7.

corner spines on both faces; nail long, $0.4\times$ total length of dactylus, 1 seta along anterior margin and 3 setules at hinge. Gnathopod 2: basis width: length is $0.34:1$. Ischium with 2 sets of postero-distal setae. Carpus $0.3\times$ length of basis and $0.56\times$ length of propodus; anterior margin of carpus with 1 distal set of setae; carpus posteriorly with 3 lateral sets of setae. Propodus small (compared to the body) and same length as propodus of gnathopod 1; propodus sub-rectangular, palm straight, with cutting margin smooth and shorter than posterior margin; posterior margin with 4 sets of stiff setae; anterior margin with 2 sets of setae; antero-distal group with 5 setae; palmar margin with short, notched setae along outer and inner faces, palmar angle with a group of 5 distally-notched, strong corner spines on both faces; dactylus similar to that of gnathopod 1.

PEREOPODS 3–7 (Figs 9A–B, 10A–C). Lengths of pereopods 3–4 equal. Dactylus 4 $0.5\times$ propodus 4; nail length $0.5\times$ total dactylus length. Dactyli 3–4 with dorsal plumose seta; inner margin with 1 stiff seta and 1 thin seta at hinge. Lengths of pereopods 5:6:7 is $0.9:1:0.9$. Pereopod 7 length $0.47\times$ body length. Bases 5–7 narrowed distally; posterior margin with postero-proximal lobes; posteriorly marginal serrations with stiff setae (with thin setae in basis 5); anteriorly 3 notched spines. Dactylus 7 length $0.37\times$ propodus 7 length. Dactyli 5–7 with dorsal plumose seta; inner margin with 1 stiff, notched seta and 1 thin seta at hinge.

PLEOPODS (Fig. 9C–F). Pleopods 1–3 sub-equal, each with 2 coupling setae accompanied by 1 stiff seta; peduncular articles fringed with long, thin setae; proximal article of inner rami fringed with 3 bifurcate setae. Pleopods 1–3 rami with 10–15 articles each.

UROPODS (Figs 2, 9H–J). Uropod 1 protopodite without basofacial spine, with 3 dorso-lateral spines and 1 dorso-medial spine; exopodite:endopodite length is $0.95:1$; rami straight and unarmed along outer margins; both with 5 strong, notched spines apically and sub-apically. Uropod 2 exopodite slightly curved and $0.2\times$ shorter than endopodite. Uropod 3 protopodite with 2 groups of strong notched spines on apex; endopodite $0.4\times$ of protopodite length, with 3 long setae apically; exopodite $1.16\times$ longer than protopodite, with 2 groups of lateral spines, long simple setae along inner margin, 3 spines and 4 setae apically.

Female (paratype X44043/Cr-1649-FEFU)

Body length 8.3 mm, with sexually dimorphic characters (Fig. 11). Smaller than male, with more slender body. Antenna 2 slender, peduncular article 4 with bundle of long setae on distal margin. Gnathopods 1 and 2: bases slender, with densely setose posterior margin; propodi sub-similar, sub-rectangular, but propodus of gnathopod 2 larger than on gnathopod 1; palmar margins sub-transverse, palm straight, with cutting margin acanthaceous; nail very long, $0.5\times$ total length of dactylus. Uropod 3 weakly armed; endopodite with 2 long setae apically. Telson with 1 spine per lobe. Oostegites 2–5 on gnathopod 2 and pereopods 3–5, very broad, with marginal setae.

Variability

Flagellum of antenna 1 with 21–23 articles. Uropod 3 endopodite with 2–3 setae apically. One individual had an abnormal 2-articulated accessory flagellum. The population of *Z. sandroruffoi* sp. nov. inhabiting streams in the Orlineo Gnezdo cave differs slightly by having a smaller body size and further shortened antenna 1, but are otherwise indistinguishable.

Ontogenetic variation

Almost all adults presented with significantly threadbare (Fig. 8F) or broken spines on the outer plate of maxilla 1. Thus, the first three of the most powerful spines turned out to be broken off in almost of all of the specimens.

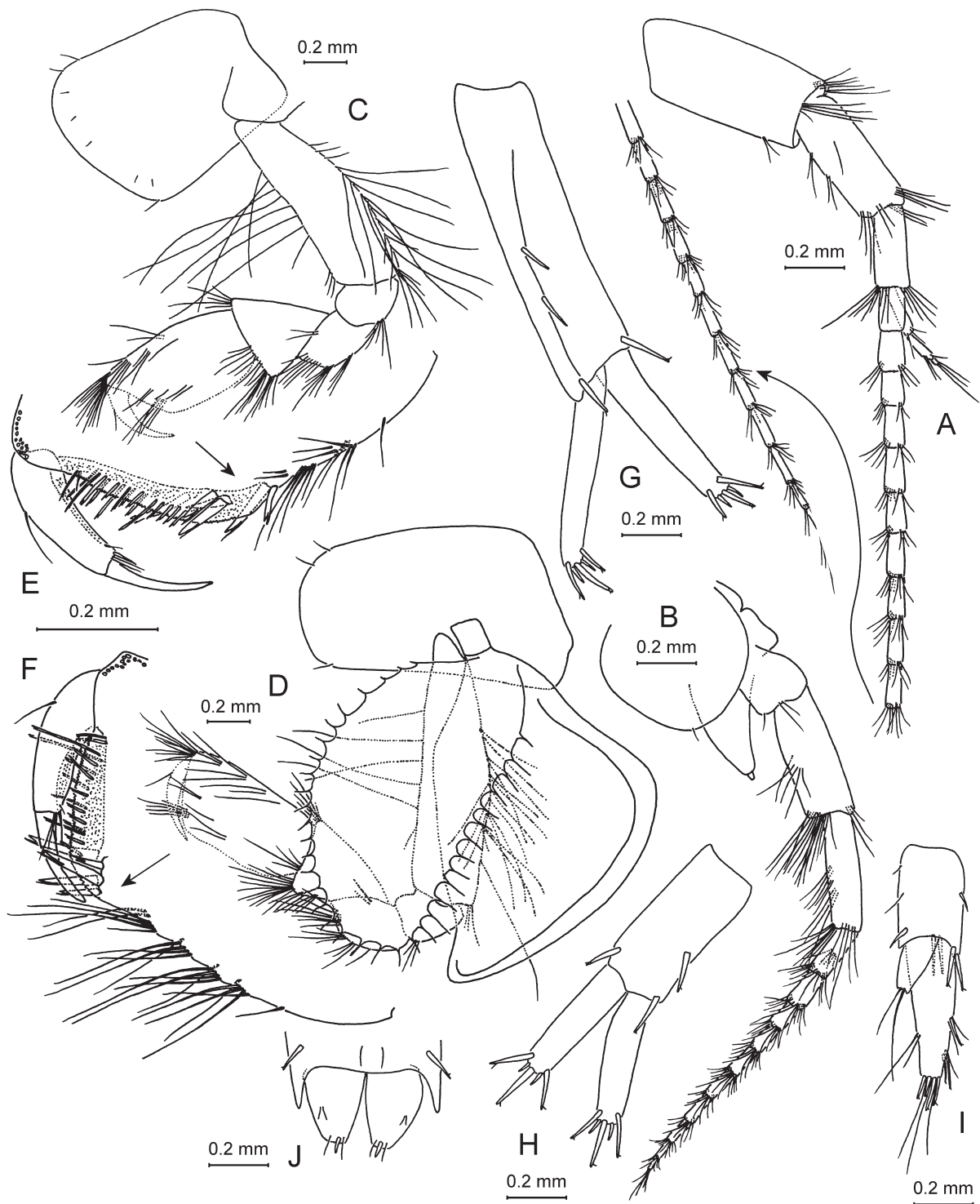


Fig. 11. *Zenkevitchia sandroruffoi* sp. nov. Paratype, ♀, 8.3 mm, X44043/Cr-1649-FEFU. **A.** Antenna 1. **B.** Antenna 2. **C.** Gnathopod 1. **D.** Gnathopod 2. **E–F.** Palmar margins of gnathopods 1 and 2 propodi. **G.** Uropod 1. **H.** Uropod 2. **I.** Uropod 3. **J.** Telson.

Distribution and ecology

Zenkevitchia sandroruffoi sp. nov. inhabits aquatic biotopes in several caves (Fig. 1) in the Eastern Arabika massif and it apparently avoids deep cave habitats. This species was observed in the Sarma Cave not deeper than -350 m (Fig. 2), in the nearby Trojka cave at a depth of -30 m and in the not-far distant Orlineo Gnezdo cave at -75 m. The setae on the antennal appendages of all specimens were densely covered (Fig. 7C) with attached filamentous algae (cyanobacteria?). The nature of the morphological variability and divergence of COI gene sequences (pairwise distances <2.2%) suggests that, in the Orlineo Gnezdo cave, the other population of the same species is present.

Genus *Adaugammarus* gen. nov.

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Type species

Adaugammarus pilosus sp. nov., by monotypy.

Generic diagnosis

Stout and gentle, large-sized species of gammarid-like habitus (sexual dimorphism marked, i.e., some males larger than females, antenna 2, both gnathopods and uropods 1–3 sexually dimorphic). Antenna 1 short, reaching 50% length of body; antenna 2 short, reaching about 50% length of antenna 1, gland cone short. Maxilla 1 inner plate trapezoidal, with 10 plumose setae, outer plate of non-filtration type (?scraper type), with 14 multi-toothed, comb-like spines; palps asymmetric and long. Mandibular palp article 3 with 2 A groups, 2 B groups, 13 D setae and 4 E setae. Gnathopods 1–2 relatively small, with propodus not larger than corresponding coxa; palmar angles of both gnathopods undefined, each bearing a group of notched, strong palmar spines; dactyli with 1 seta along outer margin, nails rather long. Pereopods 5–7 bases distinctly broader in proximal part; inner margin of dactyli of pereopods 3–7 with 1 stiff seta. Urosomites with dorsolateral groups of spines. Pleopods 1–3 with 2 coupling setae (retinacula), each accompanied by 1 seta (2+1). Uropods 1–3 extremely setose, with dense bundles of long swirling setae; uropod 1 exopodite broad and curved; uropod 3 exopodite broad, 1.6× longer than protopodite (in males). Telson with 1 or 2 distal spines per lobe. Coxal gills 2–7 stalked, triangular or sacciforme, largest on gnathopod 2, successively smaller on pereopods 3 to 7, gill 7 the smallest. Body length 12.5–16.5 mm (♀♀), 11.5–17.5 (♂♂).

Etymology

The generic epithet (*Adaugammarus*) is derived by the combination of *Adau*, the name of fearsome malicious giants in Abkhazian mythology, with *Gammarus*, a closely related genus. Gender masculine.

Discussion of affinities

Adaugammarus gen. nov. is an interesting taxon possessing features typical for a number of groups, but tending more towards *Typhlogammarus* because of the following characters: lateral cephalic lobe with recess, propodi of both gnathopods with palmar angles undefined, uropod 3 exopodite distinctly broad in males. *Adaugammarus* gen. nov. is related to the *sandroruffoi*-group of *Zenkevitchia* and *Typhlogammarus* in the similar structure of the outer plate, which has 14 multi-toothed spines. The urosomal segments are armed in a similar manner to those of *Zenkevitchia*. *Adaugammarus* gen. nov. differs from *Metohia* in the absence of dorsal cuticular elements and from *Accubogammarus* in having a short antennal gland cone, in variramus uropod 3, and differs in having 14 multi-toothed spines on the outer plate of maxilla 1, in contrast to the 38 very densely toothed spines present in *Accubogammarus*. Superficial comparison with the other “deep dweller”, cf. *Zenkevitchia* sp. *sensu* Jaume in Sendra & Reboleira (2012) from the Krubera-Voronja cave, revealed that the two taxa differ significantly from each other by the body shape and by the extremely large body size (~19.0–28.0 mm in females from Krubera) (pers. obs.).

Adaugammarus pilosus gen. et sp. nov.

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Figs 2, 4I–K, 12–16

Diagnosis (both sexes)

As for the genus. *A. pilosus* gen. et sp. nov. is readily distinguished from the other cavernicolous typhlogammarids by the sexually dimorphic uropods. See the section ‘Discussion of affinities’ and the key below.

Etymology

The species epithet (*pilosus*, Latin), meaning “covered with hairs”, refers to the extremely setose uropods in males.

Material examined

Holotype

GEORGIA: sequenced ♀ (carrying 10 eggs), 13.5 mm, Sarma Cave (43°4158 N, 40°3633 E, approx.), 2346 m a.s.l., Transsib meander (sampling depth -1270 m), Arabika massif, Gagra District, Western Caucasus, 15 Sep. 2011, coll. P.V. Rudko (X44046/Cr-1652-FEFU).

Paratypes

GEORGIA: ♂, 11.5 mm, ♀ (oostegites developed, setose), 12.5 mm, ♀ (carrying 21 eggs), 16.5 mm, same data as holotype; ♂, 17.5 mm, Sarma Cave, pit K25 Vodoprovod, (sampling depth -1700 m), 21 Sep. 2011, coll. P.V. Rudko (X44047/Cr-1653-55-FEFU).

Description

Holotype

BODY LENGTH. 13.5 mm.

GENERAL BODY MORPHOLOGY (Figs 2, 4I–J, 14C, G). Body smooth, with median and lateral thin setae, lacking dorsal cuticular elements (keel or tubercles). Head shorter than first pereon segment; rostrum indistinct; lateral cephalic lobe with recess; inferior antennal sinus shallow, sub-rounded. Eyes absent. Urosomites 1–3 on dorsal surface with lateral spines and setae; armed with notched spines in the following manner: 1 (0-0), 2 (1-1), 3 (1-0-1). Epimeral plate 1: postero-ventral corner prominent; posterior and ventral margins convex; 3 stiff setae along ventral margin, 5 setae along posterior margin. Epimeral plate 2: postero-ventral corner prominent; posterior margin straight; ventral margin convex; 3 stiff setae along ventral margin, 3 setae along posterior margin. Epimeral plate 3: postero-ventral corner prominent; posterior margin straight; ventral margin convex; 3 stiff setae along ventral margin, 1 seta along posterior margin. Telson: width: length ratio is 0.9: 1; cleft 0.9 of length; 2 apical spines per lobe, each accompanied by 2 setae.

ANTENNAE (Figs 2, 12A–B). Antenna 1 0.5× of body length; main flagellum with up to 34 articles; each article with 2–7 setae; peduncular articles in ratio 1:0.6:0.4; accessory flagellum 4-articulated. Length ratio of antenna 1 to antenna 2 is 1:0.5; flagellum of antenna 2 with 13 articles, each article densely setose; length ratio of peduncle articles 4 and 5 is 1:0.9; flagellum 0.2× longer than peduncle (articles 4+5); peduncular articles 4 and 5 densely setose, with tight bundles of long stiff setae on lateral and medial faces; gland cone very short.

MOUTH PARTS (typical gammarid, Figs 4K, 13). Labrum rounded, clypeus unfused, longer than broad. Inner lobes of labium absent, outer lobes broad, with stiff curved setae marginally, mandibular process distinct (narrow). Left mandible: incisor with 5 teeth, lacinia mobilis with 4 teeth; between lacinia and

molar a row of 11 serrate spines. Right mandible: incisor process with 4 teeth, lacinia mobilis bifurcate, with several small denticles, between lacinia and molar a row of 9 serrate spines; triturative molar process with long plumose seta. Mandibular palp article 2 longer than article 3 (distal); proximal palp article without setae; second article with 21 setae; distal article narrowed, with 2 A groups of 2 and 7

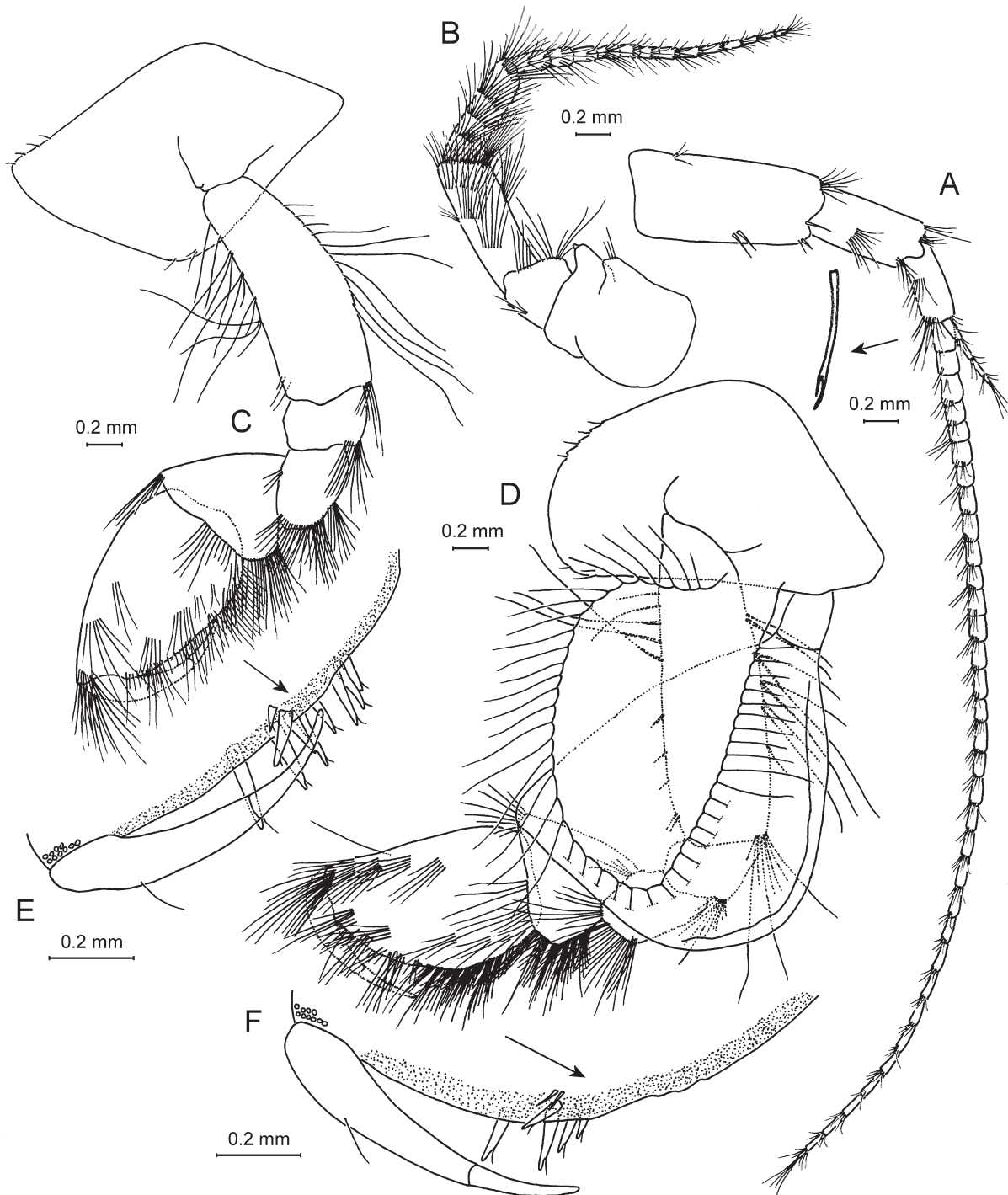


Fig. 12. *Adaugammarus pilosus* gen. et sp. nov. Holotype, ♀, 13.5 mm, X44046/Cr-1652-FEFU. A. Antenna 1. B. Antenna 2. C. Gnathopod 1. D. Gnathopod 2. E–F. Palmar margins of gnathopods 1 and 2 propodi (setation omitted).

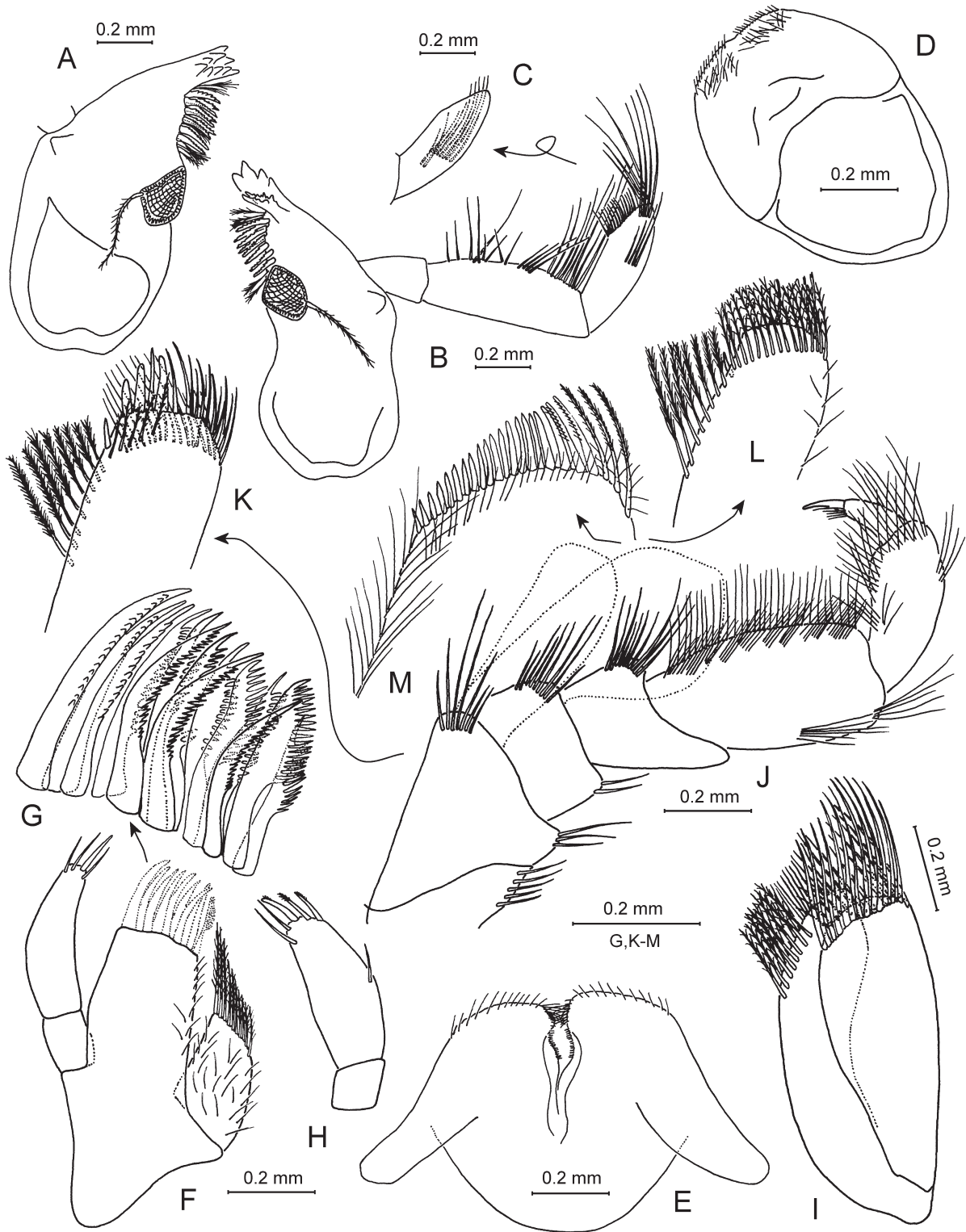


Fig. 13. *Adaugammarus pilosus* gen. et sp. nov. Holotype, ♀, 13.5 mm, X44046/Cr-1652-FEFU. **A.** Left mandible. **B.** Right mandible. **C.** Article 3 of mandibular palp, ventral setation. **D.** Upper lip. **E.** Lower lip. **F.** Maxilla I. **G.** Outer plate of maxilla 1. **H.** Palp of right maxilla 1. **I.** Maxilla 2. **J.** Maxilliped. **K.** Inner plate of maxilliped, inner face. **L.** Inner plate of maxilliped, outer face. **M.** Outer plate of maxilliped.

setae, respectively, 2 B groups of 3 and 4 setae, respectively, 13 D setae and 4 E setae. Maxilla 1 palp long, distal article with 1 or 3 apical spines accompanied with setae (both palps asymmetric, right palp broader, with 1 seta on outer margin); outer plate with 14 multi-toothed spines; inner plate trapezoidal, with 10 plumose setae. Maxilla 2 with both plates narrowed, inner plate with oblique row of 8 plumose setae; both of them apically with numerous setae in two rows. Maxilliped palp article 2 broad, with

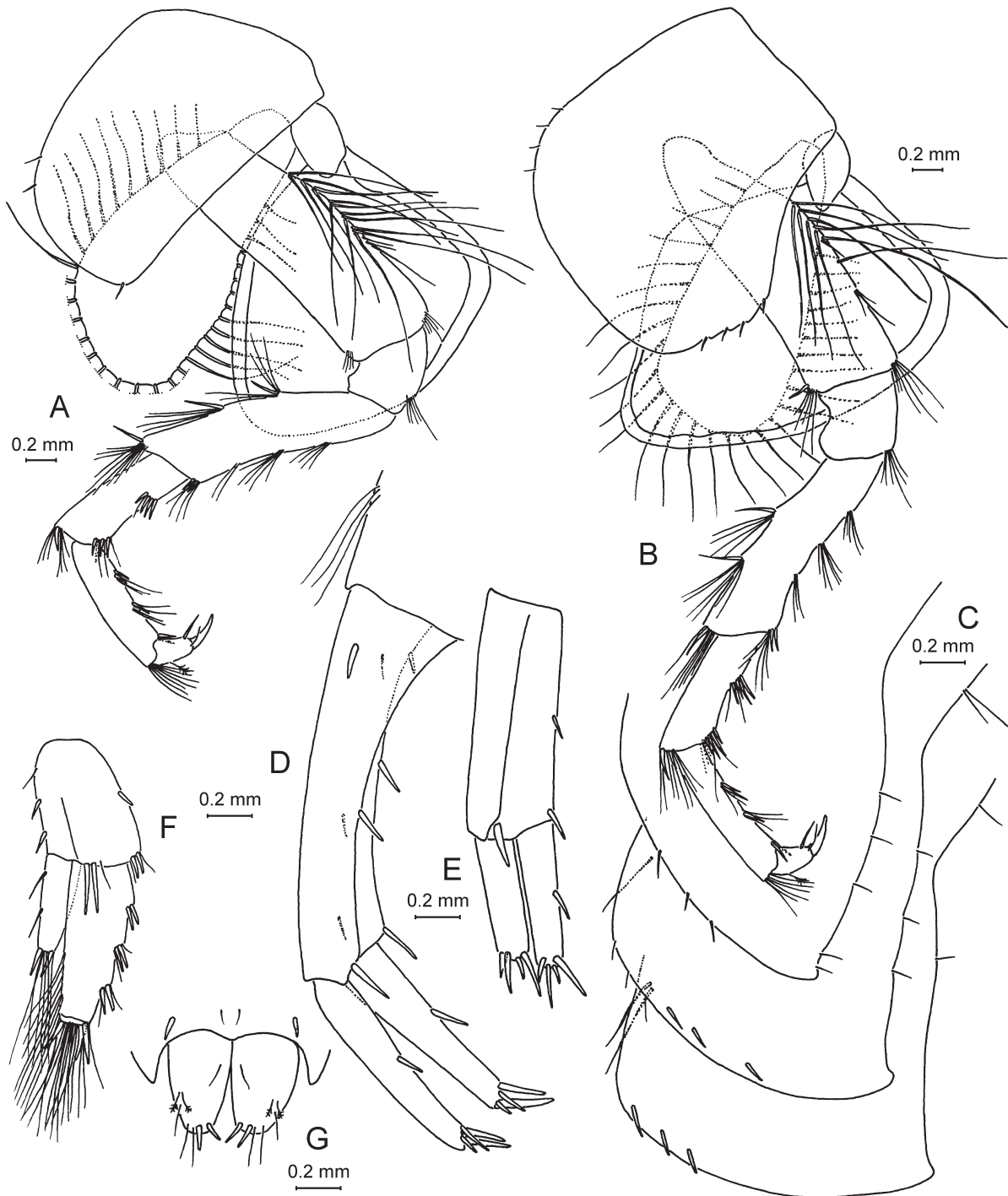


Fig. 14. *Adaugammarus pilosus* gen. et sp. nov. Holotype, ♀, 13.5 mm, X44046/Cr-1652-FEFU. A. Pereopod 3. B. Pereopod 4. C. Epimeral plates 1–3. D. Uropod I. E. Uropod 2. F. Uropod 3. G. Telson.

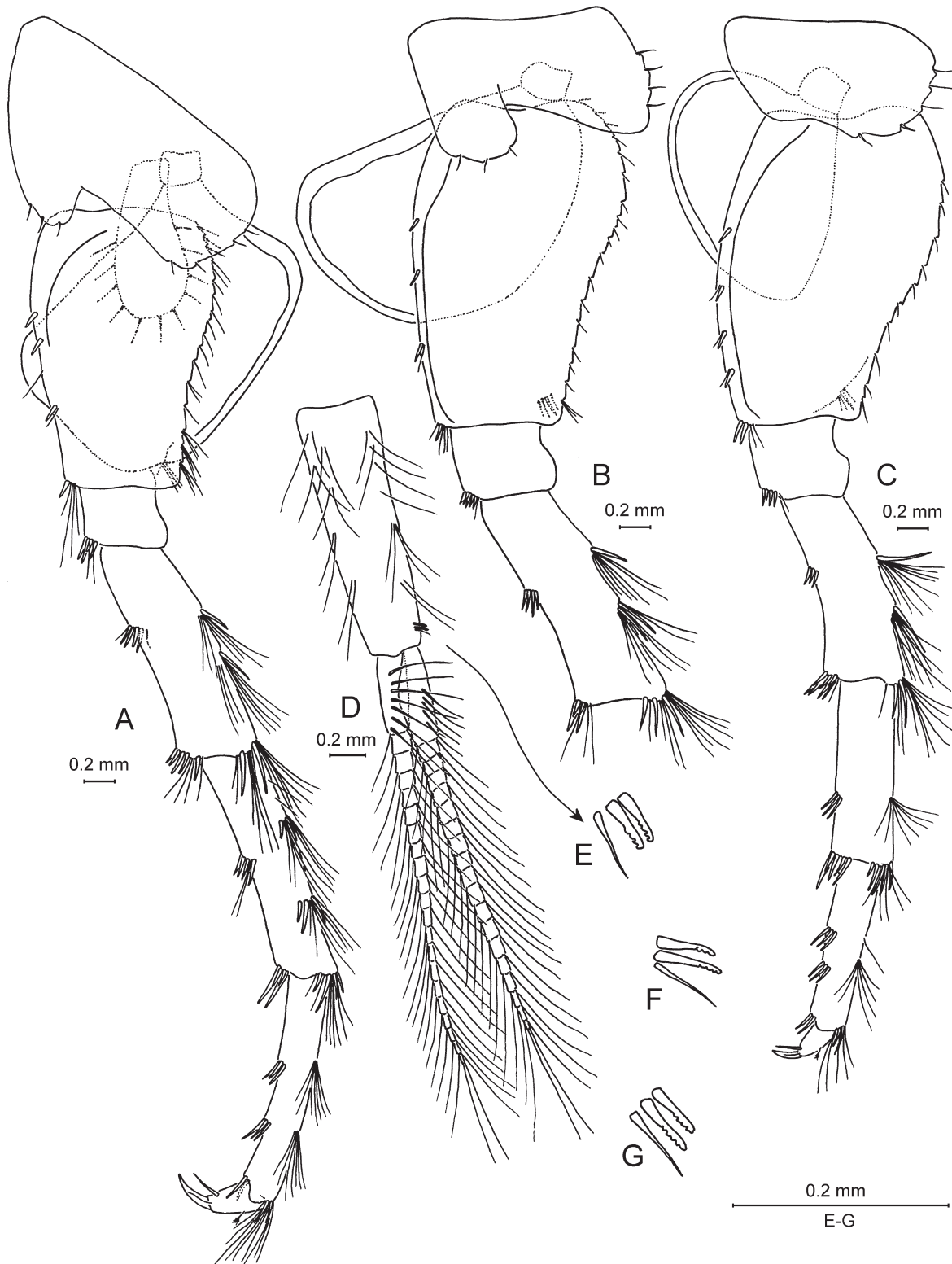


Fig. 15. *Adaugammarus pilosus* gen. et sp. nov. Holotype, ♀, 13.5 mm, X44046/Cr-1652-FEFU. A. Pereopod 5. B. Pereopod 6, part. C. Pereopod 7. D. Pleopod 1. E–G. Coupling setae of pleopods 1–3.

about 75 setae (some of them in 8 oblique clusters) along inner margin; article 3 narrow, densely setose, with long setae on inner face; article 4 (distal) with dorsal seta, bearing 5 setae at nail base, nail half as long as pedestal; outer plate with 18 flattened, naked spines, 2 long serrate spines and 3 long plumose setae on apex; inner plate with 3 strong spines (1 supplemental spine on medial face) and 13 stiff, naked setae apically and sub-apically, 24 plumose setae on ventral face, 5 stiff denticulate setae on dorsal face. Foregut lateralialia with 17 strong pectinate spines, with densely setose row of stiff setae.

COXAL PLATES, GILLS AND OOSTEGITES (Figs 12C–D, 14A–B, 15A–C). Coxal plate 1 of rectangular shape, antero-ventral margin extended, with sparse setae. Coxal plate 2 of sub-rectangular shape, antero-ventral margin narrowed with, sparse setae. Coxal plate 3 width: depth is 0.5: 1, antero-ventral margin narrowed, with 3 setae. Coxal plate 4 of sub-quadrate shape, as long as broad; posteriorly with broad excavation; along ventral margin sparse setae. Coxal plates 5–7 progressively smaller towards the posterior; coxal plates 5–6 with anterior lobe well-developed; posterior margin pointed, with 4 or 5 setae. Coxal plate 7 sub-rectangular, along posterior margin 3 setae in shallow serration. Coxal gills 2–7 stalked, large but progressively smaller towards the posterior; gills 2–4 sub-triangular, gills 5–7 saccular or irregularly ovoid. Oostegites 2–5 on gnathopod 2 and pereopods 3–5, very broad, with long marginal setae.

GNATHOPODS 1–2 (Figs 12C–F). Gnathopod 1: ischium broadly setose, with stiff setae on distal and lateral margins. Carpus 0.36× length of basis and 0.4× length of propodus; anterior margin of carpus with 1 group of setae; carpus posteriorly with transverse row of lateral and marginal setae. Propodus almond-shaped, palm convex, with cutting margin smooth and longer than posterior margin; along posterior margin a row of simple setae; anterior margin with 3 sets of setae, antero-distal group with 10 setae; palmar margin with short, notched setae along outer and inner faces, palmar angle undefined, a group of 10 distally-notched, strong spines on both faces (with 2 strong mid-palmar spines in the place where tip of nail close); nail long, 0.4× total length of dactylus, 1 seta along anterior margin, without setules at hinge. Gnathopod 2: basis width: length is 0.3: 1. Ischium broadly setose, with stiff setae on distal and lateral margins. Carpus 0.27× length of basis and 0.4× length of propodus; anterior margin of carpus with 1 distal set of setae; carpus posteriorly with 5 lateral sets of setae and transverse row of marginal setae. Propodus small (compared to the body) and same length as propodus of gnathopod 1; propodus pyriform, palm convex with cutting margin smooth and shorter than posterior margin; posterior margin with 8 sets of stiff setae; anterior margin with 5 sets of setae; antero-distal group with 10 setae; palmar margin with short, notched setae along outer and inner faces, palmar angle undefined, a group of 5–6 distally-notched, strong spines on both faces in the place where tip of nail close (with 1 strong mid-palmar spine); dactylus similar to that of gnathopod 1.

PEREPODS 3–7 (Figs 14A–B, 15A–C). Lengths of pereopods 3–4 is 0.95: 1. Dactylus 4 0.5× propodus 4; nail length 0.5× total dactylus length. Dactyli 3–4 with dorsal plumose seta; inner margin with 1 stiff seta and 1 thin seta at hinge. Lengths of pereopods 5:6:7 is 0.9: 1: 0.9. Pereopod 7 length 0.5× body length. Bases 5–7 narrowed distally; length: width is 1: 0.5–0.6; posterior margin curved (distinctly in basis 7), without postero-distal lobes; marginal serrations with short setae posteriorly (expressed in basis 5); 3–4 notched spines anteriorly. Dactylus 7 length 0.28× of propodus 7 length. Dactyli 5–7 with dorsal plumose seta; inner margin with 1 stiff seta and 1 thin seta at hinge.

PLEOPODS (Fig. 15D–G). Pleopods 1–3 sub-equal, each with 2 coupling setae accompanied by 1 stiff seta; peduncular articles fringed with long, thin setae; proximal article of inner rami fringed with 5 simple setae. Pleopods 1–3 rami with 19–21 articles each.

UROPODS (Figs 2, 14D–F). Uropod 1 protopodite with 1 basofacial spine, 2 dorso-lateral spines and 3 dorso-medial spines; exopodite: endopodite length is 1: 0.8; rami straight, with single spines along outer margins; both with 5 spines apically and sub-apically (two of them strong). Uropod 2 exopodite 0.2×

shorter than endopodite. Uropod 3 protopodite with 2 groups of spines on apex; endopodite $0.7\times$ of protopodite length, with 2 spines and 6 long setae apically; exopodite $1.3\times$ longer than protopodite, with 3 groups of lateral spines, long simple setae along inner margin, 3 spines and about 13 setae apically.

Male (paratype X44049/Cr-1655-FEFU)

Body length 17.5 mm, with sexually dimorphic characters (Fig. 16). Larger than female, with more stout body. Antenna 2 densely setose. Gnathopods 1 and 2 propodi sub-similar, almond-shaped, but propodus of gnathopod 2 larger than propodus of gnathopod 1; palmar margins beveled, palm straight, with

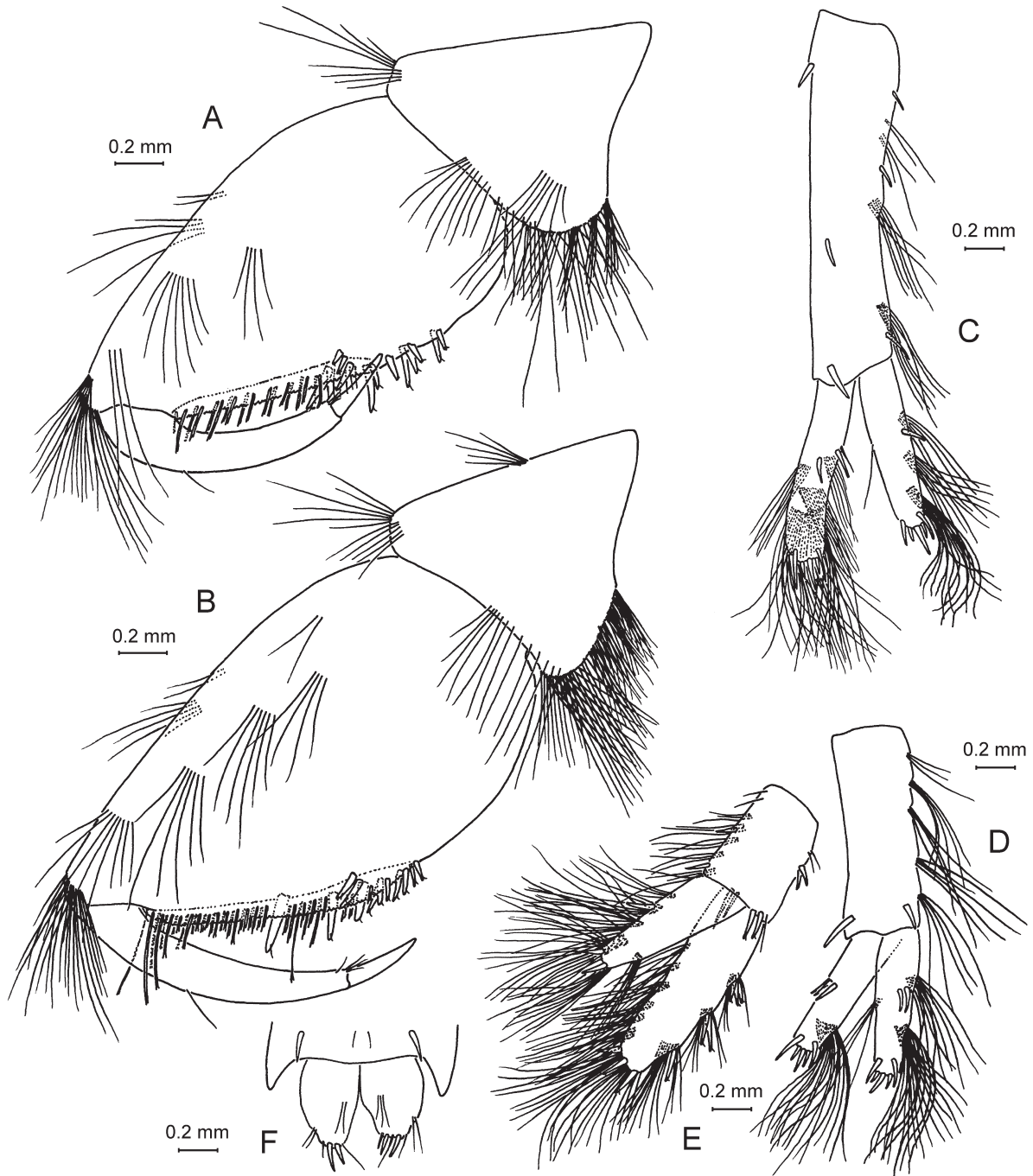


Fig. 16. *Adaugammarus pilosus* gen. et sp. nov. Paratype X44049/Cr-1655-FEFU, ♂, 17.5 mm. A. Gnathopod 1, part. B. Gnathopod 2, part. C. Uropod 1. D. Uropod 2. E. Uropod 3. F. Telson.

Table 2. Estimates of pairwise sequence divergence (uncorrected p-distances) of partial mitochondrial COI gene among and within species (bold type) of the Balkan and Caucasian Typhlogammaridae. Numbers in brackets correspond to geographic locality on Fig. 1; n/a = not applicable.

Species	Number of sequences	1	2	3	4	5	6	7	8
1. <i>Zenkevitchia sandroruffoi</i> [1]	6	0.0034							
2. <i>Adaugammarus pilosus</i> [2]	4	0.159	0.0009						
3. <i>Zenkevitchia yakovi</i> [5]	3	0.142	0.141	0.0024					
4. <i>Metohia carinata</i>	1	0.245	0.235	0.237	n/a				
5. <i>Typhlogammarus mrazeki</i>	1	0.241	0.246	0.243	0.217	n/a			
6. <i>Typhlogammarus</i> sp.	1	0.247	0.234	0.248	0.217	0.138	n/a		
7. <i>Zenkevitchia admirabilis</i> [4]	2	0.138	0.150	0.128	0.239	0.233	0.247	0.0783	
8. <i>Zenkevitchia revazi</i> [6]	1	0.206	0.210	0.210	0.255	0.246	0.251	0.207	n/a

cutting margin acanthaceous; nail short, 0.3x total length of dactylus. Uropods 1–3 extremely setose. Uropod 1 protopodite with 3 sets of long setae along inner margin; exopodite broad and curved, longer than endopodite; rami setose, with dense bundles of long, swirling setae. Uropod 2 protopodite with 5 sets of long setae along inner margin; exopodite as long as endopodite; rami setose, with dense bundles of long, swirling setae. Uropod 3 protopodite with 5 sets of long setae along inner margin; endopodite 1.3× longer than protopodite, with 2 spines along inner margin and 2 spines on apex; exopodite broad, 1.6× longer than protopodite, with 3 groups of lateral spines, 3 spines on apex; rami setose, with dense bundles of long, swirling setae.

Variability

Not observed.

Distribution and ecology

Adaugammarus pilosus gen. et sp. nov. inhabits aquatic biotopes in the Sarma Cave (Figs 1–2) in the eastern Arabika massif (species was observed at depths of -1270 m and -1700 m) and revealed an ability to move in a hygropetric zone.

Phylogenetic analysis

To access the affinities of the newly described taxa and confirm their genetic distinctness, we sequenced a partial *mt-cox1* gene from *Z. sandroruffoi* sp. nov. (6 accessions, Table 1) and *Adaugammarus* gen. nov. (4 accessions) and assembled a data set including their putative relatives, *Accubogammarus*, *Metohia*, *Typhlogammarus*, and *Zenkevitchia* spp. (Table 1). Specimens of *Zenkevitchia sandroruffoi* sp. nov. from the Trojka (-30 m depth) and Sarma caves (-350 m) produced identical sequences (KT427522 and KT427521, respectively), as did two further specimens from the Orlinoe Gnezdo cave (-75 m; KT427523 and KT427524); the intraspecific distance is 0.34 ± 0.17 SE (Table 2). All four specimens of *Adaugammarus pilosus* gen. et sp. nov. from the deepest part of the Sarma Cave (-1270 to -1700 m; KT427516 – KT427519) were also almost identical in sequence; the intraspecific distance is 0.09 ± 0.09 SE (Table 2). Redundant sequences were excluded from the analyses. The resulting topology (Fig. 3) was generally in agreement with that previously obtained for a smaller data set (Sidorov *et al.* 2015). Species of *Zenkevitchia* were members of a clade (81% BP) that also included *Accubogammarus* and *Adaugammarus* gen. nov. Topologically, *Z. revazi* was a basal divergence in this lineage. *Adaugammarus* gen. nov. was resolved as a sister (96%) to a cluster composed of *Z. sandroruffoi* sp. nov., *Z. admirabilis*, and *Z. yakovi*. The branching pattern among these species remained unresolved. Four highly similar

(*p*-distances 0.002–0.01) *Z. sandroruffoi* formed a robust (100%) clade characterized by a relatively long branch. Accessions from the Sarma and Trojka caves shared two synapomorphic substitutions and were clustered together to the exclusion of specimens from Orlineo Gnezdo.

Discussion

Brief observation on the vertical distribution of Amphipoda in the Sarma cave

An integrated comparative morphological and genetic analysis of the new amphipod taxa in the Sarma Cave revealed their obvious dissimilarity, which in turn allows us to pay attention to the structure of this cave. The system of the Sarma Cave is heterogeneous in its physical structure. Following Burmak (unpubl.) there are three parts: upper, middle and lower. In the upper part, down to -350 m, *Z. sandroruffoi* sp. nov. was discovered; in the lower part, down to -1700 m, *A. pilosus* was present. In the middle part amphipods were not detected, but we can't exclude that they were overlooked. In the lower level (from -900 m to -1100 m) in the zone of major faulting leading to the deepest part, the cave abruptly changes direction (see Fig. 2). In this part of the cave thick deposits of red clay are observed. There is also a strong flowing stream in this part of the cave.

Zenkevitchia sandroruffoi sp. nov. is not endemic to the Sarma Cave and was noted in two other caves. The most remote of the investigated caves, Orlineo Gnezdo, is located about 3.5 km to the south of Sarma. This suggests that *Z. sandroruffoi* sp. nov. is vagile, settling in suitable biotopes in the eastern Arabika massif. The affinity of *Z. sandroruffoi* sp. nov. to the *Zenkevitchia* lineage and its limited distribution suggest a relatively young phylogenetic age of this species. In contrast, *A. pilosus* is, in our view, morphologically closer to *Typhlogammarus* and hence its cohabitation with *Z. sandroruffoi* sp. nov. in the same cave at different depths is apparently not a result of parapatric speciation. Although there are no reliable data about the geophysical structure and history of the Sarma Cave, it seems that the lower part of the cave belongs to another speleological system, probably older than the overlying cave system.

Key to the genera of Typhlogammaridae

- 1 Pleosomal (abdominal) segments 1–3 with a pair of bilateral teeth dorsally ... *Metohia* Absolon, 1927
– Pleosomal segments without teeth 2
- 2 Uropods in males setose with bundles of stiff, long setae *Adaugammarus* gen. nov.
– Uropods ordinary 3
- 3 Antennal gland cone short *Typhlogammarus* Schäferna, 1907
– Antennal gland cone long 4
- 4 Maxilla 1 outer plate filtrative, multisetose *Zenkevitchia* (*admirabilis*-group)
– Maxilla 1 outer plate ordinary 5
- 5 Uropod 3 parviramous, with inner ramus half as long as outer ramus
..... *Zenkevitchia* (*sandroruffoi*-group)
– Uropod 3 almost aequiramous, with inner ramus somewhat shorter
..... *Accubogammarus* G. Karaman, 1974

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