

**Research article**

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**Review of the genus *Caucaseuma* Strasser, 1970, with the description of a new cavernicolous species from the Western Caucasus and an updated key and distribution (Diplopoda, Chordeumatida, Anthroleucosomatidae)**Dragan ANTIĆ <sup>1,\*</sup> & Slobodan MAKAROV<sup>2</sup><sup>1,2</sup>University of Belgrade – Faculty of Biology, Institute of Zoology,  
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**Abstract.** A new species of the genus *Caucaseuma* Strasser, 1970, *Caucaseuma strasseri* Antić sp. nov., is described from a cave in the Western Caucasus, representing the eighth species of the genus, and the fourth presumed troglobiontic *Caucaseuma*. An updated key to and a distribution map of all eight species of *Caucaseuma* is presented, including new records. In addition, the cave millipede fauna of the Caucasus is briefly discussed, with the inclusion of the most relevant references.

**Keywords.** Cave, millipedes, taxonomy, troglomorphies.

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**Introduction**

The millipede genus *Caucaseuma* Strasser, 1970 was established as monospecific to accommodate the species *C. lohmanderi* Strasser, 1970. This species was the first cavernicolous chordeumatidan described from the Caucasus, and until recently the sole member of this mostly Western Caucasian genus. Almost half a century later, in their monographic study of Caucasian Anthroleucosomatidae Verhoeff, 1899, Antić & Makarov (2016) described another six species of *Caucaseuma*. Besides *C. lohmanderi*, known so far from more than 10 caves in the Sochi region, Antić & Makarov (2016) considered another two narrow endemics, viz., *C. elephantum* Antić & Makarov, 2016 and *C. minellii* Antić & Makarov, 2016, as “recent” troglobionts. All three species present some troglobiomorphic features such as completely or partially depigmented tegument, somewhat reduced pigmentation in ommatidia in some, elongated appendages and a larger, robust body (see Antić & Makarov 2016).

Another species of the genus *Caucaseuma*, *C. fanagoriyskaya* Antić & Makarov, 2016, is presently known exclusively from Fanagoriyskaya Cave. Based on the overall lack of troglobiontic characters seen in the previous three congeners, it was not considered a troglobiont (Antić & Makarov 2016). The remaining three species of this genus, viz., *C. glabroscutum* Antić & Makarov, 2016, *C. kelasuri* Antić & Makarov, 2016 and *C. variabile* Antić & Makarov, 2016, are known exclusively from epigean habitats.

Here, we describe a new, fourth presumably troglobiontic species of the genus *Caucaseuma*, from the Kirovskaya (= Tigrovaya) Cave in the Sochi region, Western Caucasus. We also present an identification key to and a distribution map for all eight described species of the genus.

## Material and methods

### Preservation, dissecting, imaging, map

Specimens preserved in 70% ethanol were examined with a Nikon SMZ 745T binocular stereo microscope. All taxonomically important structures were dissected and mounted in glycerine as temporary microscope preparations and observed with a Carl Zeiss AxioScope 40 microscope. Pictures of the specimens and legs were taken using a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller attached to a Nikon SMZ 1270 binocular stereo microscope. All pictures were stacked with a Zerene Stacker. Line drawings of the gonopods were obtained using tracing paper placed on a computer monitor displaying pictures of those structures made with a Canon PowerShot A80 digital camera connected to a Carl Zeiss AxioScope 40 microscope. For scanning electron microscopy (SEM) samples were (1) cleaned in an ultrasonic bath (50–60 Hz) for 5 to 10 seconds (maximum), (2) dehydrated in an ascending alcohol series (70%, 80%, 90%, 96% EtOH, 2 × 10–15 min each) and acetone; and (3) air dried. Samples were mounted on aluminium stubs equipped with sticky aluminium tape, coated with platinum (Leica EM SCD500) and studied with a JEOL JSM 6610-LV scanning electron microscope at an accelerating voltage of 15 kV (Natural History Museum Vienna, Austria). Figures were processed and assembled in Adobe Photoshop CS6.

The distribution map was created using Google Earth Pro (ver. 7.3.4.8248) and Adobe Photoshop CS6. The final images were processed with Adobe Photoshop CS6.

### Abbreviations of gonopodal structures

#### Anterior gonopods

- aA = anterior part of angiocoxite
- bp = bone-like process of angiocoxite
- Cv = coxal vesicle
- pA = posterior part of angiocoxite
- pp = posterior projection of angiocoxite
- S = gonopodal sternum
- Sp = sternal process
- tp = triangular process of angiocoxite

#### Posterior gonopods

- A = angiocoxite
- Cv = coxal vesicle
- Cx = coxite
- S = gonopodal sternum
- T = telopodite

### Abbreviations of indices of body ring 15

- CIX = macrochaetal index = distance between exterior and median macrochaetae/distance between interior and median macrochaetae  
MA = macrochaetal angle = angle between the arm created by the median and exterior macrochaetae and the arm formed by the median and interior macrochaetae  
MIX = median index = distance between interior macrochaetae and axial suture/distance between interior and median macrochaetae  
PIX = paratergal index = (width of metazonite – width of prozonite)/(2 × length of paratergum)

### Museum and collection acronyms

- DSTU = Don State Technical University, Rostov-on-Don, Russia  
IZB = Institute of Zoology, University of Belgrade – Faculty of Biology, Belgrade, Serbia  
NHMW = Naturhistorisches Museum Wien, Vienna, Austria  
ZMUM = Zoological Museum of Moscow State University, Moscow, Russia

## Results

### Taxonomy

- Class Diplopoda de Blainville in Gervais, 1844  
Order Chordeumatida Pocock, 1894  
Suborder Craspedosomatidea Cook, 1895  
Superfamily Anthroleucosomatoidea Verhoeff, 1899  
Family Anthroleucosomatidae Verhoeff, 1899

Genus *Caucaseuma* Strasser, 1970

*Caucaseuma* Strasser, 1970: 199.

*Caucaseuma* – Antić & Makarov 2016: 28.

### Type species

*Caucaseuma lohmanderi* Strasser, 1970, by original designation.

### Other included species

- Caucaseuma elephantum* Antić & Makarov, 2016  
*Caucaseuma fanagoriyskaya* Antić & Makarov, 2016  
*Caucaseuma glabroscutum* Antić & Makarov, 2016  
*Caucaseuma kelasuri* Antić & Makarov, 2016  
*Caucaseuma minellii* Antić & Makarov, 2016  
*Caucaseuma strasseri* Antić sp. nov.  
*Caucaseuma variabile* Antić & Makarov, 2016

### Diagnosis

Differs from all other genera of the family Anthroleucosomatidae, except the genus *Heterocaucaseuma* Antić & Makarov, 2016, by the presence of two pairs of flagelliform processes originating from the base of the angiocoxites of the posterior gonopods. From the genus *Heterocaucaseuma*, it differs by the presence of more complicated anterior gonopods, characterized by angiocoxites clearly differentiated into anterior and posterior parts. The anterior parts are shield-like, separated, partially fused or completely fused, with a visible furrow. The genus *Heterocaucaseuma* is characterized by somewhat simplified anterior gonopods with angiocoxites differentiated into a medial part, fully fused, and two lateral parts.

## Distribution

The genus *Caucaseuma* includes mainly narrow endemics confined to the Western and North Western Caucasus, with the exception of *C. variable* with a rather disjunct distribution in the western, northern and central Caucasus (Fig. 1).

### *Caucaseuma strasseri* Antić sp. nov.

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Figs 1–6, 7H

## Diagnosis

*Caucaseuma strasseri* Antić sp. nov. is the only species in the genus characterized by the presence of anterior triangular processes on the angiocoxites of the anterior gonopods.

## Etymology

The new species is named after the late Carlo Strasser (1903–1981), a well-known and always inspiring diplopodologist, who made an immeasurable contribution to the knowledge of European millipedes. At the same time, Strasser described the first cave chordeumatidan taxon from the Caucasus, *Caucaseuma lohmanderi*. A noun in the genitive case.

**Material examined** (7 ♂♂, 4 ♀♀, 30 juvs)

### Holotype

RUSSIA • ♂; Western Caucasus, Krasnodar Province, Greater Sochi, near Lazarevskoye, Kirovskaya (= Tigrovaya) Cave; 2 May–12 Aug. 1996; A.G. Koval leg.; Barber pitfall traps; ZMUM.

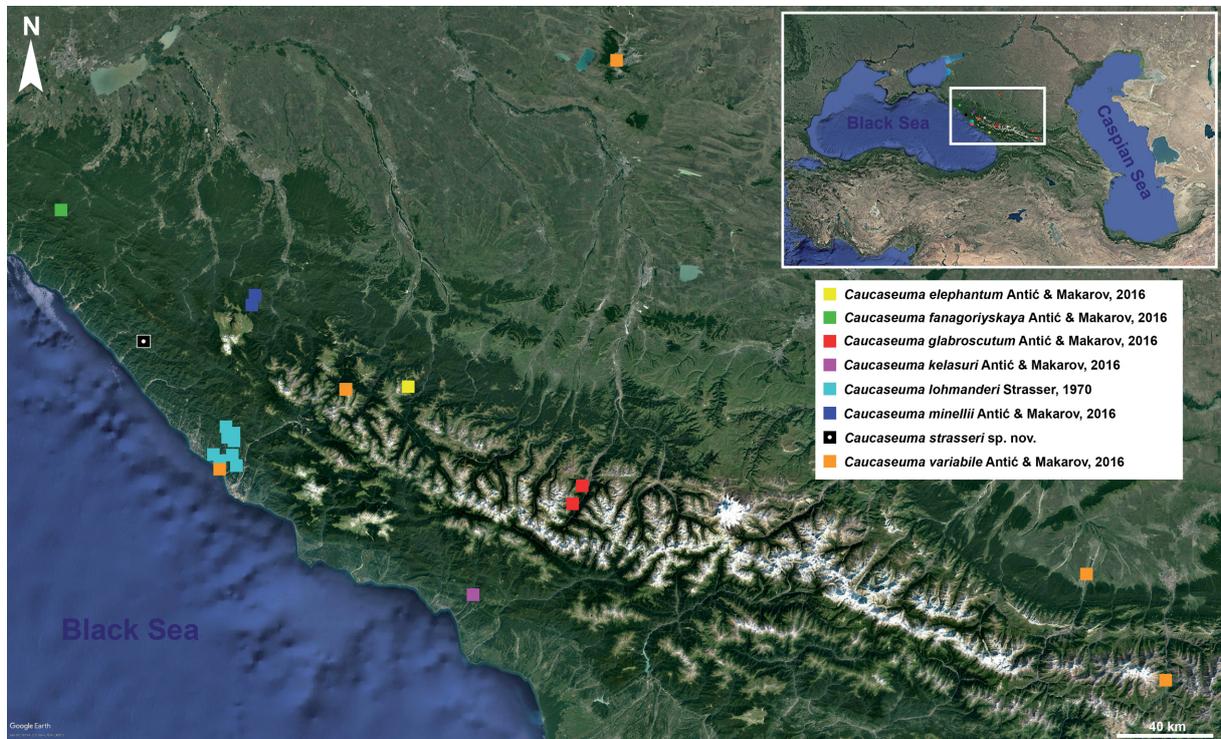


Fig. 1. Distribution of the genus *Caucaseuma* Strasser, 1970.

### **Paratypes**

RUSSIA • 1 ♂ (used for SEM); same collection data as for holotype; NHMW MY10260 • 4 ♂♂ (2 without posterior body rings); same collection data as for holotype; ZMUM • 1 ♂ (without posterior body rings); same collection data as for holotype; IZB • 1 ♀; same collection data as for holotype; ZMUM.

### **Other material**

RUSSIA • 2 ♀♀ (without posterior body rings); same collection data as for holotype; IZB • 1 ♀ (without posterior body rings); same collection data as for holotype; ZMUM • 30 juvs (12 without posterior body rings); same collection data as for holotype; IZB.

### **Description**

**SIZE AND NUMBER OF BODY RINGS.** Body in adults with 30 rings (including telson). Holotype male 20 mm long, vertical diameter of largest ring 1.35 mm. Paratype males 16.5–17 mm long, vertical diameter of largest ring 1.3 mm. Paratype female 18.5 mm long, vertical diameter of largest ring 1.6 mm.

**COLORATION** (Fig. 2). After more than two decades in ethanol yellowish. Ommatidia brownish (Fig. 2B–C).

**HEAD** (Figs 2B–C, 3A–E). Setose, frontal side convex in both sexes. Labrum with three medial teeth and 4+4 or 6+6 labral and 2+2 supralabral setae (Fig. 3B). Promentum triangular, without setae. Lingual plates with 6+7 setae arranged in irregular row. Stipites with ca 30 setae each. Antennae 3.1 mm long in holotype male. Length of antennomeres (in mm): I (0.11), II (0.30), III (0.88), IV (0.43), V (0.85), VI (0.30), VII (0.22) and VIII (0.04). Length/breadth ratios of antennomeres I–VII: I (1), II (2), III (7), IV (3), V (6), VI (2) and VII (2). Antennomeres II, IV, V, VI and VII with one, three, one, four and one sensillum trichoideum, respectively (Figs 2B, 3A). Antennomeres V and VI distally with sensilla basiconica (Fig. 3D–E). Lateral to antennal sockets a group of papillae-like outgrowths present (Fig. 3C). Number of ommatidia: 20–25 (mainly 23) in 6 rows in both sexes, arranged in irregular subtriangle (Figs 2C, 3C).

**COLLUM.** Narrower than head, with six macrochaetae, as all body rings. Anterior edge semi-circular, posterior margin gently concave.

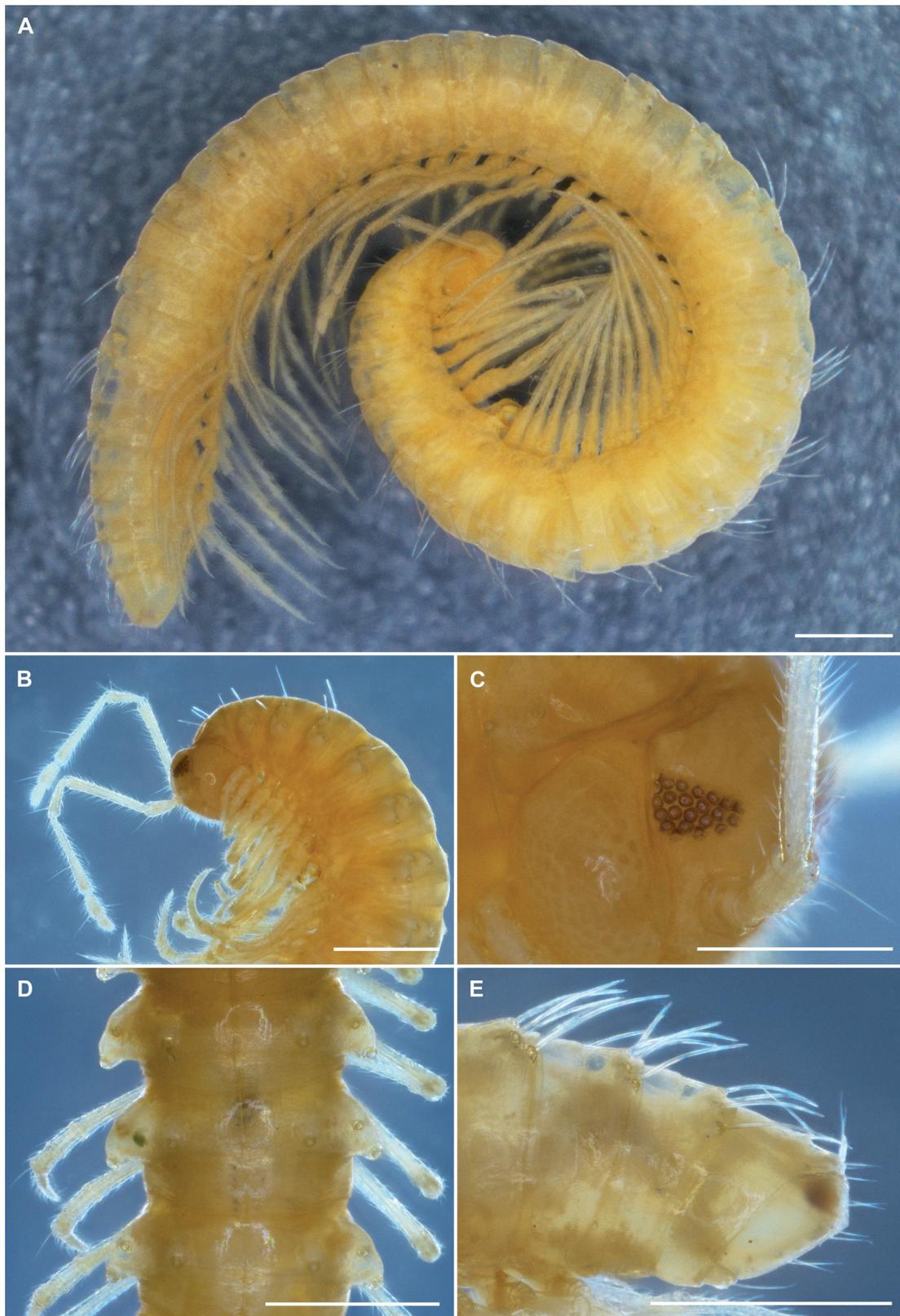
**BODY RINGS** (Figs 2A–B, D–E, 3G–H). Lateral keels well-developed. Macrochaetae long and trichoid (Fig. 4E–F). CIX (ring 15) ~ 0.7; MIX (ring 15) ~ 1.2; PIX (ring 15) = 0.6; MA (ring 15) ~ 105°. Prozonites with hexagonal tiles. Metazonites with scale-like structures.

**TELSON** (Fig. 2E). Epiproct with a pair of spinnerets and 3+3 setae (1+1 paramedian, 2+2 marginal). Hypoproct with 1+1 distal setae. Paraprocts with 3+3 marginal setae.

**LEG-PAIRS 1 AND 2** (Figs 3F, 4A–B). In both sexes, femora, postfemora and tibiae with long and robust setae; tarsi with comb of setae.

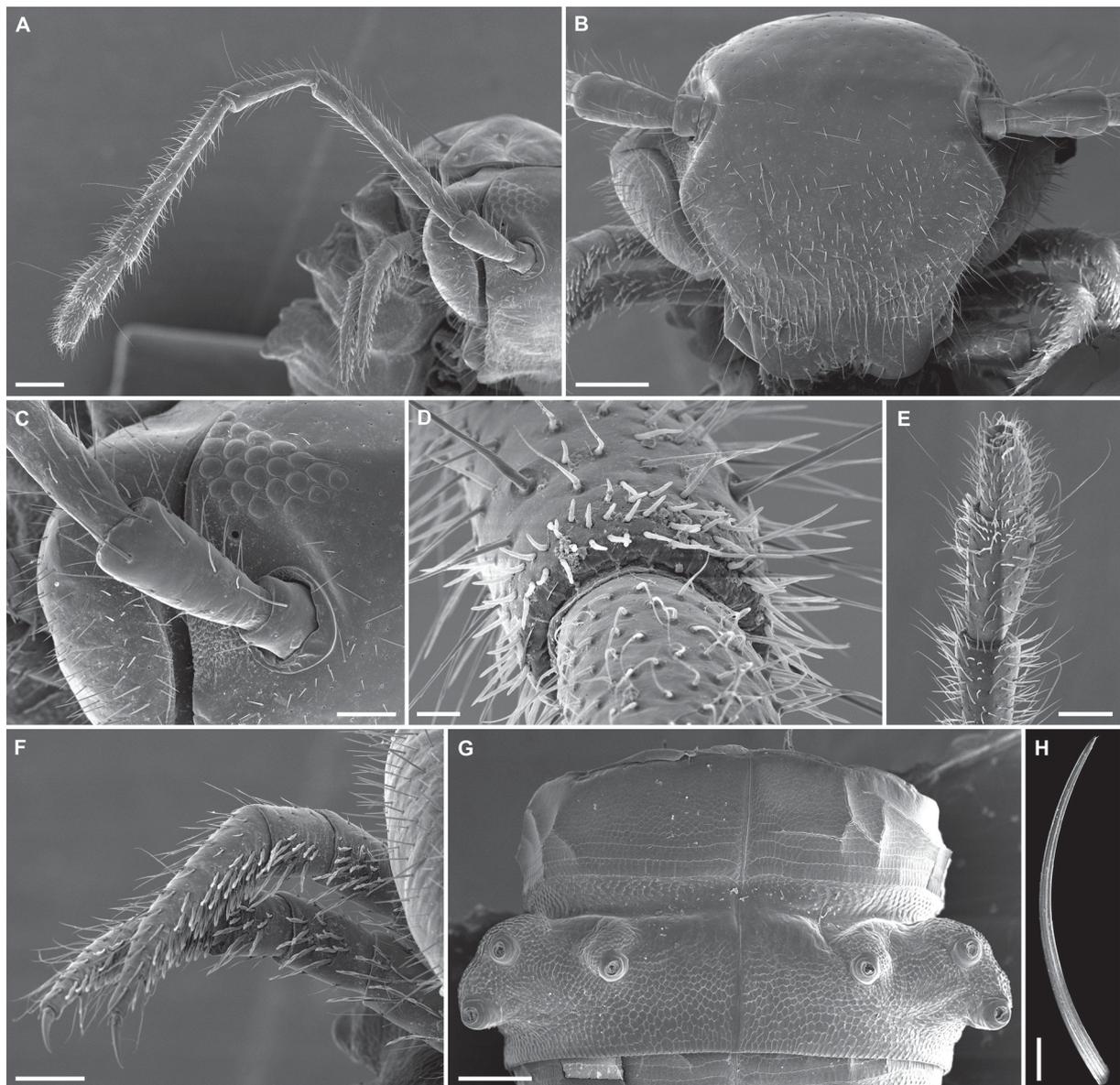
**MALE SEXUAL CHARACTERS** (Figs 2B, 4). Leg-pair 2 with genital openings on coxae (Fig. 4B). Leg-pairs 3–7 enlarged. Leg-pairs 3 and 4 each with a basal external protrusion on prefemur (Fig. 4C–D). Leg-pairs 5 and 6 without peculiarities (Fig. 4E–F). Leg-pair 7 with ventral side of coxae densely setose, with a shallow excavation posteriorly; ventral side of prefemora densely tuberculated; tarsi elongated (Fig. 4G). Leg-pairs 10 and 11 with coxal sacks; no other peculiarities (Fig. 4H–I).

**ANTERIOR GONOPODS** (Figs 5A–C, 6A–F, 7H). Gonopodal sternum (S) well-developed, wide, with anterior triangular, long sternal process (Sp) covered with hair-like outgrowths. Anterior parts (aA) of angiocoxites shield-like, medially completely fused, only with anterior furrow, almost fully rounded in

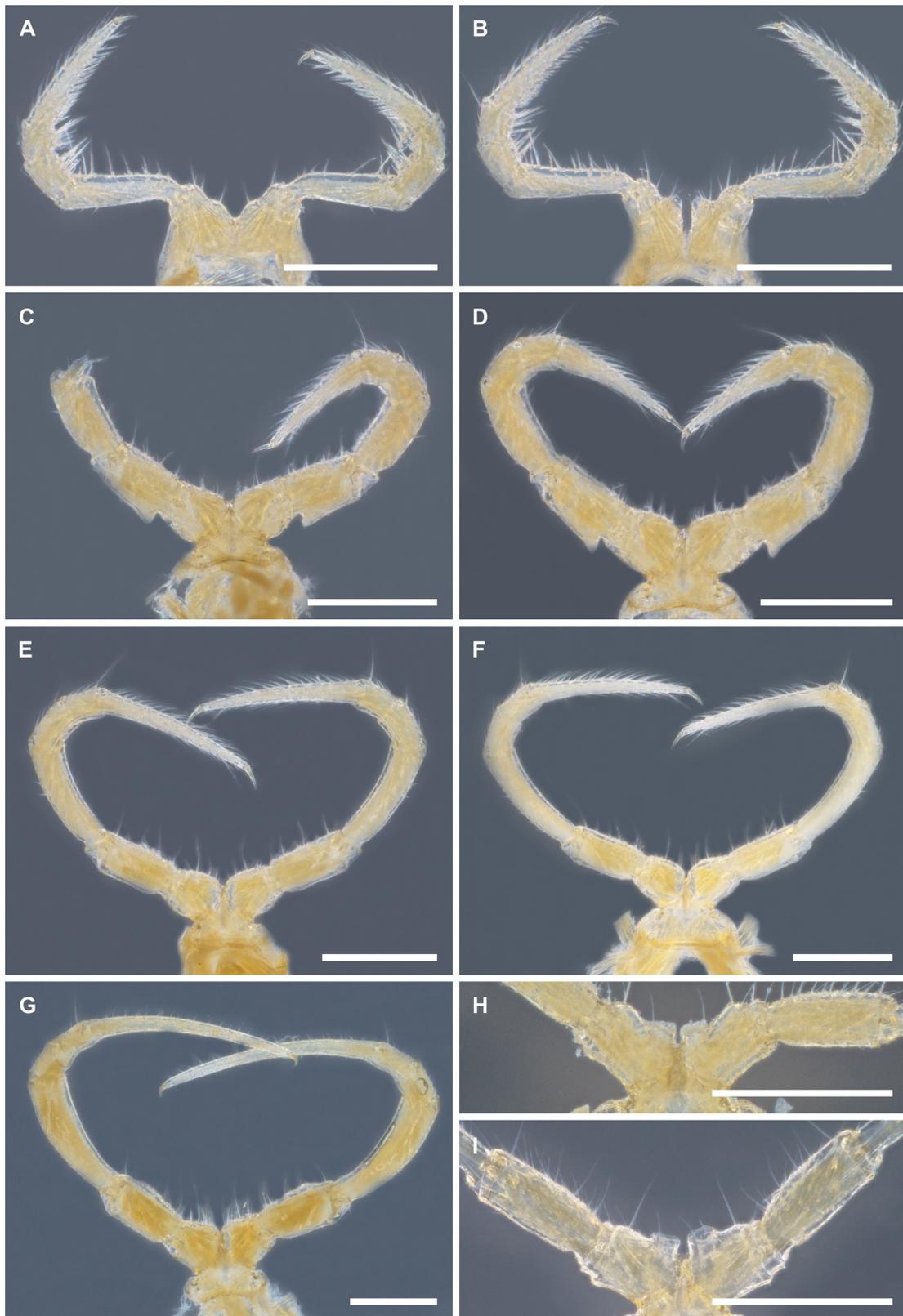


**Fig. 2.** *Caucaseuma strasseri* Antić sp. nov. **A.** Holotype, ♂ (ZMUM). **B–E.** Paratype, ♂ (IZB). **A.** Habitus, lateral view. **B.** Anterior part of the body, lateral view. **C.** Field with ommatidia, lateral view. **D.** Midbody rings, dorsal view. **E.** Telson, lateral view. Scale bars = 1 mm.

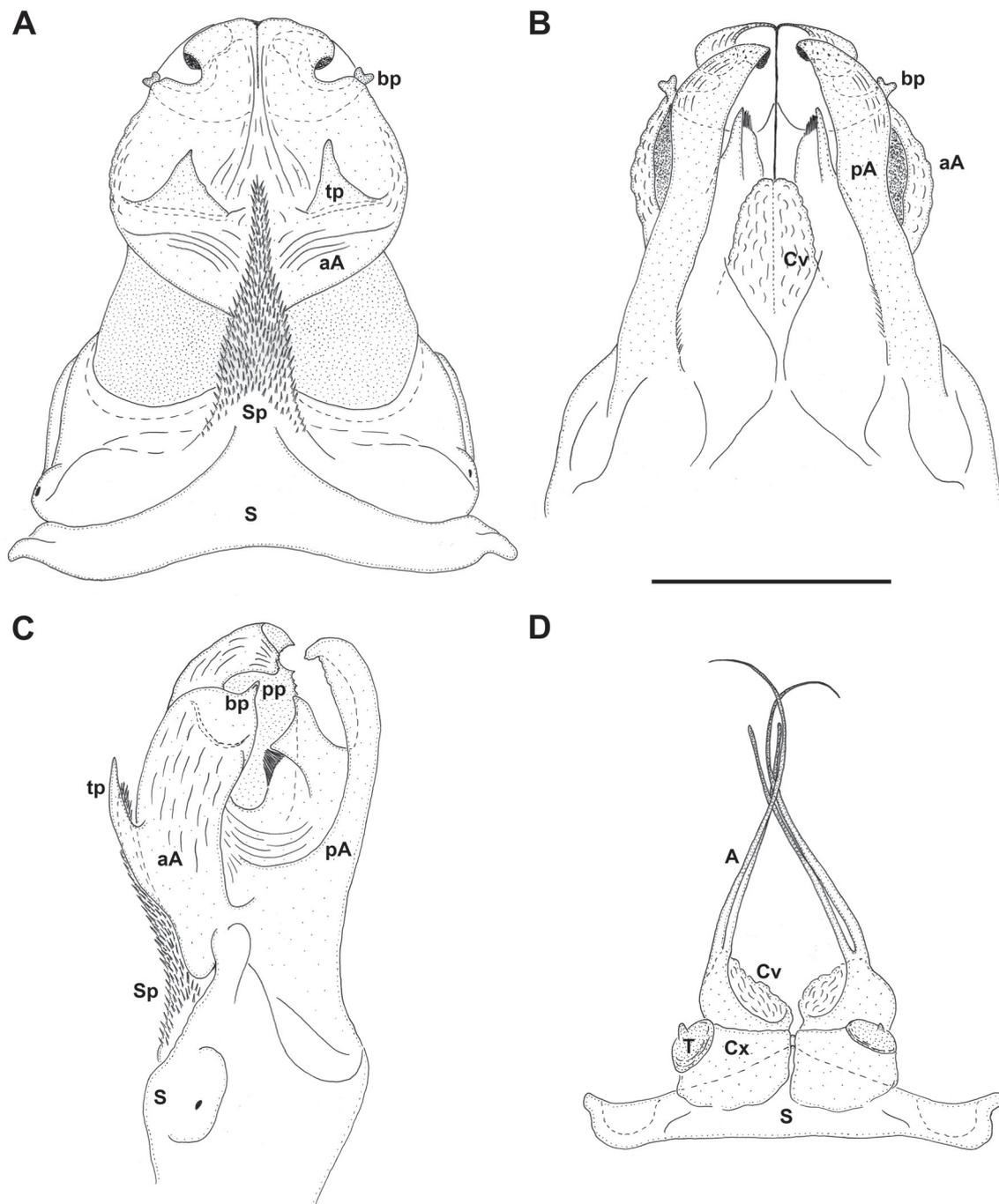
anterior view; subdistally with a pair of notches and short, lateral, bone-like processes (bp); distally with medial structure mushroom-shaped in anterior view with lateral margins curved posteriad; posteriorly, at site of fusion of anterior parts of angiocoxites, with a posterior projection (pp), denticulate distally, and extending between posterior parts of angiocoxites. A pair of characteristic anterior triangular (tp) processes present on angiocoxites. Posterior parts (pA) of angiocoxites in form of elongate levers in posterior view, with distal parts curved anteriad; anteriorly with additional lamellar and setose projections. Between posterior parts of angiocoxites coxal vesicles (Cv) visible.



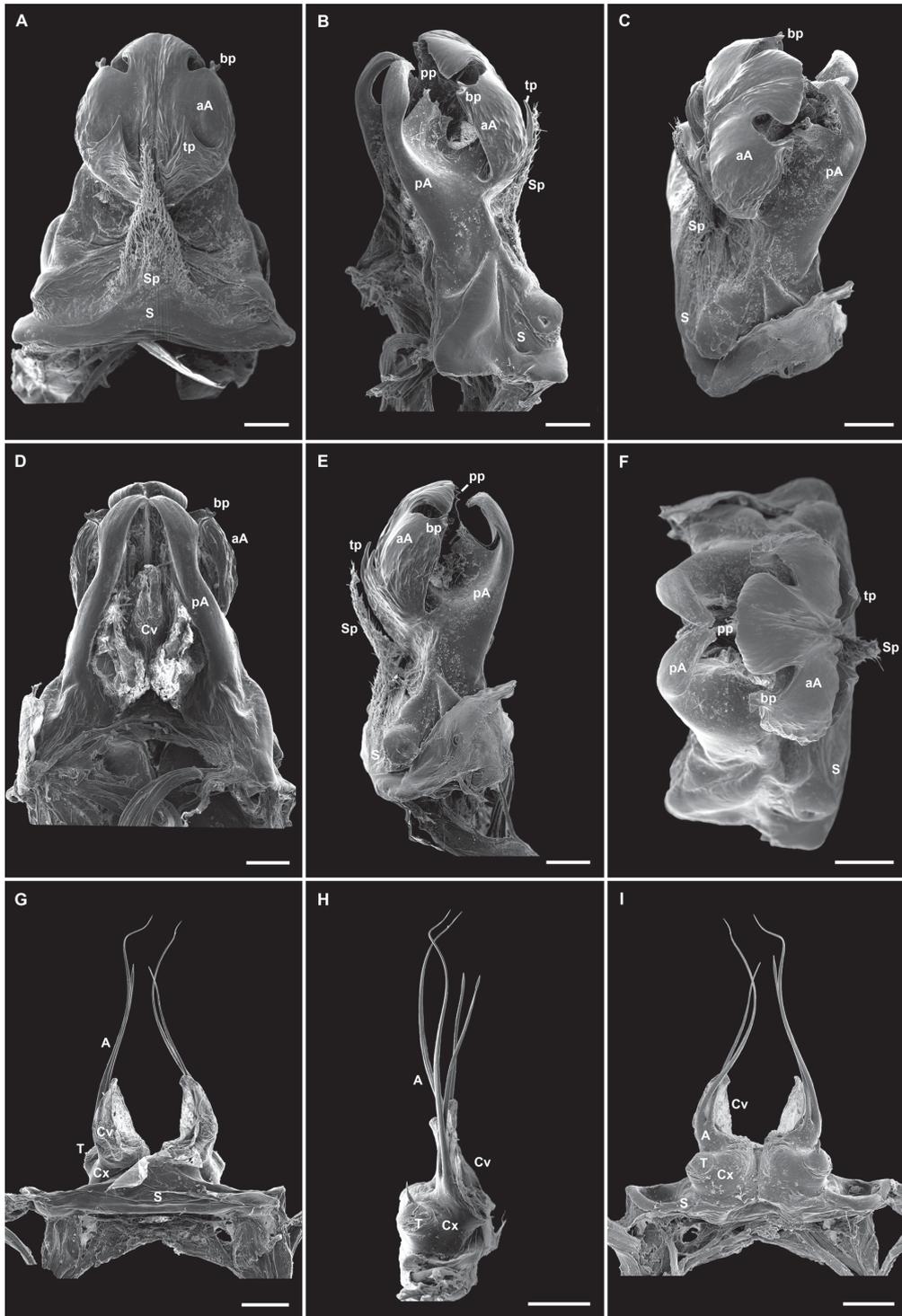
**Fig. 3.** *Caucaseuma strasseri* Antić sp. nov., paratype, ♂ (NHMW MY10260). SEM images of some habitual structures. **A.** Anterior part of the body, anterolateral view. **B.** Head, anterior view. **C.** Head, right side, lateral view. **D.** Left antennomeres 6 and 7, detail. **E.** Tip of right antenna. **F.** Right legs 1 and 2, anteroventral view. **G.** Ring 15, dorsal view. **H.** Posterior macrochaeta. Scale bars: A–B, G = 0.2 mm; C, E–F = 0.1 mm; D = 0.02 mm; H = 0.05 mm.



**Fig. 4.** *Caucaseuma strasseri* Antić sp. nov., paratype, ♂ (IZB). Legs in anterior view. **A.** Leg-pair 1. **B.** Leg-pair 2. **C.** Leg-pair 3. **D.** Leg-pair 4. **E.** Leg-pair 5. **F.** Leg-pair 6. **G.** Leg-pair 7. **H.** Leg-pair 10. **I.** Leg-pair 11. Scale bars = 0.5 mm.



**Fig. 5.** *Caucaseuma strasseri* Antić sp. nov., paratype, ♂ (IZB). Gonopods. **A–C.** Anterior gonopods, anterior, posterior and lateral views, respectively. **D.** Posterior gonopods, posterior view. Abbreviations: A = angiocoxite; aA = anterior part of angiocoxite; bp = bone-like process of angiocoxite; Cv = coxal vesicle; Cx = coxite; pA = posterior part of angiocoxite; pp = posterior projection of angiocoxite; S = gonopodal sternum; Sp = sternal process; T = telopodite; tp = triangular process of angiocoxite. Scale bar = 0.3 mm.



**Fig. 6.** *Caucaseuma strasseri* Antić sp. nov., paratype, ♂ (NHMW MY10260). SEM images of gonopods. **A–F.** Anterior gonopods, anterior, posterolateral, anterodistolateral, posterior, lateral and distal views, respectively. **G–I.** Posterior gonopods, anterior, lateral and posterior views, respectively. Abbreviations: A = angiocoxite; aA = anterior part of angiocoxite; bp = bone-like process of angiocoxite; Cv = coxal vesicle; Cx = coxite; pA = posterior part of angiocoxite; pp = posterior projection of angiocoxite; S = gonopodal sternum; Sp = sternal process; T = telopodite; tp = triangular process of angiocoxite. Scale bars = 0.1 mm.

POSTERIOR GONOPODS (Figs 5E, 6G–I). Gonopodal sternum (S) well-developed, wide, with a deep pit laterally. Coxites (Cx) divided, each with a small telopodite (T) posteriorly and coxal vesicle (Cv) and angiocoxite (A) anteriorly. A pair of flagelliform processes originating from base of angiocoxite.

### Remarks

This species is known only from a cave and shows certain troglobiomorphic features such as reduced body and ommatidia pigmentation, elongated antennae and walking legs, as well as a larger and more robust body compared to epigean congeners.

### Distribution

*Caucaseuma strasseri* Antić sp. nov. is known so far only from its type locality, Kirovskaya (= Tigrovaya) Cave (Fig. 1). This cave is the type locality of two more cave animals, viz., the troglobiontic isopod *Pseudobuddelundiella ljevuschkini* Borutzky, 1967 and the stygobitic copepod *Speocyclops psezuapsensis* Borutzky, 1965 (Turbanov *et al.* 2016a).

### Previously described species

*Caucaseuma elephantum* Antić & Makarov, 2016  
Figs 1, 7A

*Caucaseuma elephantum* Antić & Makarov, 2016: 29, figs 18–20.

### Remarks and distribution

A troglobiont. So far known only from the holotype described from Yuzhnyj Slon Cave (= “Southern Elephant Cave”), Mt Dzentu, Karachaevo-Cherkessia Republic in Russia (Antić & Makarov 2016) (Fig. 1).

*Caucaseuma fanagoriyskaya* Antić & Makarov, 2016  
Figs 1, 7B

*Caucaseuma fanagoriyskaya* Antić & Makarov, 2016: 32, figs 21–23.

### Material examined (1 ♀)

RUSSIA • 1 ♀; Western Caucasus, Krasnodar Province, Goryachiy Klyuch, near Fanagoriyskoye, Fanagoriyskaya Cave; 1 Dec. 2018; P.V. Somchenko leg.; IZB.

### Remarks and distribution

A troglophile. So far known only from the type locality, Fanagoriyskaya Cave, Krasnodar Province in Russia (Fig. 1).

*Caucaseuma glabroscutum* Antić & Makarov, 2016  
Figs 1, 7D

*Caucaseuma glabroscutum* Antić & Makarov, 2016: 36, figs 24–28.

### Remarks and distribution

Epigean species. So far known only from the type series described from two localities at ca 2000 m a.s.l. in the Teberda Nature Reserve in Russia (Antić & Makarov 2016) (Fig. 1).

*Caucaseuma kelasuri* Antić & Makarov, 2016

Figs 1, 7E

*Caucaseuma kelasuri* Antić & Makarov, 2016: 39, figs 29–31.

**Remarks and distribution**

Epigeal species. So far known only from the holotype described from near Kelasuri Cave, Sukhumi District in Georgia/Abkhazia (Antić & Makarov 2016) (Fig. 1).

*Caucaseuma lohmanderi* Strasser, 1970

Figs 1, 7F

*Caucaseuma lohmanderi* Strasser, 1970: 200, figs 1–6.

*Caucaseuma lohmanderi* – Golovatch 1985: 48. — Antić & Makarov 2016: 44, figs 32–34. — Turbanov *et al.* 2016b: 1311.

**Material examined** (53 ♂♂, 71 ♀♀, 3 juvs)

RUSSIA • 7 ♂♂, 5 ♀♀; Western Caucasus, Krasnodar Province, Greater Sochi, Khosta, Partizanskaya Cave; 30 Apr.–24 Aug. 1992; A.G. Koval leg.; Barber pitfall traps; ZMUM • 10 ♂♂, 13 ♀♀, 1 juv.; Western Caucasus, Krasnodar Province, Greater Sochi, Khosta, Mount Akhun, Bolshaya Akhunsкая Cave; 26 Apr.–26 Aug. 1992; A.G. Koval leg.; Barber pitfall traps; ZMUM • 2 ♂♂, 14 ♀♀; same collection data as for preceding but 13 Aug.–24 Sep. 1988; pitfall traps; ZMUM • 18 ♂♂, 22 ♀♀; same collection data as for preceding but 28 Apr.–23 Aug. 1990; IZB • 15 ♂♂, 17 ♀♀, 2 juvs; same collection data as for preceding but 4 Apr.–22 Jun. 1990; ZMUM • 1 ♂; Western Caucasus, Krasnodar Province, Greater Sochi, Akhshtyr Karst Massif, Avgust Cave; 9 Sep. 2015; I. Turbanov leg.; ZMUM.

**Remarks and distribution**

A trogloniont. This is the most abundant of all *Caucaseuma* species. So far, over 230 specimens from 11 caves in Sochi District, Russia, are known. Here is an updated list of caves from which this species is known, arranged in alphabetic order: Ametist, Akhunsкая (= Bolshaya Akhunsкая), Avgust, “Baribana” (= Grot Baribana) (type locality!), Dolgaya, Labirintovaya, Navalishenskaya (= Muzeynaya), Partizanskaya, Shirokopokosskaya (= Bozhyey Materi = “Our Lady”), Vorontsovskaya (= Bolshaya Vorontsovskaya; also includes Khod Kuzmenko) and Zapovednaya (= Tisovaya) (Fig. 1).

*Caucaseuma minellii* Antić & Makarov, 2016

Figs 1, 7C

*Caucaseuma minellii* Antić & Makarov, 2016: 47, figs 35–37.

**Material examined** (7 ♂♂, 2 ♀♀, 7 juvs)

RUSSIA • 4 ♂♂, 1 ♀; Krasnodar Province, Apsheronsky District, Lago-Naki Mt Range, Azish Tau Ridge, Piketnaya Cave; 6 Nov. 2020; I. Turbanov leg.; ZMUM • 3 ♂♂, 1 ♀, 7 juvs; same collection data as for preceding; IZB.

**Remarks and distribution**

A trogloniont. So far this species is known from three caves in Krasnodar Province, near Apsheronsk, Russia: Sukhaya (type locality!), Bolshaya Azishskaya and Piketnaya (Fig. 1).

*Caucaseuma variabile* Antić & Makarov, 2016  
Figs 1, 7G

*Caucaseuma variabile* Antić & Makarov, 2016: 50, 38–42.

**Material examined** (2 ♂♂, 2 ♀♀)

RUSSIA • 2 ♂♂, 2 ♀♀; Krasnodar Province, Caucasian Nature Reserve, valley of Khodzhibi river; 43°49.388' N, 40°31.138' E; 2050 m a.s.l., 6 Nov. 2020; Y. Chumachenko leg.; *Abies* and *Betula* forest; DSTU.

**Remarks and distribution**

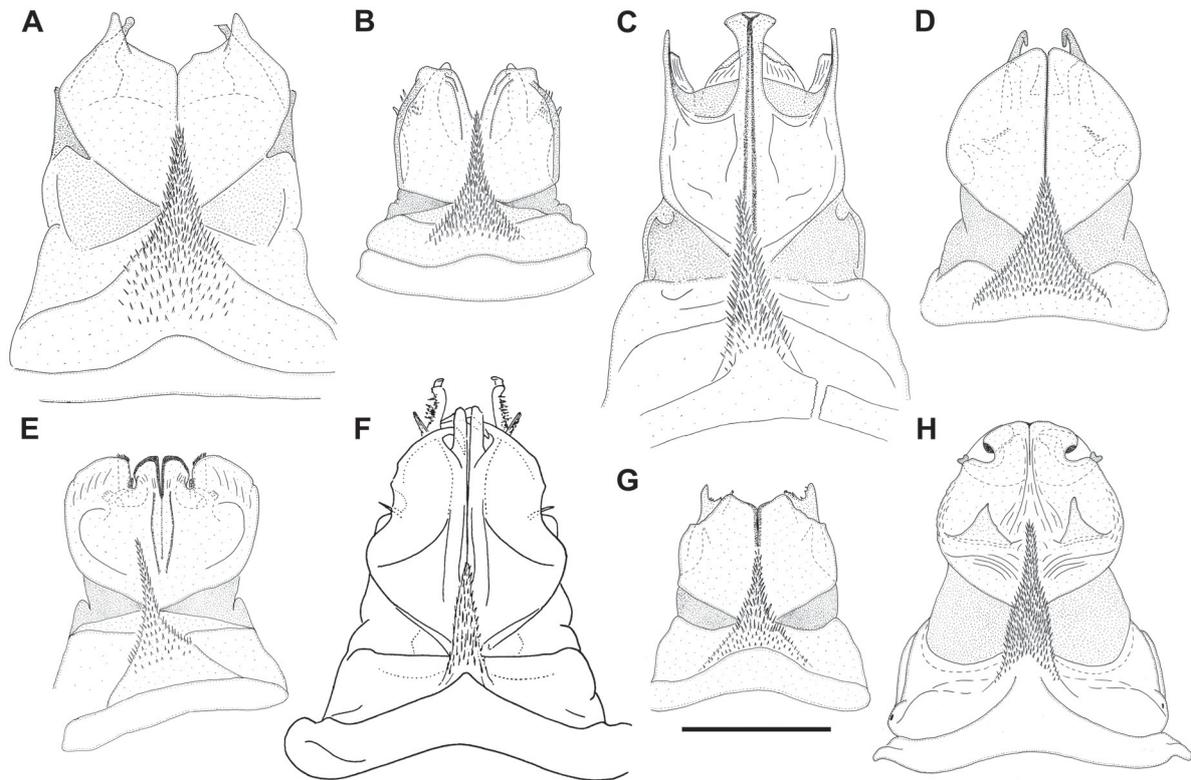
Epigeal species. This species shows a disjunct distribution so far. It is known from Russia, from North Ossetia, near Alagir (type locality!), from Krasnodar Province, near Sochi and from Stavropol Botanical Garden in Stavropol Province. Also, it is known from the Mtskheta-Mtianeti region in Georgia (Fig. 1).

**Key to the species of the genus *Caucaseuma* Strasser, 1970**

(based on the anterior gonopods of males)

1. Anterior part of angiocoxites with a pair of distal notches ..... 2  
– Anterior part of angiocoxites without a pair of distal notches ..... 5
2. Anterior parts of angiocoxites with a pair of anterior triangular processes (Fig. 7H) .....  
..... *C. strasseri* Antić sp. nov.  
– Without such processes ..... 3
3. Medial projection of anterior part of angiocoxites fused distally (Fig. 7C) .....  
..... *C. minellii* Antić & Makarov, 2016  
– Medial projection of anterior part of angiocoxites not fused distally ..... 4
4. Lateral projections of angiocoxites distally rounded; smaller species, 11 mm (Fig. 7E) .....  
..... *C. kelasuri* Antić & Makarov, 2016  
– Lateral projections of angiocoxites distally in the form of elongated processes strongly curved posteriad; larger species, 16–17 mm (Fig. 7F) ..... *C. lohmanderi* Strasser, 1970
5. Anterior part of angiocoxites with two distinctive, bifurcated, posterior projections/processes (see Antić & Makarov 2016: 31, fig. 20b, c, bp1 and bp2; Fig. 7A) .....  
..... *C. elephantum* Antić & Makarov, 2016  
– Without such posterior projections/processes ..... 6
6. Anterior parts of angiocoxites with a deep V-shaped incision distally (Fig. 7B) .....  
..... *C. fanagoriyskaya* Antić & Makarov, 2016  
– Anterior parts of angiocoxites without a deep V-shaped incision distally ..... 7
7. Margins of the anterior parts of angiocoxites circular (Fig. 7D) .....  
..... *C. glabroscutum* Antić & Makarov, 2016  
– Margins of the anterior parts of angiocoxites subquadrangular (Fig. 7G) .....  
..... *C. variabile* Antić & Makarov, 2016

To easily distinguish all eight species of the genus *Caucaseuma*, see also Figure 7.



**Fig. 7.** Anterior gonopods in the genus *Caucaseuma* Strasser, 1970, anterior views. **A.** *C. elephantum* Antić & Makarov, 2016. **B.** *C. fanagoriyskaya* Antić & Makarov, 2016. **C.** *C. minellii* Antić & Makarov, 2016. **D.** *C. glabroscutum* Antić & Makarov, 2016. **E.** *C. kelasuri* Antić & Makarov, 2016. **F.** *C. lohmanderi* Strasser, 1970. **G.** *C. variabile* Antić & Makarov, 2016. **H.** *C. strasseri* Antić sp. nov., paratype, ♂ (IZB). A–E, G after Antić & Makarov (2016), F after Strasser (1970). Scale bar = 0.3 mm for all, except for F (not to scale).

## Discussion

Just over 70 years ago, the pioneer of biospeleological research in the former USSR, Birsetein (1950), recognized the biological potential of karst in the Western Caucasus. A few decades later, Culver *et al.* (2006) were of the opinion that there are potential subterranean hotspots of biodiversity in the Western Caucasus. Numerous descriptions of new subterranean taxa in this region during the last decade are very much in favour of these assumptions.

In terms of cave millipedes of the Caucasus, from Birsetein's (1950) pioneering study until the end of the second and the beginning of the third decade of the 21<sup>st</sup> century, only a few species have been described (see also Golovatch 1985). As mentioned above, the first cavernicolous chordeumatidan from the Caucasus, *C. lohmanderi*, was described by Strasser (1970) based on samples found in two caves in the Sochi region. From then until recently, only one other cavernicolous taxon of Chordeumatida has been described from the Caucasus, a monospecific *Ratcheuma* Golovach, 1985, known from only one cave in the Racha region in Georgia. In the same paper, Golovatch (1985) added new cave localities for *C. lohmanderi*, but also mentioned some other, at that time still undescribed, cave chordeumatidans. These and other species have only recently been examined by Antić & Makarov (2016), Golovatch & Makarov

(2011) and Antić *et al.* (2018). Thus, the number of cavernicolous chordeumatidans in the Caucasus has increased from two to 11 taxa, including three genera (besides *Ratcheuma*) known exclusively from underground habitats, viz., *Brachychaetosoma* Antić & Makarov, 2016, *Georgiosoma* Antić & Makarov, 2016 and *Heterocauseuma* Antić & Makarov, 2016. The genus *Heterocauseuma* contains the deepest-dwelling chordeumatidan and at the same time one of the deepest-occurring terrestrial arthropod species ever found, *H. deprofundum* Antić & Reboleira in Antić *et al.*, 2018, described from Krubera-Voronja and Sarma caves in the Arabika Massif (Antić *et al.* 2018).

Species of the genus *Causeuma* include both cavernicolous and epigean forms. It is interesting that none of, not only *Causeuma*, but also other cave chordeumatidans from the Caucasus, are without ommatidia, while some cave-dwelling species have a large number of ommatidia. This was precisely why Golovatch (1985) considered them as probably troglaphiles. However, with the increase in the number of described chordeumatidans from the Caucasus, both cave and epigean, it has become clear that most exclusively cave-dwelling taxa present certain troglobiontic features. These adaptations are reflected in the reduction in pigment of both body and ommatidia, in the reduction of the number of ommatidia in some, in the elongation of the antennae and/or walking legs, and a more robust and larger habitus (cave gigantism) (cf. Antić & Makarov 2016; Liu *et al.* 2017; Antić *et al.* 2018). These are best seen in cases where subterranean and epigean species occur within the same genus, as is the case with the genus *Causeuma*. All four presumed troglobiontic species (including *C. strasseri* Antić sp. nov.) are larger and more robust when compared to the four epigean congeners (16–20 mm vs 8–15 mm); they also have pale bodies and somewhat elongated legs and antennae. The number of ommatidia does not differ significantly between cavernicolous and epigean *Causeuma*, but it seems that in some cave-dwellers they are, although darkly pigmented, still less pigmented compared to epigean forms. Within these presumed troglobiontic *Causeuma*, it appears that three species, *C. lohmanderi*, *C. minellii* and *C. strasseri*, show a similar degree of subterranean adaptation, which is mostly reflected in the partially depigmented body and elongated antennae and legs. On the other hand, *C. elephantum* has even more pronounced troglomorphic adaptations, which in addition to the above includes a densely setose gnathochilarium, as well as a reduced number of ommatidia compared to the remaining three cavernicolous congeners (11–12 vs 20–25) (see also Antić & Makarov 2016). Recently collected material of *C. minellii* showed that all adults have a brownish pigment dorsally, while the ventral parts are yellowish, and dark brown to almost black ommatidia. Thus, differences in the degree of adaptation can be noticed within the cavernicolous *Causeuma* species. A similar pattern of hypothetical gradual evolution in cave-dwelling *Causeuma* can be observed in the genus *Heterocauseuma* (see Antić *et al.* 2018). All this suggests that they are probably neotroglobionts, in the process of subterranean adaptation, rather than troglaphiles. This is supported by the fact that these robust animals were not found on the surface, as well as that some populations were relatively large.

In addition to several representatives of the order Chordeumatida and the family Anthroleucosomatidae, there are a few other families of millipedes with cavernicolous members in the Caucasus. These are mainly individual troglobiontic representatives from the families Glomeridae Brandt, 1833, Glomeridellidae Cook, 1896, Trichopolydesmidae Verhoeff, 1910 and Blaniulidae C.L. Koch, 1847 (see Golovatch 1976, 1985; Enghoff 1984; Golovatch & Turbanov 2017, 2018). In the Caucasus, the only millipede family that can match the Anthroleucosomatidae in the number of troglobiontic species is the family Julidae Leach, 1814. Probably the most iconic genus of cave millipedes in this region is *Leucogeorgia* Verhoeff, 1930. Until recently, this genus included four species, three of which were known exclusively from caves (see Verhoeff 1930; Lohmander 1936; Golovatch 1983). Antić & Reip (2020) increased the number of species in the genus to 15, describing 11 new species, of which as many as 10 are troglobiontic. The genus *Leucogeorgia*, as well as the monospecific genus *Martvilia* Antić & Reip, 2020, includes some interesting forms that are characterized by highly modified mouthparts, and have a semiaquatic life, occasionally entering cave waters where they can presumably feed by filtering (Antić & Reip

2020). In addition, the genus *Leucogeorgia* includes the world's deepest terrestrial arthropod ever found, *Leucogeorgia profunda* Antić & Reip, 2020, with one specimen collected in Vervovkina Cave at a depth of -2204 meters (Antić 2021).

In the last decade, the number of newly described and discovered troglobiontic millipedes in the Caucasus has increased significantly. This not only provides a greater understanding concerning regional subterranean fauna, but has also led to additional questions concerning the ecology and evolution in underground habitats. The description of another cavernicolous millipede in this paper clearly indicates that the number of cave representatives of this group in the Caucasus is far from fully known, and that we can expect new discoveries and surprises in the future.

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