

***Protuberator novaki* gen. nov., sp. nov., a new anthroleucosomatid millipede (Diplopoda: Chordeumatida: Anthroleucosomatidae) from the Caucasus**

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Summary. The present study describes a new monospecific chordeumatidan genus, *Protuberator* gen. nov., and its type species, *Protuberator novaki* gen. nov., sp. nov., from Machakhela National Park in Adjara, Georgia. This new millipede is characterized by a profoundly modified head, with a very large anterior bulge, as well as distinctive tarsi on leg-pair 6, and unique gonopods in male. These unique features make the taxon easily distinguishable, not only from the Caucasian Anthroleucosomatidae, but also from all other members of the family. The new genus and species are described and diagnosed in detail, and illustrations of the male habitus, legs and gonopods are provided. The affinities of the new genus with other members of the family Anthroleucosomatidae and head modifications in general are also briefly discussed.

Keywords: Adjara, biodiversity, Georgia, head modifications, Lesser Caucasus, taxonomy.

INTRODUCTION

The chordeumatidan family Anthroleucosomatidae is among the most heterogeneous members of the order; the family is clearly non-monophyletic, and currently includes 92 species in 36 genera (Antić and Makarov 2016; Antić 2017; Antić et al. 2020, 2023, 2025; Šević et al. 2022). The distribution of chordeumatidan family Anthroleucosomatidae is almost exclusively confined to the Western Palaearctic, with the main centers of diversification located in the Balkan Peninsula and the Caucasus.

More than half of the described taxa within the family are known from the Caucasus ecoregion. Interestingly, this level of diversity remained largely hidden until recently, as only seven species were known prior to 2016 (Antić and Makarov 2016). However, over the past decade alone, as many as 45 new species and 15 new genera of anthroleucosomatids

have been described. Today, with 20 genera and 52 species, Anthroleucosomatidae represents one of the most diverse millipede groups in the region (Antić and Makarov 2016, 2022; Antić et al. 2018, 2023, 2025).

In the present study, we describe a remarkable new anthroleucosomatid genus from the Caucasus, which is characterized by a strongly modified head in the male.

MATERIAL AND METHODS

A single male specimen (holotype) is preserved in 70% ethanol and deposited in the collection of the Naturhistorisches Museum Wien, Austria (NHMW). The specimen was examined using Nikon SMZ745T, Nikon SMZ1270, and Carl Zeiss Stemi 2000-C binocular stereo microscopes. All taxonomically important structures were dissected and mounted in glycerin as temporary microscope preparations, and ob-

served with a Carl Zeiss Axioscope 40 microscope. Habitus photographs were taken using a Nikon DS-Fi2 camera equipped with a Nikon DS-L3 camera controller attached to a Nikon SMZ1270 binocular stereo microscope. Photographs of the legs were also recorded with a Nikon DS-Fi2 camera equipped with a Nikon DS-L3 camera controller attached to a Nikon SMZ1270 binocular stereo microscope; as well as with a Canon PowerShot A80 digital camera connected to a Carl Zeiss Axioscope 40 microscope. All images were stacked using Zerene Stacker Professional v1.04. Line drawings of the gonopods were made using tracing paper placed on a computer monitor displaying images of these structures taken with a Canon PowerShot A80 digital camera connected to a Carl Zeiss Axioscope 40 microscope. The final images were processed and assembled in Adobe Photoshop CS6.

The terminology used in the description follows Antić et al. (2025), with some modifications.

Abbreviations used to denote particular structures of the gonopods are explained directly in the description and figure legend.

RESULTS

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Chordeumatida Pocock, 1894
Family Anthroleucosomatidae Verhoeff, 1899

Genus *Protuberator* Antić & Makarov, gen. nov.

Diagnosis. The new genus differs from all other members of the family Anthroleucosomatidae by the presence in the male of a very large anterior bulge on the head, distinctive tarsi of leg-pair 6 with large proximal dorsal bulges covered by small nipples, and uniquely shaped anterior gonopods with a well-developed synangiocoxite. In addition, the posterior gonopods lack telopodites, while the angiocoxites are in the form of a few flagelliform processes.

Name. The genus name *Protuberator* is derived from the Latin verb *protuberare* ("to swell, bulge out"), referring not only to the large head bulge, the most distinctive feature of the genus, but also to the distal bulges of the tarsi of leg-pair 6. The name is treated as a masculine noun.

Description. Adult male with 31 body segments (including collum and telson). Body whitish with poorly developed lateral keels and rather short and trichoid macrochaete. Head strongly modified, with a large anterior bulge. Ocular field with 4+5 poorly pigmented ommatidia. Leg-pairs 3–7 strongly enlarged and modified. Leg-pair 6 with a characteristic proximal dorsal bulge on the tarsi, covered by nipples. Leg-pairs 10 and 11 with coxal glands. Leg-pair 10 with posterodistal process covered by nipples. Anterior

gonopods complex; sternum with sternal lamella with three lobes and a pair of lateral processes; angiocoxites in form of a pair of shields and bottle shaped synangiocoxite anteriorly; a pair of coxal vesicles present posteriorly. Posterior gonopods without telopodites; angiocoxites in the form of five long flagelliform processes; colpocoxites poorly sclerotized, membranous, rather subtriangular.

Type species. *Protuberator novaki* gen. et sp. nov., by present designation and monotypy.

Protuberator novaki Antić & Makarov, gen. et sp. nov.

Figs 1–5

Diagnosis. As for the genus.

Name. The species is named after colleague János Novák, a Hungarian arachnologist who collected this remarkable specimen. The name is treated as a noun in the genitive case.

Material examined. Holotype male (NHMW-ZOO-MY-10660) – Georgia, Adjara, Machakhela National Park, between Uchkhiti and Acharisaghamarti, leaf litter sifting in a forested area, 10-11-2023, leg. J. Novák.

Description. *Number of body segments and size.* Body with 31 segments (including collum and telson). Body length 13 mm, vertical diameter of the largest segment 1.1 mm.

Coloration. Whitish (Figs 1, 2).

Head (Figs 1A, 2A–E). Mostly smooth, with sparse setae; strongly modified, with a large anterior bulge; dorsally, with a longitudinal medial and two longitudinal lateral ridges, and two longitudinal depressions in between; anterior side with a central depression and two smaller lateral bulges. Labrum with three labral teeth, and 4+4 labral and 2+2 supralabral setae. Gnathochilarium normal, without peculiarities. Antennae 2.2 mm long. Length of antennomeres (in mm): I (0.11), II (0.25), III (0.60), IV (0.31), V (0.55), VI (0.20), VII (0.16) and VIII (0.02). Length/breadth ratios of antennomeres I–VII: I (1.0), II (2.0), III (5.5), IV (2.6), V (4.0), VI (1.3) and VII (1.6). Antennomeres II, IV, V, VI and VII with one, three, one, four and one long sensillum trichodeum, respectively. Ommatidia poorly developed, light brownish, barely visible; left side with 4 ommatidia in two rows, right side with 5 ommatidia in one line.

Collum. Narrower than head, with six macrochaetae as on all body segments. Anterior edge semi-circular, posterior margin gently concave.

Body segments (Figs 1, 2F). Lateral keels rounded in dorsal view. Macrochaetae rather short and trichoid in midbody segments, somewhat longer in the anterior part of body.

Telson. Normal, without peculiarities.

Leg-pairs 1 and 2. With tarsal combs; femora, post-femora and tibiae with long and robust setae (Fig. 3A).

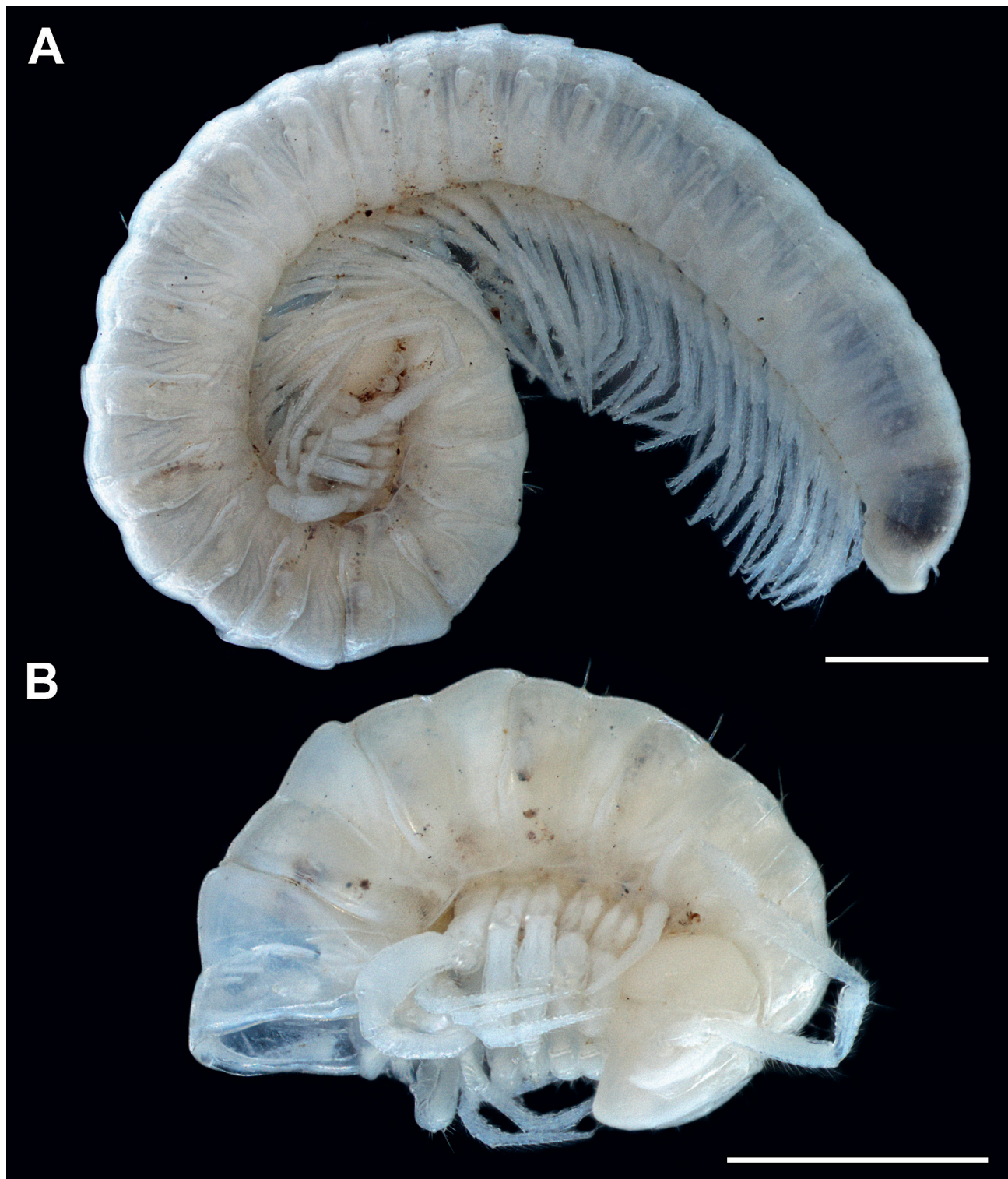


Fig. 1. *Protuberator novaki* gen. nov., sp. nov., holotype male (NHMW-ZOO-MY-10660). **A**, habitus, lateral view; **B**, anterior part of body, lateral view. (Scale bars: 1 mm).

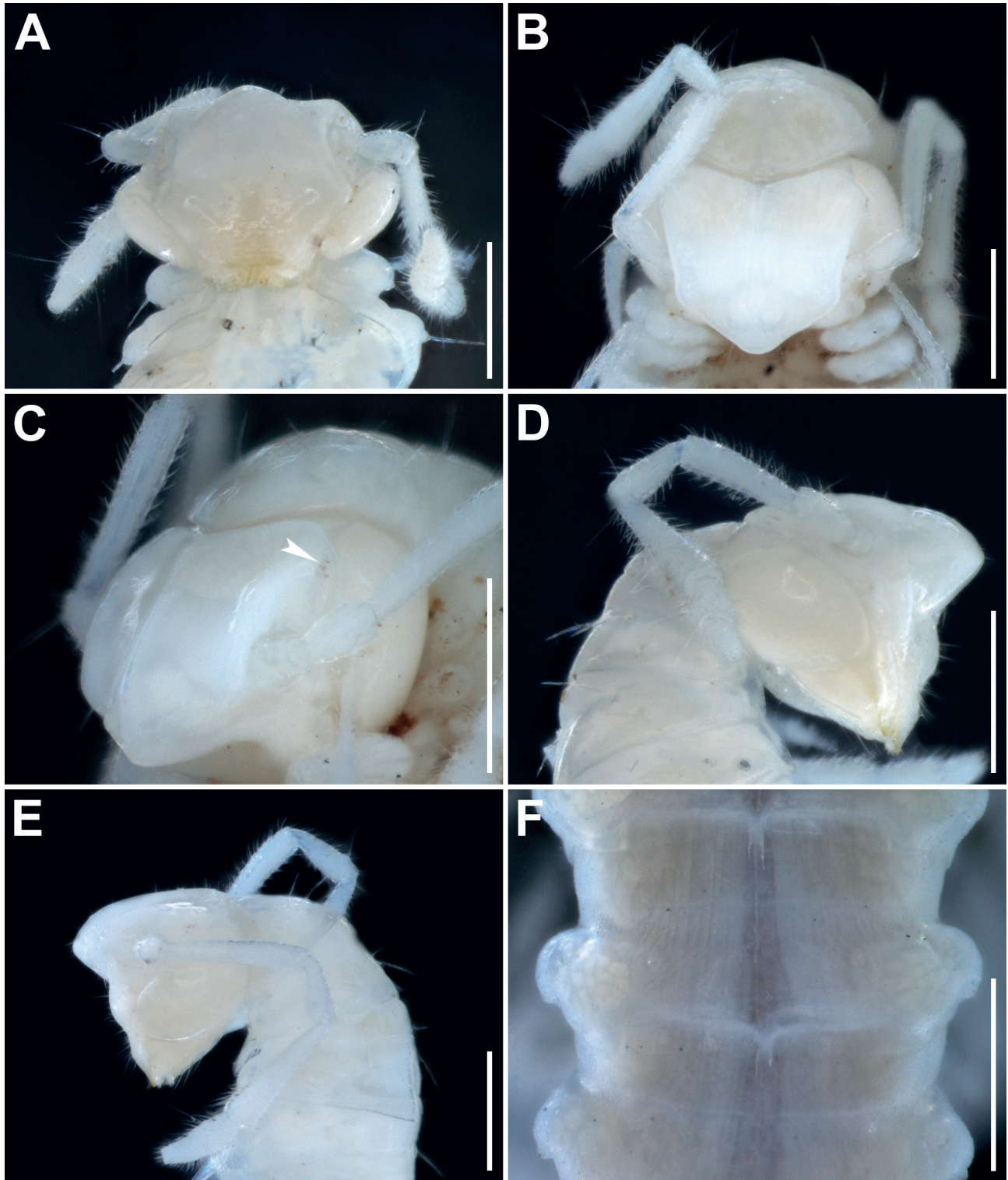


Fig. 2. *Protuberator novaki* gen. nov., sp. nov., holotype male (NHMW-ZOO-MY-10660). A–E, head in anterior, dorsal, dorsolateral, anterolateral and lateral view, respectively (white arrow indicates ommatidia); F, midbody segments, dorsal view. (Scale bars: 0.5 mm).

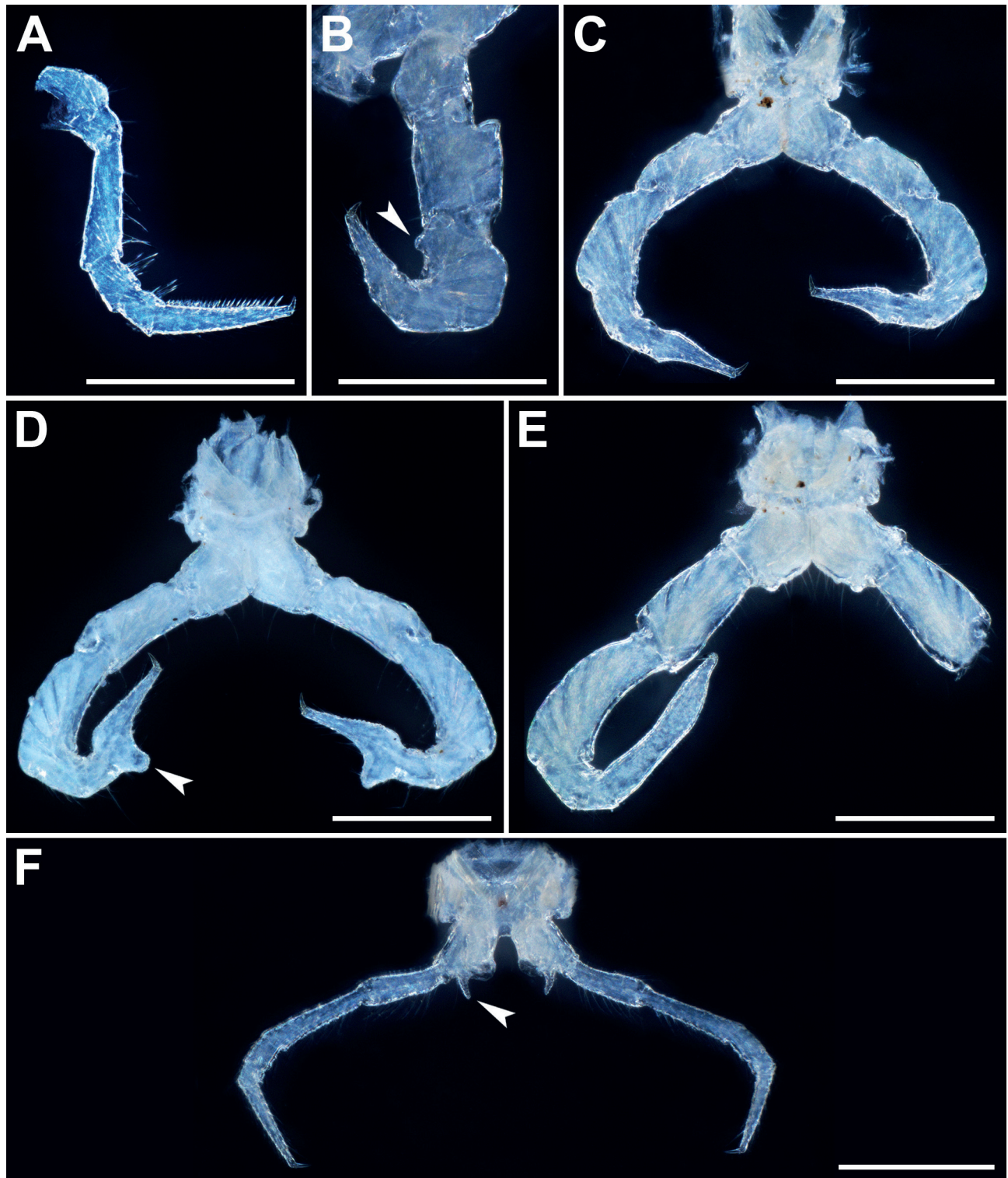


Fig. 3. *Protuberator novaki* gen. nov., sp. nov., holotype male (NHMW-ZOO-MY-10660), legs. **A**, right leg 2, anterior view; **B**, right leg 3, posterior view (white arrow indicates small proximal ventral bulge on femur); **C**, leg-pair 5, anterior view; **D**, leg-pair 6, anterior view (white arrow indicates proximal dorsal bulge on tarsus); **E**, leg-pair 7, posterior view; **F**, leg-pair 10, posterior view (white arrow indicates distal posterior process on coxa). (Scale bars: 0.5 mm).

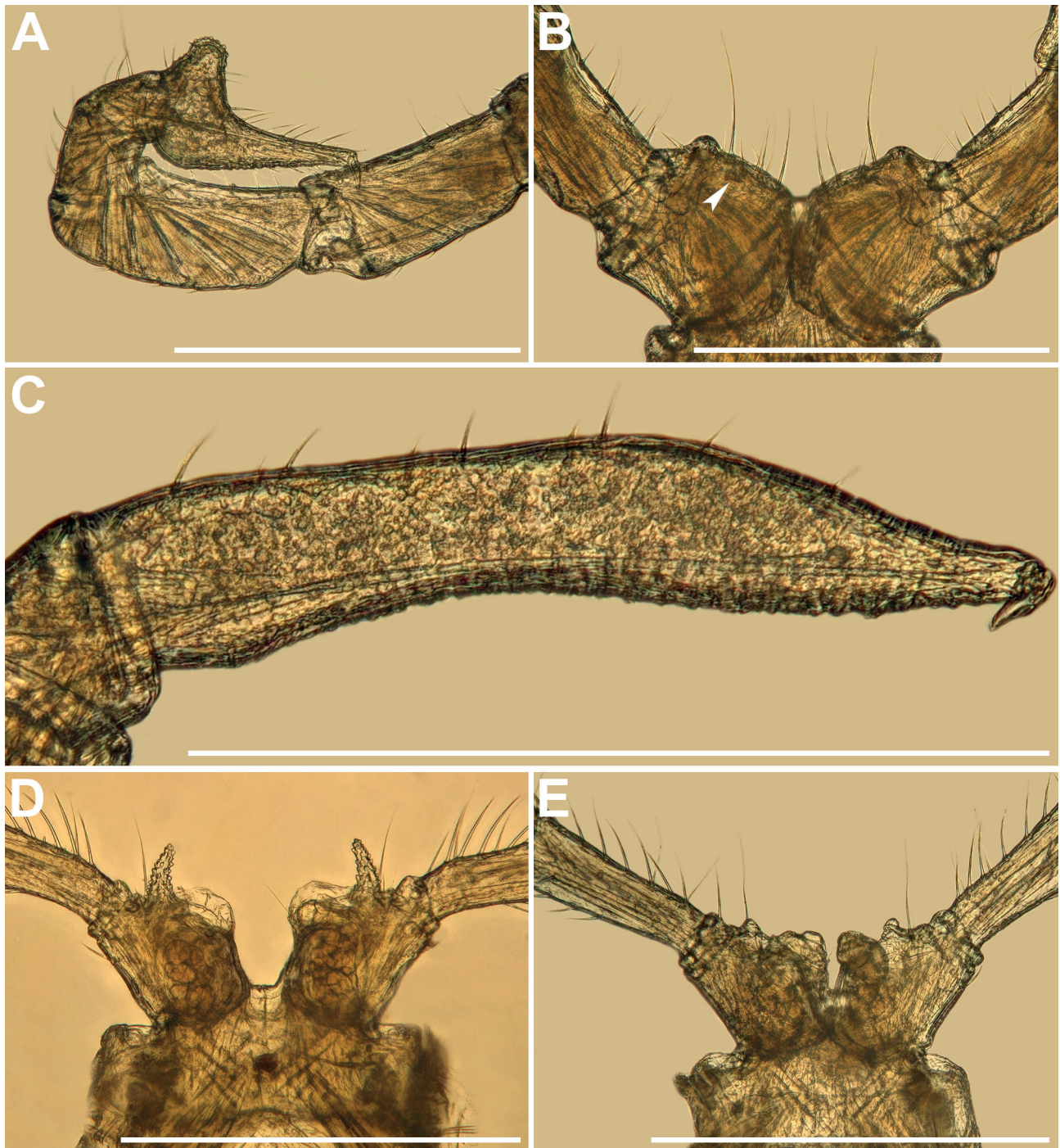


Fig. 4. *Protuberator novaki* gen. nov., sp. nov., holotype male (NHMW-ZOO-MY-10660), legs. **A**, right leg 6, posterior view; **B**, coxae 7, posterior view (white arrow indicates small posterior triangular tooth); **C**, right tarsus 7, posterior view; **D**, coxae 10, posterior view; **E**, coxae 11, posterior view. (Scale bars: 0.5 mm).

Male sexual characters. Gonopores opening mesally on coxae 2. Leg-pairs 3–7 strongly enlarged and modified (Fig. 1). Leg-pair 3 stout, prefemora and femora thick, prefemora with a proximal dorsal protrusion, femora with a small proximal ventral bulge on posterior side (Fig. 3B). Leg-

pair 4 with thick prefemora and femora, prefemora with a proximal dorsal protrusion. Leg-pair 5 with robust femora and a faint proximal dorsal bulge on tarsi (Fig. 3C). Leg-pair 6 with strongly developed femora and with peculiar tarsi a with well-developed proximal dorsal bulge covered

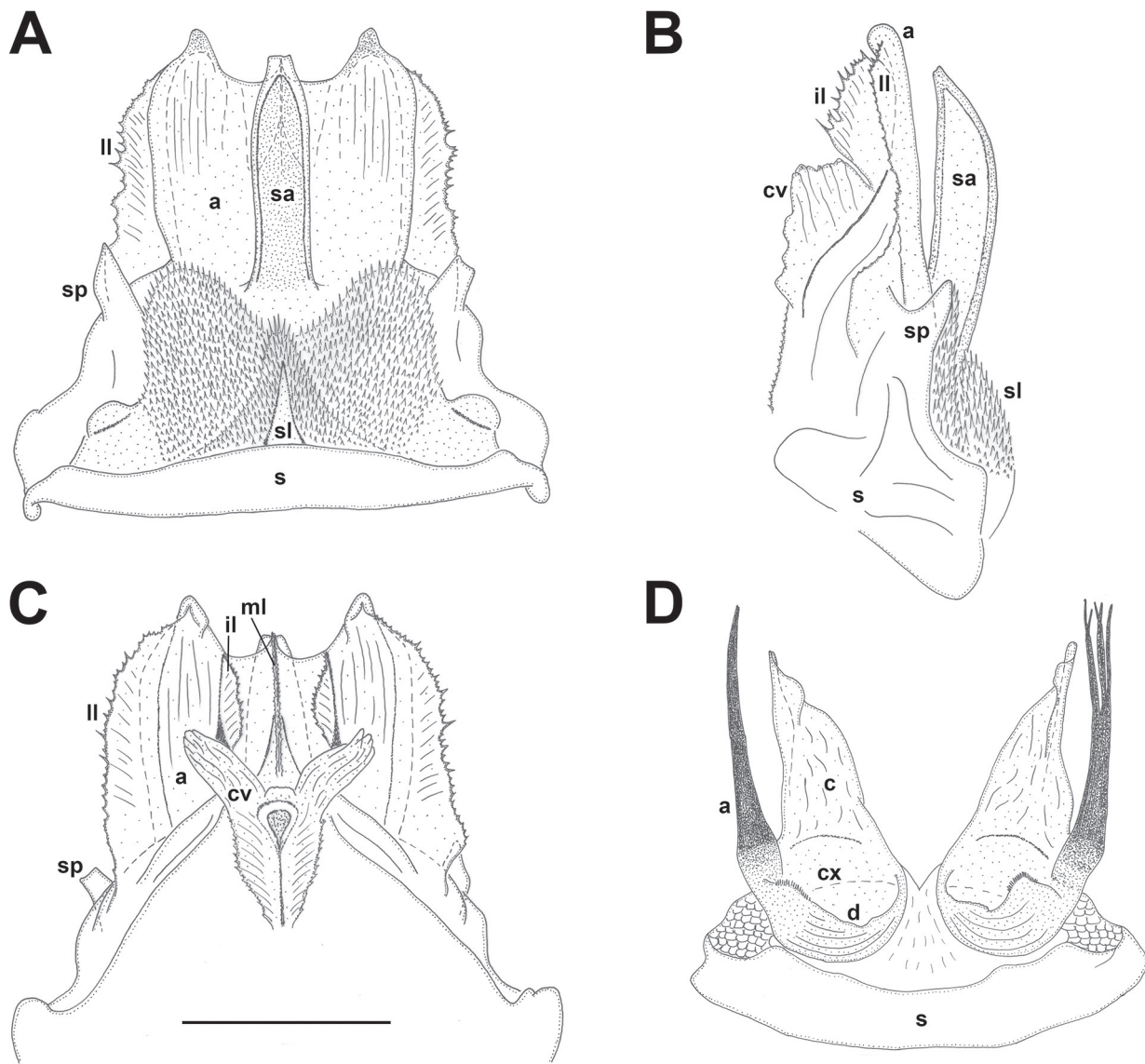


Fig. 5. *Protuberator novaki* gen. nov., sp. nov., holotype male (NHMW-ZOO-MY-10660), gonopods. A–C, anterior gonopods in anterior, lateral and posterior view respectively; D, posterior gonopods, anterior view. Abbreviations: a: angiocoxite; c: colpocoxite; cv: coxal vesicle; cx: coxite; d: anterior depression; il: intermediate lamella; ll: lateral lamella; ml: mesal lamellae; s: sternum; sa: synangiocoxite; sl: sternal lamella; sp: sternal process. (Scale bars: 0.2 mm).

by nipples and ventral side also covered by nipples (Figs 3C, 4A). Leg-pair 7 the most robust, coxae with a small, posterior, triangular, denticulate process, anteriorly with a small ventral distal bulge; prefemora with distal ventral bulge; tarsi elongate, ventral side flattened with small nipples (Figs 3E, 4B, C). Leg-pair 10 with coxal glands and distal posterior coxal processes with small denticles (Figs 3F, 4D). Leg-pair 11 with coxal glands and small distal posterior process on coxae. Leg-pairs 12 and 13 with rounded, distal bulge on coxae, more pronounced on leg-pair 12. Legs normal from leg-pair 14 onwards.

Anterior gonopods (Fig. 5A–C). Sternum (s) strongly developed, with a well-developed, fimbriate, trilobed sternal lamella (sl) on anterior side, lateral lobes higher than the medial one; a pair of anterolateral, subtriangular, sternal processes (sp) present. Angiocoxites (a) shieldlike, with thin fringed lateral lamellae (ll); medially, angiocoxites nearly fused, forming posteriorly a pair of mesal lamellae (ml); distally, shield narrowing in the form of a rounded tip; posteriorly, both angiocoxites with intermediate lamella (il). Anteriorly, strongly developed, bottle-shaped synangiocoxite (sa) presenting with narrowing distal part (broken). Coxal

vesicles (cv) well-developed, wing-like, proximal parts narrowing with fringed lateral margins.

Posterior gonopods (Fig. 5D). With developed sternum (s). Coxites (cx) short, with semicircular anterior ridge with distolateral elevation covered by minute setae. A semicircular anterior ridge borders the anterior depression (d). Angiocoxites (a) lateral in position, consisting of five flagelliform processes, slightly curved posteriad. Colpocoxites (c) arise from posterior side of the coxital depression, weakly sclerotized, lamellar, more or less subtriangular, with an anterodistal fold; shorter than angiocoxites. No traces of telopodites.

DISCUSSION

Antić and Makarov (2016) established eight complexes of genera, in which they classified all Caucasian Anthroleucosomatidae. The new genus can be provisionally placed within the *Herculina* complex. According to Antić and Makarov (2016), this complex includes only the genus *Herculina* Antić & Makarov, 2016, with two species, which is diagnosed by "...the presence of a very robust and bizarre male leg-pair 6, and by the presence of numerous arrow-like filaments on the coxites of the posterior gonopods". In addition, both *Herculina* species have a robust leg-pair 5. In the new genus, leg-pairs 5 and 6 are not as robust as in *Herculina*, but they do have somewhat enlarged femora. The second diagnostic character of the *Herculina* complex in the posterior gonopods is the presence of angiocoxites in the form of numerous flagelliform processes. The same is true for the new genus, which has angiocoxites in the form of five flagelliform structures. In addition, the colpocoxites are very similar in both *Herculina* and the new genus. While both *Herculina* species have small telopodites on the posterior gonopods, these are absent in the only representative of *Protuberator* gen. nov. It is noteworthy to mention that the telopodites are also absent from the posterior gonopods of the Caucasian monospecific genus *Ratcheuma* Golovatch, 1985 (Golovatch 1985; Antić and Makarov 2017). More generally, with the exception of these two Caucasian genera, within the family Anthroleucosomatidae, the absence of telopodites on the posterior gonopods also characterizes the Balkan representatives of the *Bulgarosoma* complex and four species of the genus *Anamastigona* Silvestri, 1898, as well as the North American species *Leschius mcallisteri* Shear & Leonard, 2004 (Shear and Leonard 2004; Antić 2017). The absence of telopodites on the gonopods of Diplopoda is a derived (apomorphic) character state; therefore, the new genus belongs to those genera within Anthroleucosomatidae that possess derived posterior gonopods. Furthermore, when comparing the new genus with *Herculina*, the structure of the anterior gonopods should also be considered. Both genera share a similar configuration of their angiocoxal shields, which bear three

types of lamellae: lateral, intermediate, and mesal. In *Herculina oligosagittae* Antić & Makarov, 2016, the lateral lamellae are bent posteriorly, whereas in *Herculina polysagittae* Antić & Makarov, 2016, and in the new genus, they are directed laterad. Both genera also have very similar structures in the distal portion of the angiocoxal shields and possess a pair of coxal vesicles posteriorly. However, the new genus clearly differs from *Herculina* in having a strongly developed, trilobate sternal lamella and a pair of anterolateral sternal processes, and by the presence of a strongly developed synangiocoxite. Among the Anthroleucosomatidae, a synangiocoxite in the form of an anterior medial process between the angiocoxal shields is also present in the monospecific Caucasian genus *Brachychaetosoma* Antić & Makarov, 2016, belonging to the *Caucaseuma* complex (Antić and Makarov 2017: 27, fig. 17A–C). However, the two genera differ markedly in numerous external and gonopodal characters. Finally, it should be noted that *Protuberator* gen. nov. and both species of the genus *Herculina* are geographically close and inhabit forest habitats in the Lesser Caucasus in Georgia.

As mentioned above, the new genus is characterized by a strongly modified male head. A modified male head is common among chordeumatidans, and is mainly reflected by the fact that males have either a flattened or slightly concave anterior part of the head, whereas in females the head is normal and slightly convex. However, the presence of a more or less pronounced anterior bulge on the head appears to be very rare among Chordeumatida. To our knowledge, a bulge on the male head characterizes some representatives of the family Anthroleucosomatidae. Among Caucasian anthroleucosomatids, apart from the new genus, the only taxon with an anterior bulge on the male head is the monospecific genus *Adshardicus* Golowatch, 1981 (see Antić and Makarov 2016: 20, fig. 10B, C). An anterior bulge is also present in some Balkan anthroleucosomatids. It is most pronounced in *Bulgarosoma bureschi* Verhoeff, 1926 (Strasser 1962: 450, fig. 17; personal observation) and *Banatosoma ocellatum* (Tabacaru, 1967; personal observation); whereas a much smaller bulge can be seen, for example, in males of three *Serbosoma* species (Ćurčić and Makarov 2000; personal observation). The examples discussed above refer to head modifications characteristic only of males. However, there is also a case of a head modification that occurs in both sexes: the North American troglobitic cleidogonid *Pseudotremia peponocranium* Shear, 2011. Adults of both sexes exhibit a large, square bulge on the head, which is smaller in females (see Shear 2011: 15, figs. 34–35). The new genus represents the most striking example of head modification known among anthroleucosomatids. Unfortunately, in the absence of collected females, it remains uncertain whether this modification is restricted to males.

It should be noted that male head modifications also

occur in the orders Callipodida and Polydesmida. Among Callipodida, this is particularly characteristic of the genus *Paracortina* Wang & Zhang, 1993 (Akkari et al. 2023), with perhaps the most bizarre example found in the Vietnamese troglomorphic species *Paracortina kyran* Nguyen, Stoev, Nguyen & Vu, 2023 (see Nguyen et al. 2023: 185, fig. 2B). Among Polydesmida, head modifications are observed in some Afro-tropical Pyrgodesmidae and Trichopolydesmidae, occurring either only in males or in both sexes (Golovatch 2018; Golovatch et al. 2018, 2019).

The function of the modified head in males remains unknown. In addition to head modifications, it is worth noting the presence of modifications of the pregonopodal legs in male Chordeumatida and Callipodida. These legs, which are often greatly thickened and bearing various extensions, are assumed to play an important role during mating by providing firmer stabilization of the female. It is possible that the modified heads of males serve a similar function, contributing to the stabilization of the female during copulation. However, such modifications are apparently rare, and are not genus-specific: occurring independently in several lineages. Furthermore, the presence of similar head modifications in both sexes of *Pseudotremia peponocranium* raises additional questions. If head modifications function in mating together with the pregonopodal legs, why do they occur in both sexes in this species, and why are they absent in other species that evidently achieve successful mating with “only” the modified pregonopodal legs of males? It is remarkable that, although these head and pregonopodal leg modifications are both conspicuous and well-documented, their functional significance remains uncertain.

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