



## The millipede tribe Leptoiulini in the Caucasus, with notes on its generic classification (Diplopoda: Julida: Julidae)

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### Abstract

The generic classification of the Palaearctic tribe Leptoiulini is revised, with 11 genera being recognized. The main differences between the genera, all presented in a tabular form, lie in the structure of the 2<sup>nd</sup> and 7<sup>th</sup> leg-pairs of the male, coupled with gonopodal conformations: the presence/absence and the degree of development of flagella on the promeres, and of the phylacum and velum on the opisthomeres. Based on abundant new material, only three genera and seven species of Leptoiulini, all keyed, mapped and properly illustrated, are shown to occur in the Caucasus: *Chatoleptophyllum flexum* Golovatch, 1979, *Kubaniulus gracilis* Lohmander, 1936, *K. lativelatus* **sp. nov.**, *Leptoiulus hastatus* Lohmander, 1932 (= *L. disparatus* Lohmander, 1936, **syn. n.**), *L. tanymorphus* (Attems, 1901), *L. meskhii* **sp. nov.**, and *L. gonopodialis* **sp. nov.** All species are endemic or subendemic to the region, while *Kubaniulus* Lohmander, 1936 represents the only genus in the tribe which is restricted to the Caucasus, in particular, the western and central parts of the Caucasus Major. The distributions are mainly allopatric, but a few pairs of species are para- or even sympatric.

**Key words:** generic reclassification, faunistics, Caucasus Major, Caucasus Minor, new species, key, distribution patterns

### Introduction

The Palaearctic millipede tribe Leptoiulini Lohmander, 1936, family Julidae, was first distinguished by Lohmander (1936) as the subfamily Leptoiulinae, downgraded to the tribal status by Hoffman (1980) who assigned the following genera to this tribe:

*Allopodoiulus* Verhoeff, 1898. Two European species.

*Hypsoiulus* Verhoeff, 1913. One species in the Central Alps.

*Kubaniulus* Lohmander, 1936. Monotypic, Caucasus.

*Leptoiulus* Verhoeff, 1894. Nine subgenera with numerous described and still undescribed species from Europe, the Caucasus and Siberia.

*Macedoiulus* Verhoeff, 1932. One species from the Republic of North Macedonia.

*Ophiulus* Berlese, 1884. Two European subgenera with 26 described and few undescribed species.

*Pachypodoiulus* Verhoeff, 1897. One species with two subspecies in the Alps.

*Peltopodoiulus* Lohmander, 1933. Monotypic, Central Asia.

*Xestoiulus* Verhoeff, 1893. Four subgenera with 12 described species.

Questions regarding the monophyly and generic composition of the Leptoiulini have repeatedly been raised since (Enghoff *et al.* 2011, 2013), but they still remain far from settled.

Morphological evidence for the isolation of this taxon has been presented by Read (1990) who highlighted several apomorphies: (1) ozopores located behind the suture dividing pro- and metazonae; (2) a free mesomere on the gonopod; (3) presence of a paracoxal process on the opisthomere; (4) concealed gonopods. However, some of these apomorphies are shared with the Julini and the Typhloiulini as well (Read 1990; Enghoff *et al.* 2011, 2013). A few other morphological characteristics of the Leptoiulini can be added: (1) male genae unmodified; (2) the first leg-pair of the male is reduced, usually unciform, with a field of papillae in the apical part of the telopodite and strong basal setae; (3) collum and body rings with whorls of setae at the caudal margin; (4) a well-developed caudal projection on the telson (= epiproct); (5) anal valves densely setose; (6) mesomere straight or only slightly curved, adjacent to the promere, with small papillae and/or scales in the apical and/or anterior part; (7) promere spoon-shaped, with small papillae in the distal part. Most of these characteristics are likewise shared with the Julini and the Typhloiulini (Read 1990; Enghoff *et al.* 2011, 2013).

The generic composition of the Leptoiulini still remains rather vague. Apparently, some genera of, if not the entire tribe, Typhloiulini could well be classified within Leptoiulini (Mauriès *et al.* 1997). A cladistic analysis of julid millipedes based on morphological evidence alone showed that the tribes Leptoiulini, Typhloiulini and Julini represent one clade and a monophyletic group (Read 1990).

Molecular data (Enghoff *et al.* 2011, 2013) demonstrate that species of the genera *Leptoiulus*, *Pacifiulus* Mikhaljova, 1982, *Ophiulus* and *Julus* Linnaeus, 1758 form one monophyletic clade, in contrast to the Typhloiulini which remains a separate lineage. Another molecular analysis (Spelda *et al.* 2011) stated the same for the genera *Leptoiulus*, *Hypsoiulus*, *Ophiulus* and *Julus*. Semiochemistry, i.e. the chemical composition of defensive secretions (Makarov *et al.* 2017), also groups the genera *Leptoiulus*, *Ophiulus*, *Xestoiulus*, *Pacifiulus* and *Julus* into one clade. These morphological, molecular and chemical analyses are still too incomplete to provide an unambiguous view of the phylogenetic relationships and generic composition of the tribe Leptoiulini. As a result, the classical work of Hoffman (1980), albeit with some changes, remains the one we basically follow here.

Contrary to Hoffman (1980) and based on overlooked or more recent publications, we add the following four genera therein to the Leptoiulini:

*Chaetoleptophyllum* Verhoeff, 1898. One species each in Europe and the Caucasus.

*Chaetoleptophyllum* was first described as a subgenus of *Leptophyllum* Verhoeff, 1894 (at present, *Enantiulus* Attems, 1894), but later transferred to Leptoiulini (Read 1990).

*Interleptoiulus* Mršić, 1988. Monotypic, Montenegro.

The attribution to Leptoiulini was established by its author (Mršić 1988).

*Pacifiulus* Mikhaljova, 1982. Monotypic, Siberia, the Russian Far East and northeastern China.

The morphological characteristics of the genus correspond to those of Leptoiulini, also supported by molecular and semiochemical data (Enghoff *et al.* 2011, Makarov *et al.* 2017). The recent assignment to the tribe Julini (Evsyukov *et al.* 2018) is thus to be reconsidered.

*Sibiriulus* Gulička, 1963. Seven species in Siberia and eastern Kazakhstan.

Originally described as a subgenus of *Cylindroiulus* Verhoeff, 1894. Lokšina and Golovatch (1979) elevated it to a full genus. Read (1990) removed *Sibiriulus* from the tribe Cylindroiulini and suggested that it belonged to the tribe Leptoiulini, based solely on morphological evidence.

Contrary to Hoffman (1980), we exclude the following two genera from the tribe Leptoiulini based on more recent publications and data:

*Pachypodoiulus*. Species with the first leg-pair of the male represented by one setose podomere, a condition typical of *Julus*. Only one of the molecular analyses groups this genus with *Cylindroiulus* (Spelda *et al.* 2011). Thus, both morphological and molecular data allow us to exclude this genus from the tribe Leptoiulini.

*Macedoiulus* is not anymore an independent member of Leptoiulini, because *M. storkani* Verhoeff, 1932 is a junior synonym of *Leptoiulus sarajevensis* Verhoeff, 1898 (Mauriès *et al.* 1997).

**TABLE 1.** The main differences between the genera of the tribe Leptoilini, based on male characters

Genus	Gnathochilarium	1 <sup>st</sup> leg-pair	2 <sup>nd</sup> leg-pair	7 <sup>th</sup> leg-pair	Flagellum	Velum	Phylacum	Height ratios of gonopod parts
<i>Altopodoiulus</i>	without modifications	reduced and unciiform	with a coxal process	with a coxal process	well-developed	small, curved, with spines	broadly rounded at tip	solenomere highest; phylacum higher than promere and mesomere; promere higher than mesomere
<i>Chaetoleptophylum</i>	without modifications	reduced and unciiform	without process	without process	absent	lamelliform, not detached from solenomere	absent	velum higher than promere, mesomere and solenomere; solenomere higher than promere; promere higher than mesomere
<i>Hypsoiulus</i>	without modifications	reduced and unciiform	with a coxal process	without process	absent	a dentiform process	small, elongated, rounded at apex	solenomere very broad and highest; phylacum(?) as high as solenomere; all parts of opisthomere higher than promere; promere higher than mesomere
<i>Interleptoiulus</i>	without modifications	reduced and unciiform	without process	without process	well-developed	small, acuminate	relatively large, separated from solenomere by a "large bay"	solenomere, phylacum and mesomere about as high as or higher than velum and promere; promere lower than other parts
<i>Kubanulus</i>	without modifications	reduced and unciiform	without process	without process	absent	relatively large, spinulate	absent	solenomere higher than promere and mesomere; velum higher or lower than solenomere; mesomere lower than promere; promere and velum same in height
<i>Leptoilulus</i>	without modifications	reduced and unciiform	usually without process, occasionally with a small coxal process	without process	developed to varying degrees, but usually present	more or less strongly developed	more or less strongly developed	solenomere usually highest; phylacum and velum developed to varying degrees; promere higher than mesomere
<i>Ophyiulus</i>	stipites strongly swollen distally	reduced and unciiform	with or without process	without process	well-developed	small, finger-shaped	broad	phylacum very broad, higher than or as high as promere; solenomere lower than phylacum; velum lower than solenomere and phylacum; promere higher than mesomere
<i>Pacificiulus</i>	without modifications	reduced and unciiform	without process	without process	well-developed	poorly-developed	small	solenomere highest; promere higher than mesomere, velum and phylacum; velum higher than phylacum

.... Continued next page

TABLE 1. (Continued)

Genus	Gnathochilarium	1 <sup>st</sup> leg-pair	2 <sup>nd</sup> leg-pair	7 <sup>th</sup> leg-pair	Flagellum	Velum	Phylacum	Height ratios of gonopod parts
<i>Peltopodiulus</i>	without modifications	reduced and unciiform, with a coxal process	without process	without process	reduced (very short and small, spiniform)	not detached from solenomere, with small spike at apex	small and rounded	solenomere highest; velum slightly higher than phylacum and both higher than promere; promere higher than mesomere
<i>Sibirius</i>	without modifications	reduced and unciiform	without process	without process	well-developed	small, tip pointed	either thin and short or absent	solenomere highest; velum and phylacum developed to varying degrees; mesomere higher than promere
<i>Xestoiulus</i>	without modifications	reduced and unciiform	without coxal process	without coxal process	well-developed	more or less strongly developed	more or less strongly developed	solenomere usually highest; phylacum and velum developed to varying degrees; promere higher than mesomere

Bearing the above considerations in mind, the tribe Leptoilulini presently comprises 11 genera: *Allopodoiulus*, *Chaetoleptophyllum*, *Hypsoiulus*, *Interleptoiulus*, *Kubaniulus*, *Leptoiulus*, *Ophiulus*, *Pacifiulus*, *Peltopodoiulus*, *Sibiriulus* and *Xestoiulus*. The main differences between those genera lie in the structure of the 2<sup>nd</sup> and 7<sup>th</sup> leg-pairs of the male, coupled with gonopodal conformations: the presence/absence and the degree of development of flagella on the promeres, and of the phylacum and velum on the opisthomeres. The generic characteristics are presented in Table 1. These are based on the traits observed in the type, several or all species (for small and monotypic genera) of the respective accepted genera.

*Leptoiulus* alone contains as many as nine subgenera, either listed as such (Hoffman 1980) or fully neglected as junior synonyms (Kime and Enghoff 2017, [https://fauna-eu.org/cdm\\_dataportal/taxon/39fc5b83-ad00-4ad1-bbbd-32ef295bd36b](https://fauna-eu.org/cdm_dataportal/taxon/39fc5b83-ad00-4ad1-bbbd-32ef295bd36b)). With this work we will not be able to solve the relationship and the eligibility of these subgenera in *Leptoiulus* and disregard them here.

Species of only three genera of Leptoilulini are found in the Caucasus: *Kubaniulus*, *Leptoiulus* and *Chaetoleptophyllum*. The genus *Kubaniulus* comprises one endemic species, *K. gracilis* Lohmander, 1936, from the Krasnodar Province (Lohmander 1936). The Palaearctic genus *Leptoiulus* is widespread in Europe and the Caucasus s.l., but marginally it occurs also in southwestern Siberia (Lohmander 1936; Mikhaljova *et al.* 2015; Kime and Enghoff 2017; Nefediev and Nefedieva 2017; Nefediev 2018). In the Caucasus, this genus is represented by three described species: *L. tanymorphus* (Attems, 1901), from Lenkoran, Azerbaijan, *L. hastatus* Lohmander, 1932, from Armenia, and *L. disparatus* Lohmander, 1936 (**syn. n.** = *L. hastatus*), from Georgia. The genus *Chaetoleptophyllum* contains one species in the Caucasus: *C. flexum* Golovatch, 1979, from Georgia, Caucasus.

The present paper provides a review of the tribe Leptoilulini in the entire Caucasus region, based on abundant new material. Two new species of *Leptoiulus* and one new species of *Kubaniulus* are described.

## Material and methods

Most of the material has been shared between the collections of the Zoological Museum of the Moscow State University (ZMUM), the private collection of the first author (AE), both Russia, the Senckenberg Museum of Natural History in Görlitz, Germany (SMNG) and the Institute of Zoology, University of Belgrade, Serbia (IZB). The specimens are stored in 70–75% ethanol. Some parts of males (antennae, gonopods, legs etc.) and females (vulva and leg-pair 2) were dissected and mounted in temporary (glycerol) or permanent microscopic slides (Canada balsam, Eukitt, Euparal). Photographs were taken using a Lomo MSP microscope and a Sony A camera. Line drawings were executed using a camera lucida attached to the same light-transmission scope. SEM micrographs were taken using a JEOL JSM-6480LV (Royal Museum for Central Africa, Tervuren, Belgium), a Zeiss CrossBeam 340 (Rostov-on-Don State Technical University, Rostov-on-Don, Russia) and JEOL JSM-6510LV (SMNG) scanning electron microscopes. After examination, SEM material was removed from stubs and returned to alcohol, now in ZMUM and SMNG.

The distribution map was created using Google Earth Pro and Adobe Photoshop CS6.

A “body segment formula” indicates the number of podous (including the gonopod-bearing segment) and apodous segments in an individual. This formula is p+a+T where p = number of podous body segments, a = number of apodous body segments, T = telson (Enghoff *et al.* 1993). Only adults have been analyzed in the present study.

Type material of previously described species has not been revised, because the descriptive accounts and illustrations available in the literature are sufficiently complete and clear to allow a safe species identification.

In the catalogue sections, D stands for a description or descriptive notes, R for new or repeated records, while M is a mere mention.

## Taxonomic part

### Genus *Chaetoleptophyllum* Verhoeff, 1898

**Type species:** *Leptophyllum montanum* Verhoeff, 1898

**Diagnosis.** Epiproct long, slightly turned down, densely setose, tip pointed. Promeres slender, without flagella. Velum not detached from solenomere. Phylacum absent (Table 1).

### Species included:

*Chaetoleptophyllum flexum* Golovatch, 1979

*Chaetoleptophyllum montanum* (Verhoeff, 1898)  
(Verhoeff 1898; Golovatch 1979)

### *Chaetoleptophyllum flexum* Golovatch, 1979

**Figs 1A, 2, 3, 4, 5, 41A, Map 1**

*Chaetoleptophyllum flexum* Golovatch, 1979: 340 (D).

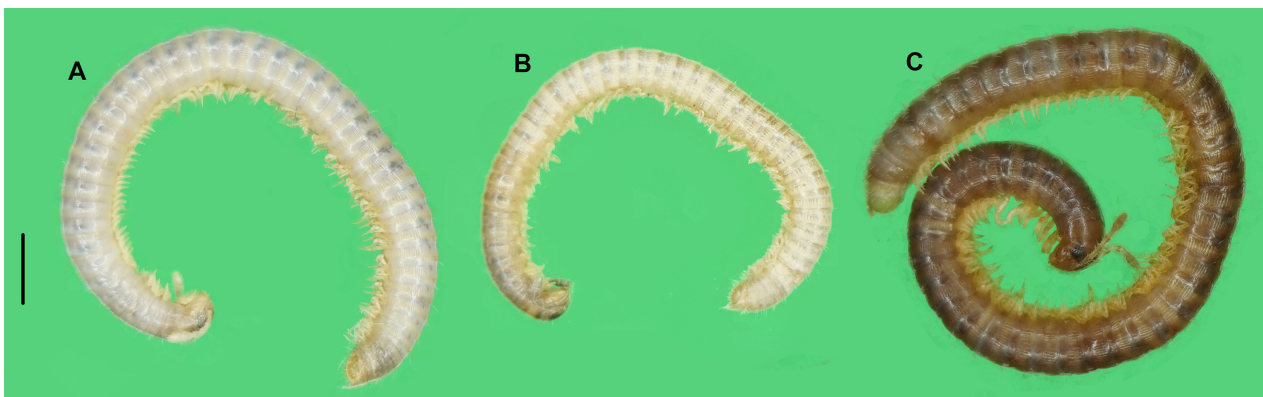
*Chaetoleptophyllum flexum*—Lokšina and Golovatch, 1979: 385 (M); Zuev, 2014: 350 (R); Chumachenko, 2016: 410 (R);  
Kokhia and Golovatch, 2018: 40 (M).

Non: *Chaetoleptophyllum* cf. *flexum*—Korobushkin *et al.*, 2016: 24 (R).

### Material examined.

**Georgia:** 5 males, 32 females (ZMUM), Ajaria, Batumi Botanical Garden, 15–20 m a.s.l., 30.V.–7.VI.1981. 3 females (ZMUM), same locality, forest, litter, 20–150 m a.s.l., 9.X.1981. 1 male, 2 females (ZMUM), Kintrish Nature Reserve, Zeraboseli, 800 m a.s.l., *Rhododendron* thicket, litter, 13.X.1981. 6 males, 17 females (ZMUM), same locality, 450–600 m a.s.l., deciduous forest, litter and under stones, 13.X.1981. 3 males, 9 females (ZMUM), same locality, 450–600 m a.s.l., 1–3.VI.1981, all leg. S. Golovatch and J. Martens. 3 males, 5 females (ZMUM), Khulo, 900 m a.s.l., *Quercus*, *Abies* and *Ulmus* forest, litter, 11.X.1981, leg. S. Golovatch. 3 males, 1 female (ZMUM), Kobuleti, between Kobuleti & Ureki, *Pinus* forest at seashore, sifted litter, 41°55'58"N, 41°45'53"E, 5 m a.s.l., 21.VII.2012. 3 females (ZMUM), Lake Shaori, mixed forest, sifted litter, 42°23'47"N, 43°01'48"E, 1180 m a.s.l., 19.VII.2012, all leg. Y.M. Marusik. 1 juv. male, 1 female, 1 juv. (ZMUM), near Keda, mixed forest, litter, X.1975. 1 female (ZMUM), same locality and date, all leg. A. Druk. 2 males (ZMUM), Svanetia, valley of Khumprer River, near Dizi, 1000 m a.s.l., forest, litter, 9.IX.1986, leg. A. Ryvkin. 2 males, 7 females (ZMUM), ca. 10 km E of Tkibuli, near Mukhura, *Carpinus* and *Fagus* forest and *Buxus* thicket, 42°20'06"N, 43°02'36"E, 1010 m a.s.l., 23.VII.2012, 1 male (ZMUM), same locality and date, all leg. Y. Marusik. 5 males, 9 females (ZMUM), Saguramo Nature Reserve, SE of Mtskheta, Zedazeni, 1100–1200 m a.s.l., *Fagus*, *Carpinus*, *Acer* etc. forest, litter and under bark, 20.V.1987, leg. S. Golovatch and K. Eskov. 1 male, 7 females (ZMUM), Surami Mt. Ridge, Pass Djvari between Gomi and Sachkhere, 850 m a.s.l., *Alnus*, *Fagus*, *Rhododendron* etc. forest, litter, 7.V.1987. 15 males, 12 females, 3 juv. (ZMUM), Algeti Nature Reserve W of Manglisi, *Fagus*, *Picea*, *Acer* etc. forest, 1400–1450 m a.s.l., litter and under bark, 16–18.V.1987. 2 males, 18 females, 4 juv. (ZMUM), Mariamdjvari Nature Reserve, ENE of Sagarejo, 1150–1250 m a.s.l., *Fagus*, *Carpinus*, *Acer*, *Pinus* etc. forest, litter, under bark and stones, 13–14.V.1987. 6 males, 18 females, 3 juv. (ZMUM), Batsaro Nature Reserve ca. 20 km N of Akhmeta, *Fagus* and *Castanea* forest, 800–850 m a.s.l., litter, 5–6.V.1987. 3 males, 10 females (ZMUM), Mukhura ca. 15 km E of Tkibuli, 700–800 m a.s.l., *Castanea*, *Fagus*, *Carpinus* etc. forest, litter, under bark and stones, 7–9.V.1987. 8 females (ZMUM), Kartli Mt. Ridge, Pass Sabaduri, ca 40 km NNE of Tbilisi, 1400 m a.s.l., *Fagus* forest, litter and under bark, 6.V.1987, all leg. S. Golovatch and K. Eskov. 1 male, 1 female (ZMUM), Rike N of Zugdidi, *Alnus* wet forest, litter, 24.IX.1986. 1 male, 5 females (ZMUM), Kutaisi Distr., Sataplia Nature Reserve, forest, litter and under stones, 25.X.1981. 3 females (ZMUM), same locality, forest, 8.VIII.1974. 3 females (ZMUM), NE of Poti, Chaladidi, *Alnus*, *Quercus*, *Fraxinus* forest on swamp, litter, 13.IV.1983, all leg. S. Golovatch. 4 males, 17 females (ZMUM), same locality, 400 m a.s.l., *Fagus* forest, 5.VI.1981, 1 male (ZMUM), same locality and date, all leg. S. Golovatch and J. Martens. 2 males, 6 females, 4 juv. (ZMUM), Racha, 10 km NE of Shovi, Gurshevi, near Mamisoni Pass, 2000–2200 m a.s.l., *Abies*, *Fagus*, *Ulmus* forest, litter and under stones, at a spring, 21.X.1981. 9 males, 21 females, 3 juv. (ZMUM), Borzhomi Distr., 8 km SE of Akhaldaba, Nedzura River valley, 1000 m a.s.l., *Picea*, *Carpinus* and *Fagus* forest, litter, logs, 12.V.1983. 6 males, 13 females (ZMUM), Svanetia, Mestia, ca. 1500 m a.s.l., *Betula* and *Rhododendron* on moraine, litter and under stones, 5 and 16.IX.1986. 8 males, 23 females (ZMUM), 40 km W of Mestia, Kherkhvashi

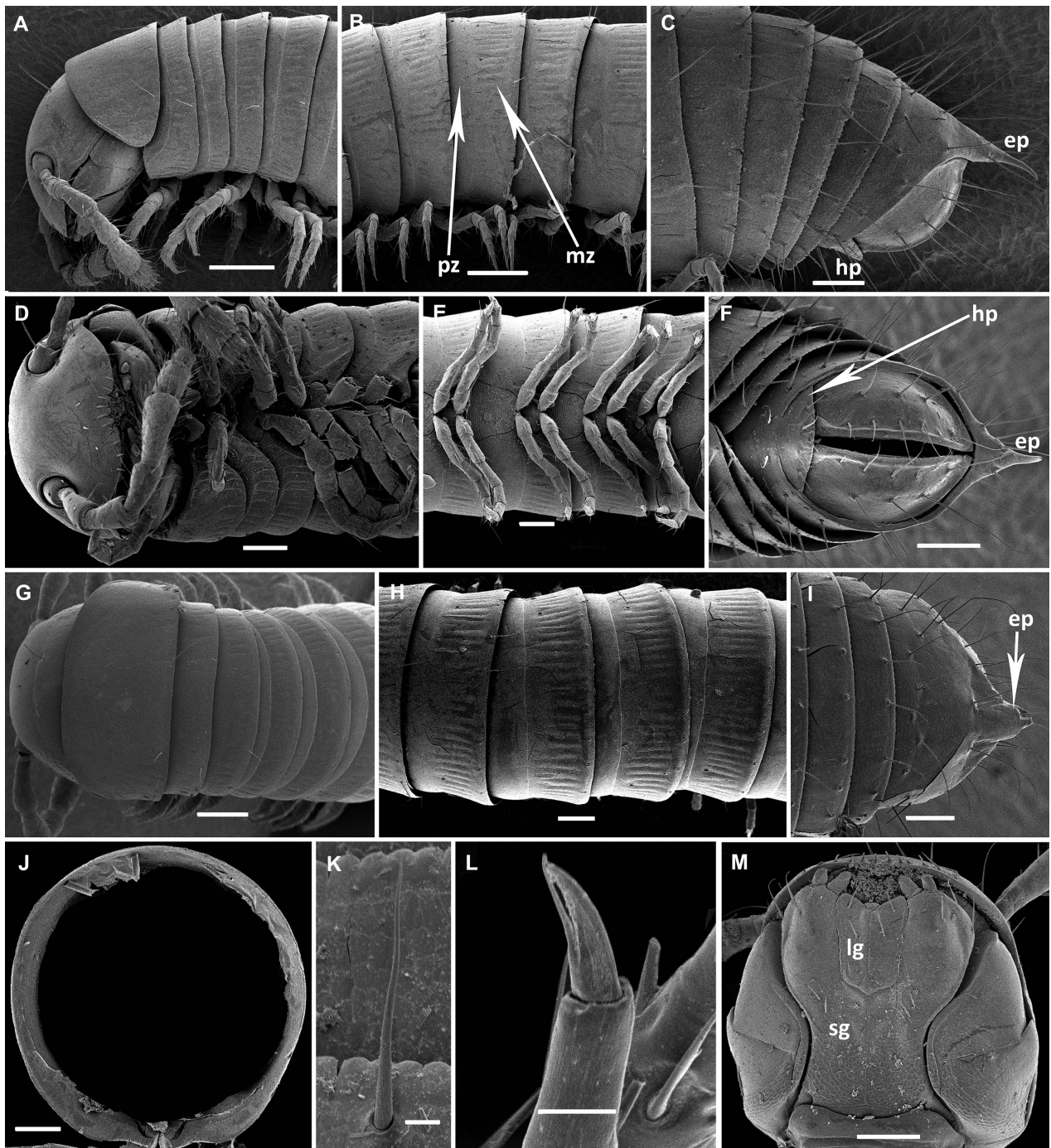
E of Nakra (= Naki), 1250-1700 m a.s.l., *Quercus*, *Fagus*, *Carpinus*, *Picea*, *Abies* etc. forest, litter and under bark, 21.VIII-21.IX.1986. 3 males, 9 females, 1 juv. (ZMUM), S of Gudauri near Krestovyi Pass, 1800 m a.s.l., *Rhododendron* bush, litter, 4.VI.1982. 4 males, 12 females (ZMUM), Surami (= Rikoti) Pass, ca. 1000 m a.s.l., *Fagus*, *Alnus*, *Castanea*, *Rhododendron* forest, litter and under stones, 14.IV and 17.V.1983. 1 male, 2 females (ZMUM), Racha, Oni Distr., Shovi, *Fagus*, *Ulmus* and *Abies*, litter and under stones, at a spring, 21.X.1981. 3 females (ZMUM), Racha, 10 km NE of Shovi, 2000-2200 m a.s.l., Gurshevi, near Pass Mamisoni, *Abies*, *Fagus*, *Ulmus* forest, litter and under stones, at a spring, 21.X.1981. 7 males, 21 females, 1 juv. (ZMUM), Tbilisi, bank of Lake Cherepashye, bush, litter, 18.X.1981. 12 females (ZMUM), 15 km W of Adigeni, *Abies*, *Picea*, *Fagus*, *Acer* etc. forest, 1500-1700 m a.s.l., litter, logs, under stones, 14-15.V.1983. 2 males, 1 female, 1 juv. (ZMUM), Khulo Distr., 3 km W of Danisparauli, deciduous forest, litter, 10.X.1981, all leg. S. Golovatch. 1 male (ZMUM), near Manglisi, *Quercus* forest, 12.XI.1984, leg. E. Kvavadze. 1 male, 3 females, 1 juv. (ZMUM), Mingrelsky (= Egrissky) Mt. Ridge, NW slope of Mount Tsekhuri, 1500-1800 m a.s.l., *Fagus* forest, litter, 18-19.VIII.1988, leg. I. Belousov. 1 female (ZMUM), Lagodekhi, *Quercus* and *Carpinus* in ravine, XI.1967, leg. T. Perel. 3 females (SMNG), Mingrelia and Upper Svanetia, Mestia, Tal Ri Glacier, *Abies* and *Fagus* forest, on slope, litter, 43.1118°N, 42.7453°E, 09.VI.2019. 1 male (SMNG), Samegrelo-Zemo Svaneti, Nikortsminda, at karst river exit, deciduous forest, litter and under stones, 42.4705°N, 43.0678°E, 14.VI.2019, all leg. H.S. Reip.



**FIGURE 1.** Habitus pictures of some species of Leptoilulini from the Caucasus, lateral views. **A:** *Chaetoleptophyllum flexum* Golovatch, 1979, male from Khulo, Georgia. **B:** *Kubaniulus gracilis* Lohmander, 1936, male from near Gelenjik, Krasnodar Prov. **C:** *Kubaniulus lativelatus* sp. nov., male paratype from Pasture Abago, Krasnodar Prov. Scale bar: 1 mm.



**MAP 1.** Distribution of some Leptoilulini species in the Caucasus: *Chaetoleptophyllum flexum* Golovatch, 1979 (red square); *Kubaniulus gracilis* Lohmander, 1936 (green triangle); *Kubaniulus lativelatus* sp. nov. (yellow star).

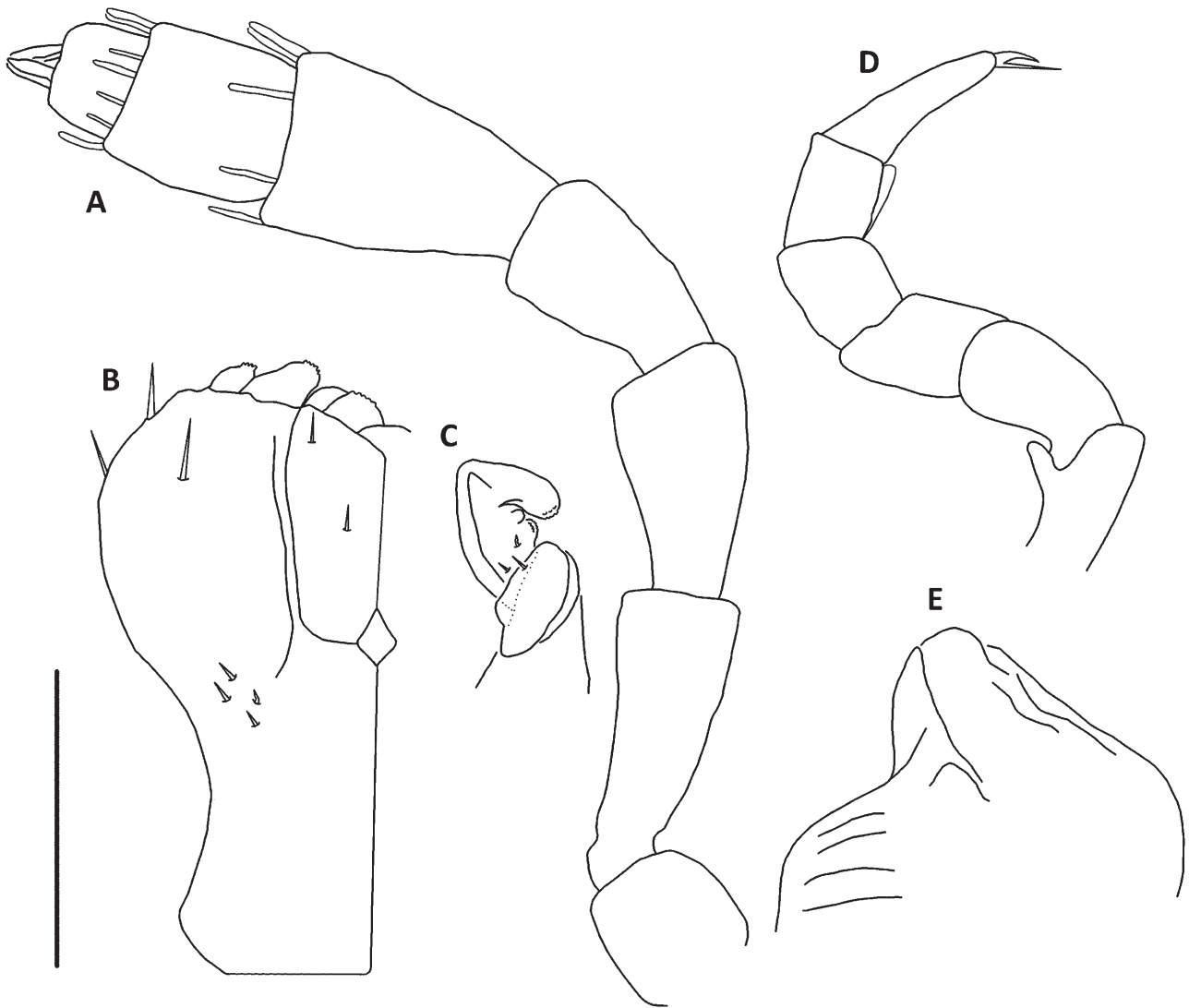


**FIGURE 2.** *Chaetoleptophyllum flexum* Golovatch, 1979, male from Sataplia Nature Reserve, Georgia. **A–C:** anterior, middle and posterior parts of body, respectively, lateral views. **D–F:** same, respectively, ventral views. **G–I:** same, respectively, dorsal views. **J:** midbody ring, frontal view. **K:** seta and limbus on a midbody ring, dorsal view. **L:** claw on leg 2, lateral view. **M:** head, ventral view. **Abbreviations:** ep, epiproct; hp, hypoproct; lg, lamella lingualis of gnathochilarium; mz, metazona; pz, prozona; sg, stipes of gnathochilarium. Scale bars: 0.2 mm (A, B, G), 0.1 mm (C–F, H–J, M) or 0.01 mm (K, L).

**Abkhazia:** 2 males (ZMUM), Sukhumi Distr., Yashtukha, *Nicotiana* plantation, 26.V.–19.VI.1981, leg. A. Markossian. 1 male, 3 females (ZMUM), Bzyb River valley, Pskhu, 700–950 m a.s.l., *Fagus*, *Quercus*, *Castanea* etc. forest, litter, under bark and stones, 15–16.VIII.1986. 1 female (ZMUM), near Lake Ritsa, mixed forest, litter, 24.X.1978, all leg. S. Golovatch. 4 males, 2 females (ZMUM), same locality, *Pinus*, *Abies*, *Polygonatum*, 12.IX.1985, leg. I. Ushakov.

**South Ossetia:** 2 males, 2 females (ZMUM), Lower Roki, S of Roksky Pass, 1500 m a.s.l., *Fagus*, *Betula* etc. forest on rock, 17.X.1987, leg. S. Golovatch.





**FIGURE 3.** *Chaetoleptophyllum flexum* Golovatch, 1979, male from near Tkibuli, Georgia. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.

**Diagnosis.** See diagnosis of genus, based also on non-regional congeners.

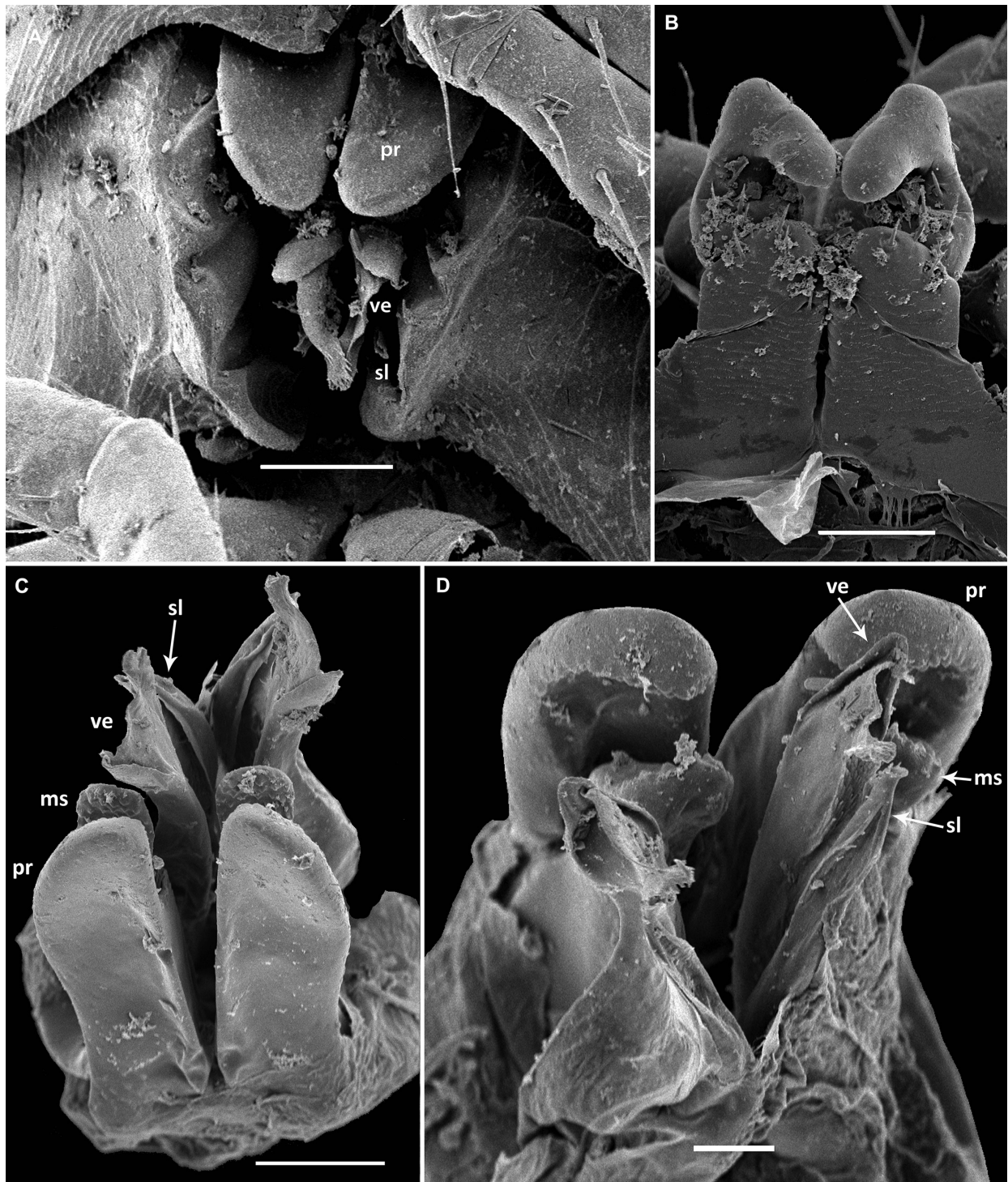
**Descriptive notes.** Length of adults 10–15 mm, width 0.5–0.9 mm. Number of segments in adults from 39+3+T to 57+2+T. Body cylindrical (Fig. 2J), marbled brownish grey, head and collum brown, legs and antennae yellow (Fig. 1A). Eye patches oval, composed of 20–25 ommatidia. Striations of metazonae relatively deep, striae not reaching the caudal margin (Fig. 2A, B, G, H). Collum and metazonae with a row of setae at posterior margin (Fig. 2A, B, C, G, H, K).

Antennae relatively long, *in situ* reaching segment 4; a complete corolla of long bacilliform sensilla on antennomeres 5 and 6; sparser and shorter on 6<sup>th</sup> (Figs 2A, D, 3A). Head with 5+5–6+6 labral setae, 2+2 supralabral setae, and 1+1–2+2 at base of antennae (Fig. 2D). Gnathochilarium with two setae on each lamella lingualis and groups of 2–4 short setae on stipites (Figs 2M, 3B). Epiproct subtriangular, slightly turned down (Fig. 2F, I). Hypoproct triangular, with smooth edges and 2+2 setae (Fig. 2F).

**MALE.** Leg-pair 1 small, unciform; coxa with a group of small setae, telopodite with a field of papillae in apical part (Figs 3C, 4B). Male leg-pair 2 without modifications, each with a pad on tibia; an accessory claw slightly longer than claw itself (Figs 2L, 3D). Penes short, bifurcated on top.

All three parts of gonopods (Figs 4C, D, 5A, D) forming a tight block. Promere (**pr**) elongated, spoon-shaped, papillate distomesally (Figs 4C, D, 5A, B, D). Flagella absent. Mesomere (**ms**) simple, lower/shorter than promere, its apical and anterior parts with a field of papillae (Figs 4C, 5A, C, D). Velum of opisthomere (**op**) triangular, not

detached from opisthomere, broadening distad, with a small apical spike and small spinules in posterior part (Figs 4C, D, 5A, D). Solenomere (sl) narrow, higher than promere, but shorter than velum (ve); apical part with a tooth, connected to velum through thin plate with folds in basal part.



**FIGURE 4.** *Chaetoleptophyllum flexum* Golovatch, 1979, male from Sataplia Nature Reserve, Georgia. **A:** segment 7, ventral view. **B:** leg-pair 1, caudal view. **C & D:** gonopods, frontoventral and ventrocaudal views, respectively. **Abbreviations:** ms, mesomere; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.05 mm (A, B, C) or 0.02 mm (D).

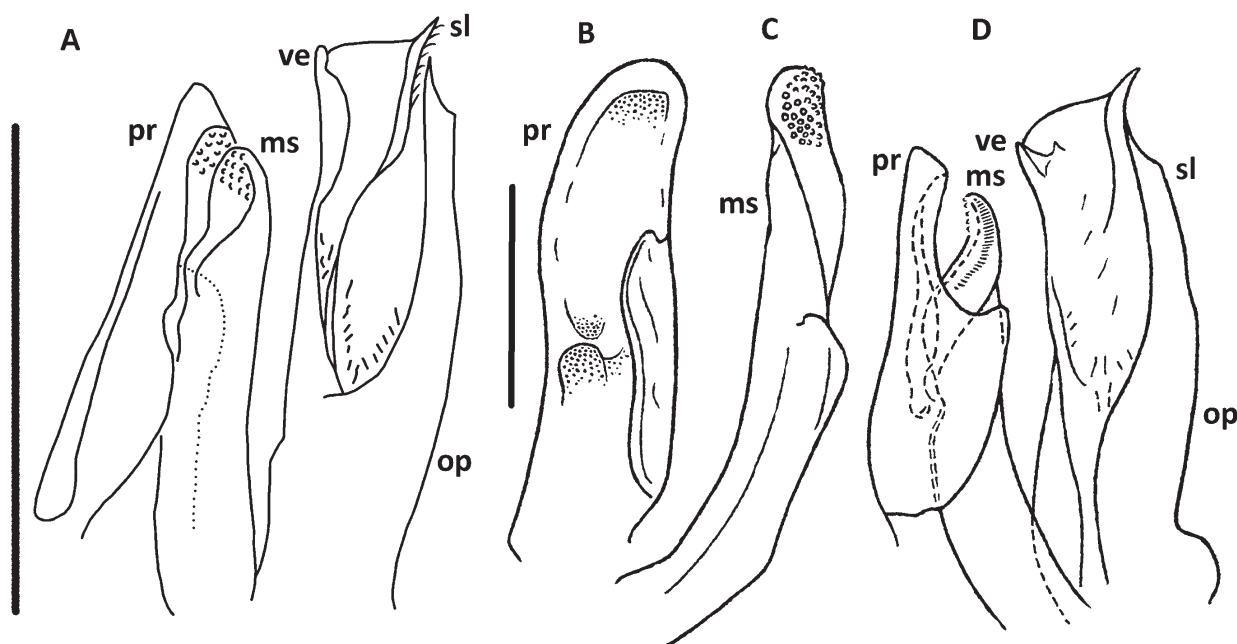
Ventral edge of male segment 7 with small curved lamellae bordering the gonopodal aperture (Figs 3E, 4A).

**FEMALE.** Leg-pairs 1 and 2 unmodified. Vulva elongated, densely setose (Fig. 41A). Operculum (om) with two small notches in apical part. Median field (mf) of bursa (bu) short and narrow, emargination (em) of mf

rounded. Receptaculum seminis (**rs**) consisting of two tubes, each ending in an ampulla (**a**): one ampulla oval, not level with the other.

**Remarks.** A widespread species recorded from Georgia, Abkhazia, South Ossetia and the Stavropol Province of Russia. It inhabits deciduous and mixed forests from the Black Sea coast up to 1800 m a.s.l.

*Leptophyllum montanum* Verhoeff, 1898, which by monotypy became the type species of the simultaneously proposed subgenus *Chaetoleptophyllum*, was described from a single male from Mount Trebević, central Bosnia and Herzegovina (Verhoeff 1898). This species seems to have never been recorded since (Kime and Enghoff 2017). As the original description was far from perfect, accompanied by only a single sketch of the opisthomere (Verhoeff 1898), and the species badly requires revision, the generic position of the above Caucasian formal congener remains provisional.



**FIGURE 5.** *Chaetoleptophyllum flexum* Golovatch, 1979, male from near Tkibuli (A) and male paratype (B–D), Georgia. **A:** gonopod, mesal view. **B:** promere of gonopod, caudal view. **C:** mesomere of gonopod, mesal view. **D:** gonopod, mesal view. **B–D:** after Golovatch (1979). **Abbreviations:** **ms**, mesomere; **op**, opisthomere; **pr**, promere; **sl**, solenomere; **ve**, velum. Scale bars: 0.2 mm (A) or 0.1 mm (B–D).

### Genus *Kubaniulus* Lohmander, 1936

**Type species:** *Kubaniulus gracilis* Lohmander, 1936

**Diagnosis.** Epiproct straight, densely setose. Promeres triangular in lateral view, without flagella. Velum well-developed, as high as or higher than promere. Phylacum absent (Table 1).

#### Species included:

*Kubaniulus gracilis* Lohmander, 1936

*Kubaniulus lativelatus* **sp. nov.**

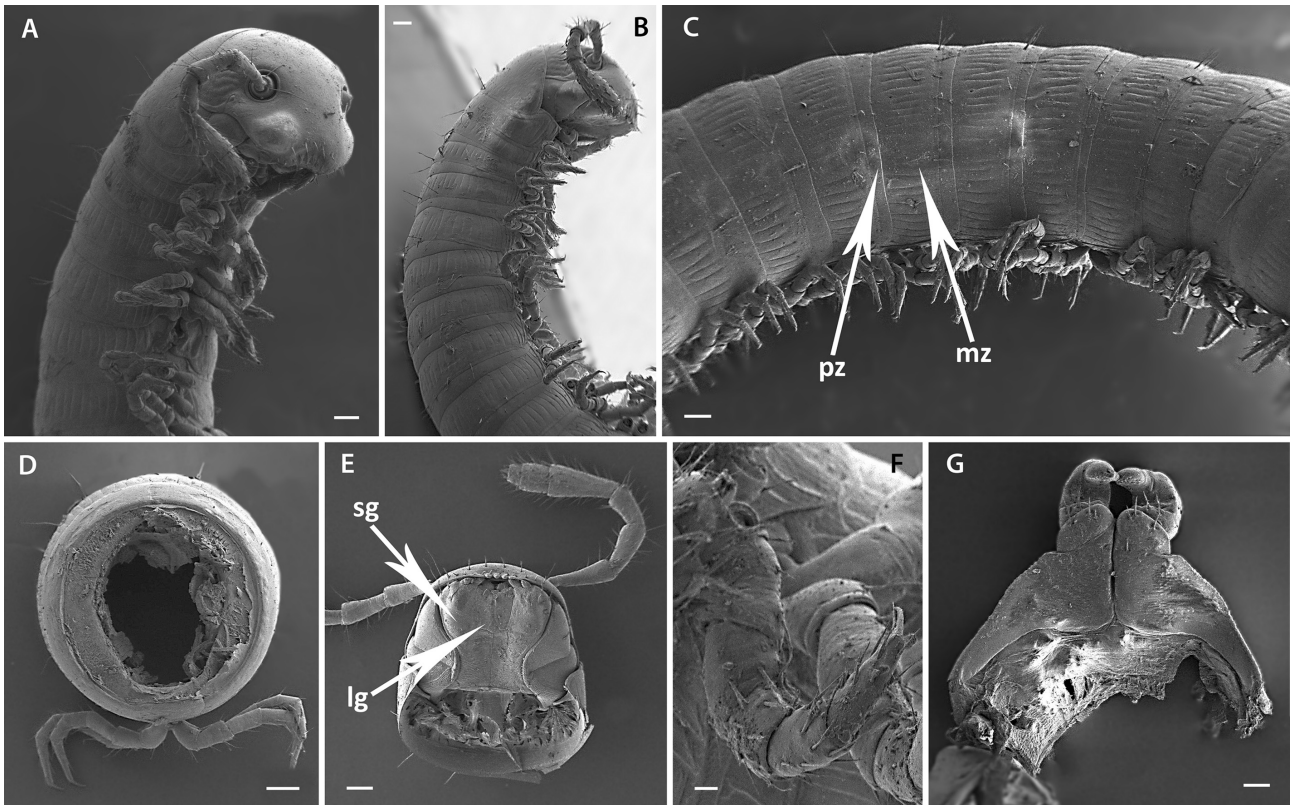
(Lohmander 1936; and hereafter)

#### *Kubaniulus gracilis* Lohmander, 1936

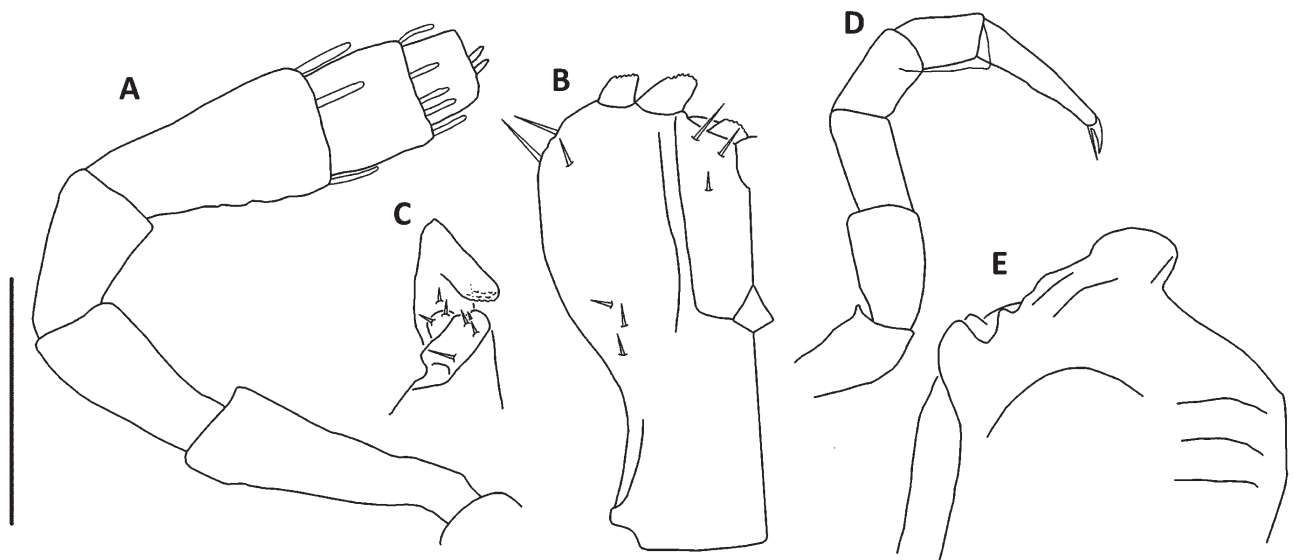
**Figs 1B, 6, 7, 8, 9, 41B, Map 1**

*Kubaniulus gracilis* Lohmander, 1936: 62 (D).

*Kubaniulus gracilis*—Lokšina and Golovatch, 1979: 386 (M); Lang, 1959: 1791 (M).



**FIGURE 6.** *Kubaniulus gracilis* Lohmander, 1936, male from pasture Abago, Krasnodar Prov. **A:** anterior part of body, ventrolateral view. **B:** anterior part of body, lateral view. **C:** middle part of body, lateral view. **D:** midbody ring, frontal view. **E:** head, ventral view. **F:** leg 2, frontolateral view. **G:** leg-pair 1, caudal view. **Abbreviations:** **lg**, lamella lingualis of gnathochilarium; **mz**, metazona; **pz**, prozona; **sg**, stipes of gnathochilarium. Scale bars: 0.1 mm (A–E) or 0.03 mm (F–G).



**FIGURE 7.** *Kubaniulus gracilis* Lohmander, 1936, male from pasture Abago, Krasnodar Prov. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.

#### Material examined.

**Russia, Krasnodar Prov.:** 5 males, 14 females, 1 juv. (ZMUM), Caucasian Nature Reserve, Pasture Abago near Guzeripl, 1700–1850 m a.s.l., *Abies*, *Fagus*, *Acer*, *Betula* etc. forest, up to timber line and in subalpine mead-

ows, litter, under bark and stones, 24–26.V.1985, leg. S. Golovatch. 2 females (ZMUM), 12 km SW of Goryachyi Klyuch, Kaverze valley, floodplain, 7.IV.1983, leg. V. Yanushev.

**Russia, Adygea:** 2 males, 4 females (ZMUM), Abadzekhskaya, *Crataegus*, *Pyrus*, *Prunus*, *Cornus* etc. forest/bush along stream, 6.X.1986, leg. V. Zherikhin. 1 male, 4 females (ZMUM), Sakhray near Novoprokhladnoye S of Maikop, 700 m a.s.l., *Fagus* and *Alnus* forest, litter, 7.VII.1986, leg. S. Golovatch. 1 male (AE), Caucasian Nature Reserve, “Juga” meteorological station, subalpine meadow, 43°53′02″N 40°28′53″E, 29.VII–04.IX.2016. 1 male (AE), Caucasian Nature Reserve, cordon Chernorechye, 43°55′60″N 40°41′00″E, 15.VI–03.VII.2017, all leg. Y. Chumachenko.

**Diagnosis.** Differs from the only other congener, *K. lativelatus* **sp. nov.**, by the deep incision of the velum dividing it from the solenomere, as well as through the shape of the solenomere.

**Descriptive notes.** Length of adults 10–18.5 mm, width 0.8–1.0 mm. Number of segments in adults from 49+3+T to 57+4+T. Body subcylindrical (Fig. 6D), brownish grey, head and collum brown, legs and antennae yellow (Fig. 1B). Eye patches oval, each composed of 15–17 ommatidia. Striations of metazonae irregular, deep, not reaching the caudal margin (Fig. 6A, B, C). Collum and metazonae with a row of setae at posterior margin (Fig. 6B).

Antennae relatively long, *in situ* reaching somite 4; a complete corolla of long bacilliform sensilla on antennomeres 5 and 6 (Figs 6A, B, 7A). Head with 5+5–6+6 labral setae, 2+2 supralabral setae, and 1+1 at base of antennae (Fig. 6A). Gnathochilarium with 1 short seta in median part and 1–2 long ones in anterior part of lamella lingualis; groups of 3–6 short setae on stipites (Figs 6E, 7B). Epiproct subtriangular, straight. Hypoproct subtriangular with 2+2 setae.

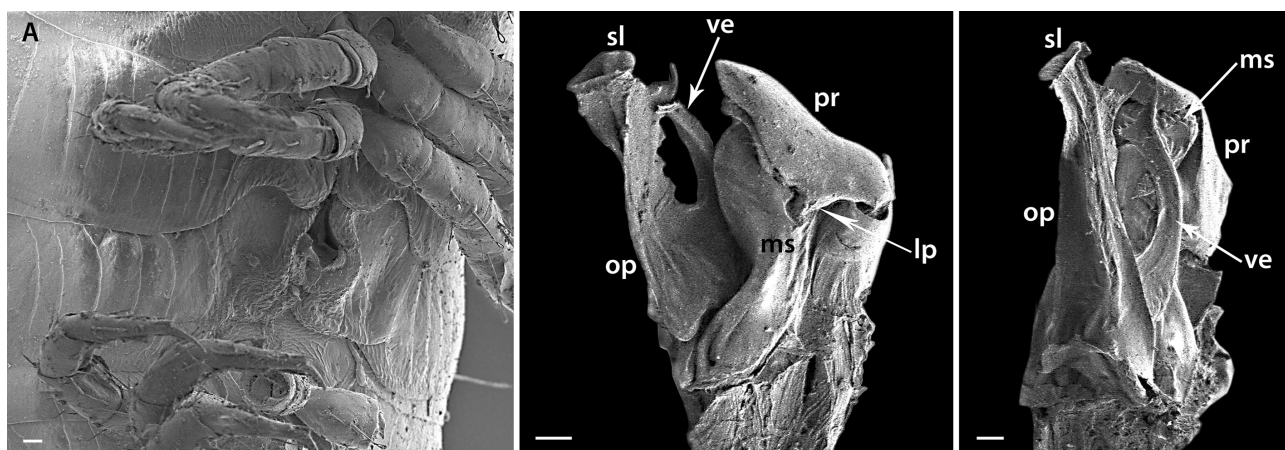
**MALE.** Leg-pair 1 small, unciform, relatively slender, with a group of setae in basal part, telopodite with a field of papillae in apical part (Figs 6G, 7C). Male leg-pair 2 with a pad on tibia (Fig. 7D); an accessory claw slightly longer than claw itself (Figs 6F, 7D). Penes short, bifurcated on top.

All three parts of gonopods (Figs 8B, C, 9B) forming a tight block. Promere (**pr**) triangular, spoon-shaped, papillate on top, with a lamella (**lp**) in basal part (Figs 8B, C, 9A, B). Flagella absent. Mesomere (**ms**) lower/shorter than promere, in apical and anterior parts with a field of papillae (Figs 8B, 8C, 9B). Velum (**ve**) of opisthomere (**op**) expanded to apical part, with a large tooth on top in anterior part, with fine fimbriae in posterior part, subequal in height to **pr** (Figs 8B, 8C, 9B). Solenomere (**sl**) very much higher than both **pr** and **ve**, with lamellae on top and a relatively large claw at anterior margin (Figs 8B, C, 9B).

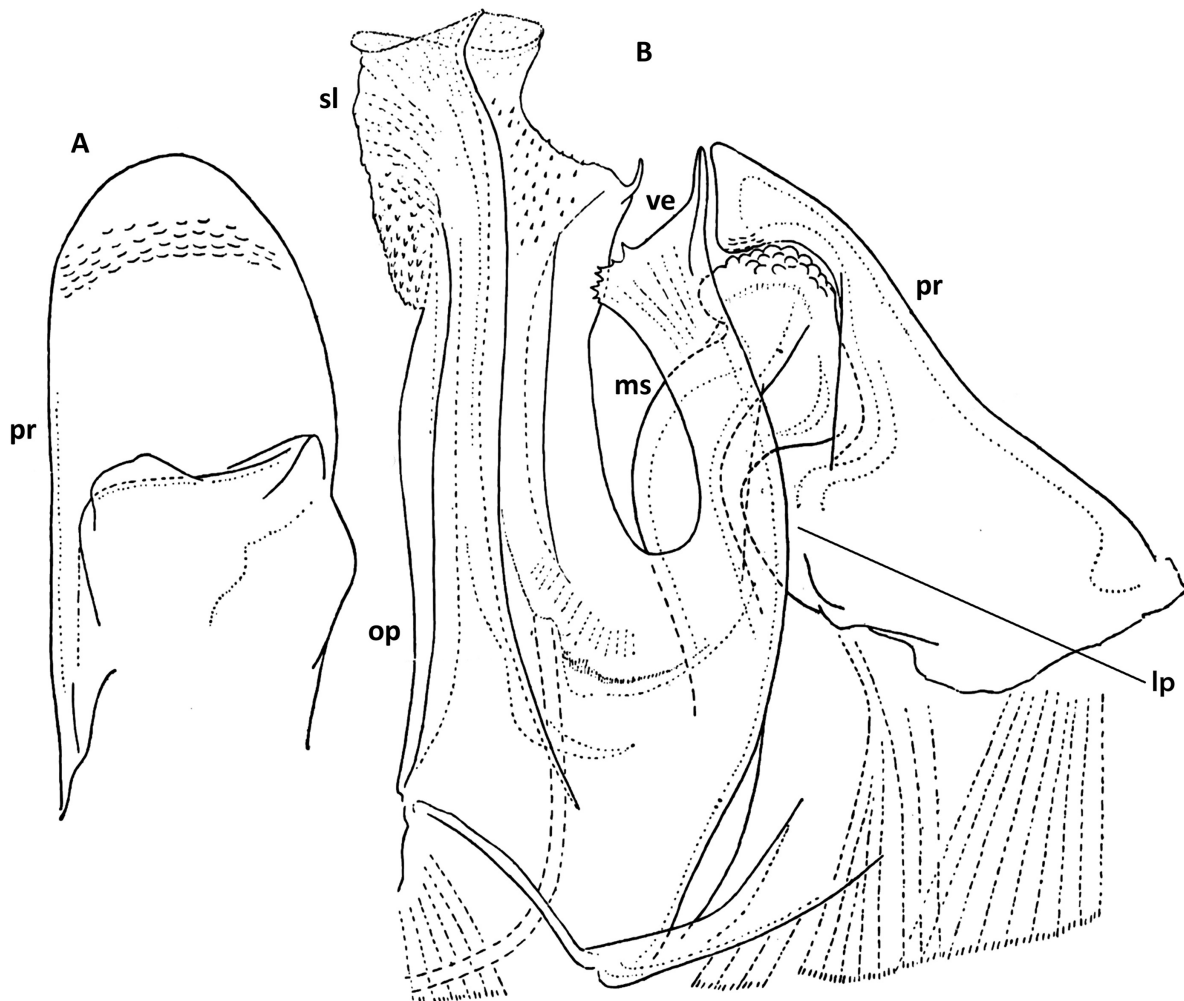
Ventral edge of male segment 7 with small curved lamellae bordering the gonopodal aperture (Figs 7E, 8A).

**FEMALE.** Leg-pairs 1 and 2 unmodified. Vulva elongated, with long setae (Fig. 41B). Operculum (**om**) very short. Median field (**mf**) of bursa (**bu**) short, emargination (**em**) of **mf** oval. Receptaculum seminis (**rs**) with two tubes, only one of which ending in a relatively large and elongated ampulla (**a**).

**Remarks.** A widely distributed species occurring in lowland to foothill deciduous and mixed forests in Krasnodar Province and Adygea, both Russia (Map 1).



**FIGURE 8.** *Kubaniulus gracilis* Lohmander, 1936, male from pasture Abago, Krasnodar Prov. **A:** segment 7, ventrolateral view. **B:** left gonopod, lateral view. **C:** right gonopod, caudal view. **Abbreviations:** **lp**, lamella of promere; **ms**, mesomere; **op**, opisthomere; **pr**, promere; **sl**, solenomere; **ve**, velum. Scale bars: 0.03 mm.



**FIGURE 9.** *Kubaniulus gracilis* Lohmander, 1936, male holotype, after Lohmander (1936). **A:** promere of gonopod, caudal view. **B:** right gonopod, mesal view. **Abbreviations:** lp, lamella of promere; ms, mesomere; op, opisthomere; pr, promere; sl, solenomere; ve, velum. Drawn not to scale.

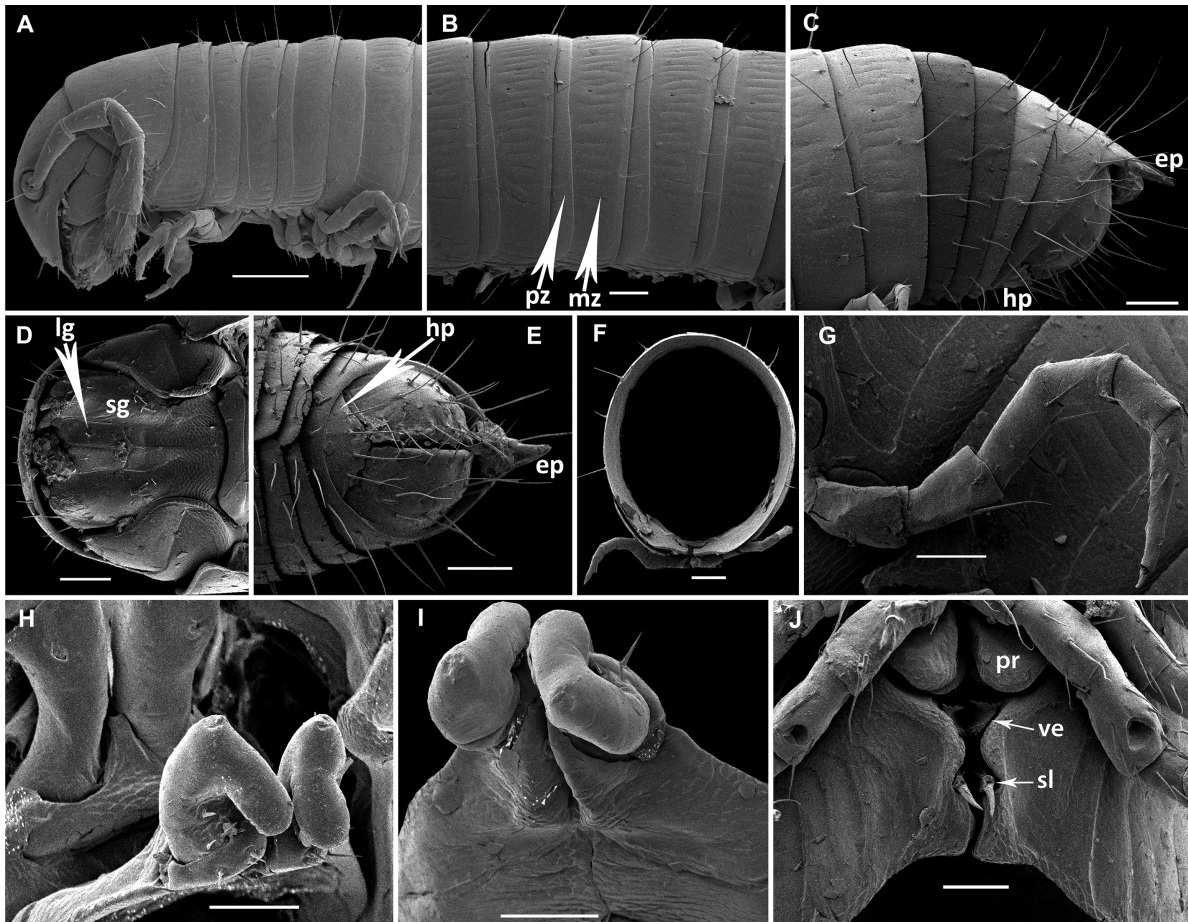
***Kubaniulus lativelatus* sp. nov.**

**Figs 1C, 10, 11, 12, 13 14, 41C, Map 1**

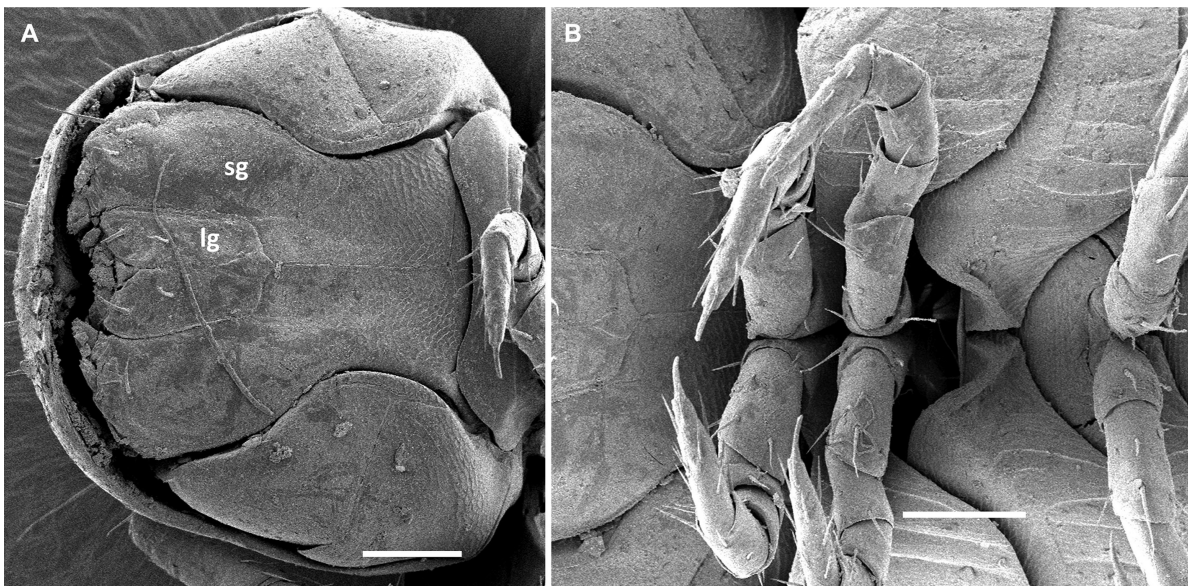
**Type material.**

**Holotype male** (ZMUM), **Russia, Krasnodar Prov.**, Sochi, ca. 8 km E of Khosta, Cave “Our Lady”, *Buxus*, *Fagus*, *Acer* etc. forest near entrance, litter and under stones, 16.V.1985, leg. S. Golovatch.

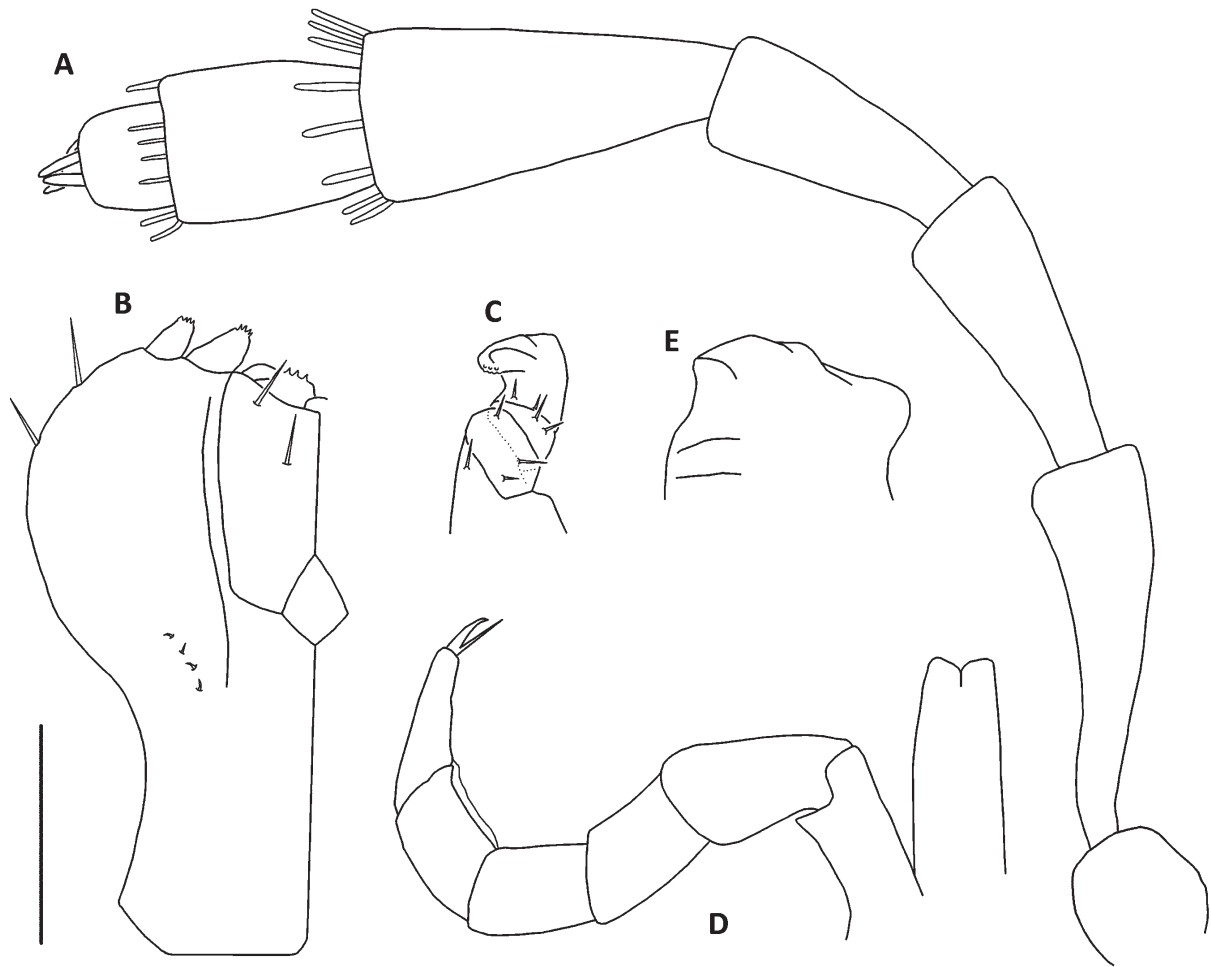
**Paratypes.** 4 males, 5 females, 1 juv. (ZMUM), same data as holotype. 1 male, 1 female (ZMUM), Sochi, Lazarevskoye, Saloniki, deciduous forest, litter, 28.X.1981. 4 males, 9 females, 3 juv. (ZMUM), Severskaya Distr., 2–10 km S of Ubinskaya, *Quercus*, *Fagus*, *Carpinus* etc. forest, 300–450 m a.s.l., litter, under bark, 3 and 4.VII.1986. 2 males (ZMUM), Sochi, Khosta, *Taxus* and *Buxus* forest with *Fagus*, litter and under stones, 15.V.1985, all leg. S. Golovatch. 1 male (slide mount, ZMUM), 25 km ENE of Aderbievka, E slope of Markotkh Mt. Ridge, 400 m a.s.l., 44°36'36"N 38°04'29"E, forest, 30.IV.2016, all leg. K. Makarov and O. Makarova. 4 males, 4 females (ZMUM), **Karachaevo-Cherkessia**, Teberda Nature Reserve, Mount Malaya Khatipara above Teberda town, ca. 1500 m a.s.l., 29–30.V.1985. 1 male, 1 female (ZMUM), **Abkhazia**, near Sukhumi, near Cave Kelassuri, litter, 11.IV.1983. 1 male (slide mount, ZMUM), Sukhumi Botanical Garden, 9.X.1978. 2 males, 10 females (ZMUM), Myussera Nature Reserve, 20–130 m a.s.l., mixed deciduous forest (*Castanea*, *Alnus* etc.), litter, under bark and stones, 8–10.IV.1983. 1 male, 1 female (ZMUM), **Georgia**, Tskhaltubo, near Cave Belaya, deciduous forest on rock, litter and under stones, 26.X.1981, all leg. S. Golovatch.



**FIGURE 10.** *Kubaniulus lativelatus* sp. nov., male paratype from near Khosta, Krasnodar Prov. **A–C:** anterior, middle and posterior parts of body, respectively, lateral view. **D:** head, ventral view. **E:** posterior part of body, ventral view. **F:** midbody ring, frontal view; **G:** leg 2, frontal view. **H & I:** leg-pair 1, caudolateral and frontoventral views, respectively. **J:** segment 7 and leg-pair 7, lateral view. **Abbreviations:** ep, epiproct; hp, hypoproct; lg, lamella lingualis of gnathochilarium; mz, metazona; pr, promere; pz, prozona; sg, stipes of gnathochilarium; sl, solenomere; ve, velum. Scale bars: 0.2 mm (A), 0.1 mm (B–F) or 0.05 mm (G–J).



**FIGURE 11.** *Kubaniulus lativelatus* sp. nov., female from near Khosta, Krasnodar Prov. **A:** head, ventral view **B:** leg-pair 2 and gonopores, ventral view. **Abbreviations:** lg, lamella lingualis of gnathochilarium; sg, stipes of gnathochilarium. Scale bars: 0.1 mm.



**FIGURE 12.** *Kubaniulus lativelatus* sp. nov., male paratype from near Khosta, Krasnodar Prov. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2 and penes, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.

**Non-type material.** 2 females (ZMUM), **Krasnodar Prov.**, W of Gelenjik, lower course of Yashamba River, 20 m a.s.l., 44°35'30"N 37°59'13"E, 2.V.2016. 1 female (ZMUM), W of Aderbievka, W slope of Mount Kotsekhur, Verbovaya cleft, 130 m a.s.l., 44°37'46"N 38°05'47"E, 3.V.2016, all leg. K. Makarov and O. Makarova. 1 female (ZMUM), **Abkhazia**, Gumista Nature Reserve, forest, litter, 6.VI.1982, leg. J. Boháč.

**Diagnosis.** This new species is assigned to the genus *Kubaniulus* primarily because of the absence of flagella from the promeres and of a phylacum from the opisthomere, even though these characters are shared with *Chaetoleptophyllum* as well. In addition, the velum of the opisthomere being not completely detached from the solenomere is also characteristic of both *Kubaniulus* and *Chaetoleptophyllum*. However, a subtriangular promere brings the new species closer to *Kubaniulus*. Differs clearly from *K. gracilis*, the only known congener, by the conformation of the opisthomere which shows a shorter velum, while the margins of both velum and solenomere are jagged.

**Etymology.** To emphasize the broad velum of the gonopod opisthomere; adjective.

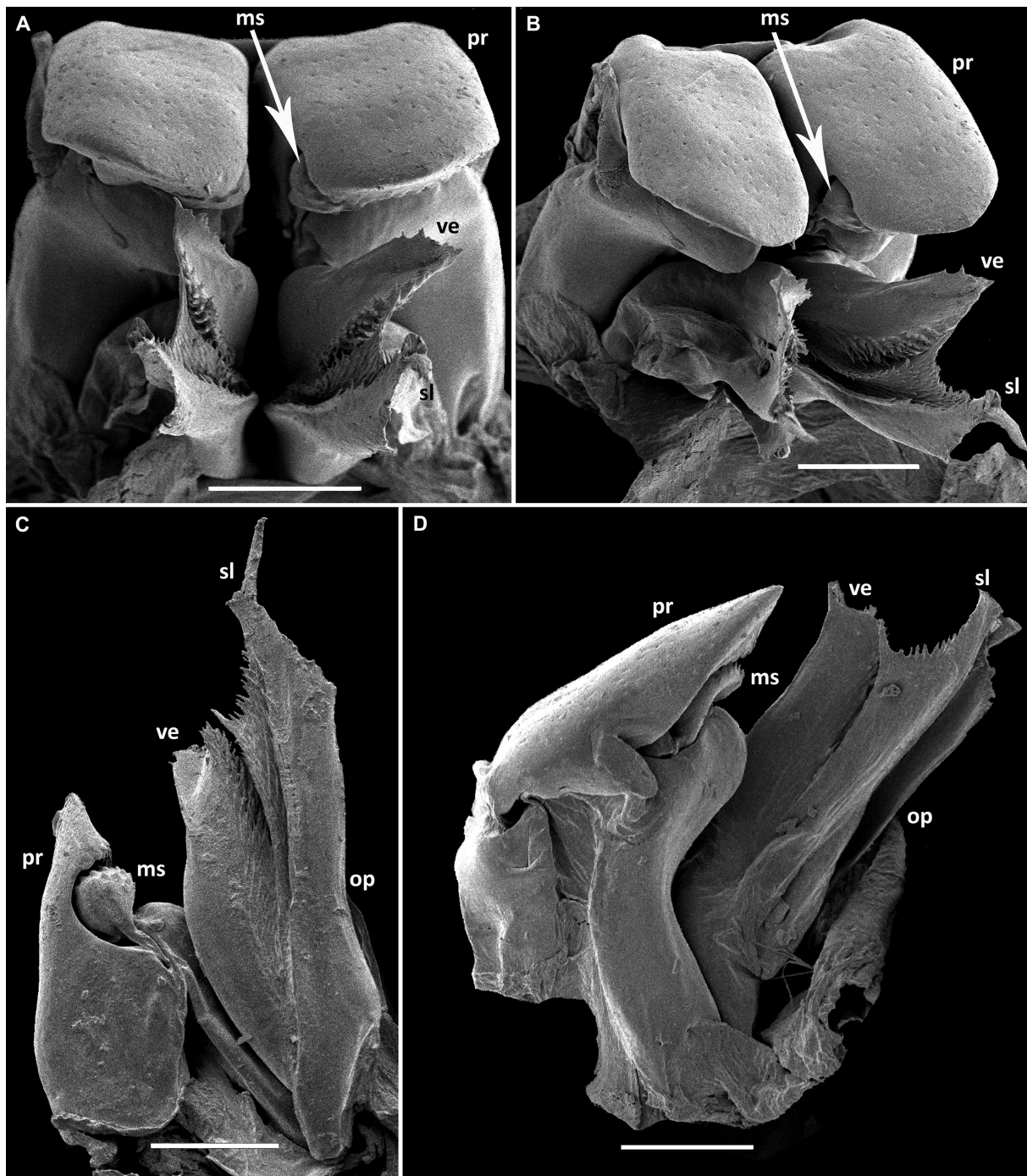
**Description.** Length 15–20 mm, width 1.0–1.2 mm (females), or length 15–17 mm, width 1.0–1.2 mm (males). Body segment formula: from 44+5+T to 50+4+T (males) and from 45+3+T to 61+3+T (females). Body greyish yellow; head, collum, legs and antennae yellow (Fig. 1C).

Eye patches subtriangular, each with 18–20 ommatidia. Epicranial setae 1+1, supralabral setae 2+2, labral setae 4+4–5+5, and 2+2–3+3 at base of antennae. Genae unmodified. Antennae relatively short, *in situ* reaching segment 3 when stretched laterally; a complete corolla of long bacilliform sensilla on antennomeres 5 and 6 (Figs 10A, 12A).

Each lamella lingualis of gnathochilarium with two long setae. Each stipe with a group of 4 or 5 setae (Figs 10D, 12B).



Body subcylindrical (Fig. 10F). Male segment 7 thicker than others. Suture dividing pro- and metazonae distinctly constricting both. Ozopores small, lying behind suture without touching it (Fig. 10B). Metazonae with relatively dense and regular striations reaching the hind margin, the latter with dense rows of setae (Fig. 10A–C). Epiproct subtriangular, with long setae (Fig. 10C). Anal valves convex, densely setose. Hypoproct with an undulate caudal margin and 2+2 setae (Fig. 10E).



**FIGURE 13.** *Kubaniulus lativelatus* sp. nov., male paratype near Khosta, Krasnodar Prov. **A & B:** both gonopods, ventral and ventrolateral views, respectively. **C:** left gonopod, mesal view. **D:** right gonopod, lateral view (solenomere is broken). **Abbreviations:** ms, mesomere; op, opisthomere; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.05 mm.

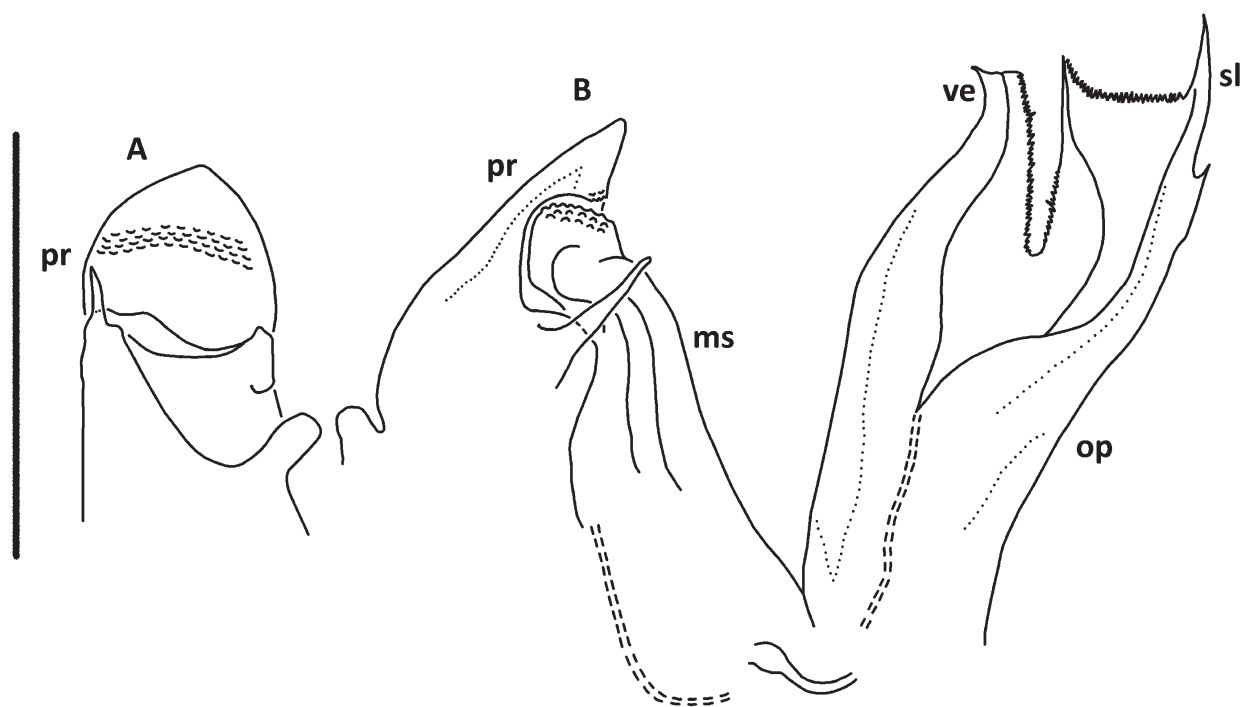
**MALE.** Ventral edge of segment 7 with small curved lamellae bordering the gonopodal aperture (Figs 10J, 12E). Leg-pair 1 small, unciform; a group of short setae in basal part, telopodite with a field of papillae in apical part (Figs 10H, I, 12C). Leg-pair 2 with a pad on postfemur (Fig. 12D); an accessory claw slightly longer than claw itself (Fig. 12D). Penes short, bifurcated on top. Leg-pair 7 with a pore on femur (Fig. 10J).

All three parts of gonopods (Figs 13A–D, 14B) forming a tight block. Promere (**pr**) spoon-shaped, with a field of papillae in upper part, medial part along external margin either with a rounded lamella and a relatively long and thin spike at mesal margin (Figs 14A, 14B) or only with a lamella (Fig. 13C). Flagella absent. Mesomere (**ms**) simple, lower/shorter than promere, in apical and anterior parts with small tubercles (Figs 13A–D, 14B). Velum (**ve**) of opisthomere (**op**) broad, rounded to top, separated from opisthomere only by a shallow notch with a finely denticulate margin (Figs 13C, D, 14B). Solenomere (**sl**) rather narrow, higher than **pr**, with a spike-like apical process (Figs 10J, 13C).

FEMALE. Gnathochilarium without setae on stipites (Fig. 11A). First two leg-pairs unmodified (Fig. 11B).

Vulva broad and densely setose (Fig. 41C). Operculum (**om**) with long and short setae on caudal side. Median field (**mf**) of bursa (**bu**) long, emargination (**em**) of **mf** oval. Ampullae (**a**) rounded, both placed at the same level.

**Remark.** This species seems to be endemic to the Colchidan region of the Caucasus within Krasnodar Province, Karachaevo-Cherkessia, Abkhazia, and Georgia (Map 1). Both *K. gracilis* and *K. lativelatus* **sp. nov.** are parapatric in the region concerned and both tend to mostly occur in lowland Black Sea coastal woodlands.



**FIGURE 14.** *Kubaniulus lativelatus* **sp. nov.**, male paratype from near Khosta, Krasnodar Prov. **A:** promere of gonopod, caudal view. **B:** gonopod, mesal view. **Abbreviations:** **op**, opisthomere; **pr**, promere; **ms**, mesomere; **sl**, solenomere; **ve**, velum. Scale bar: 0.2 mm.

## Genus *Leptoiulus* Verhoeff, 1894

**Type species:** *Julus trilineatus* C.L. Koch, 1847

**Diagnosis.** Epiproct straight, densely setose. Promere slightly lower/shorter than opisthomere, with well-developed flagella. Both velum and phylacum strongly developed (Table 1).

### Species included:

*Leptoiulus arabistanus* Lohmander, 1932

*Leptoiulus hastatus* Lohmander, 1932

*Leptoiulus tanymorphus* Lohmander, 1936

*Leptoiulus tigirek* Mikhajlova, Nefediev, Nefedieva & Dyachkov, 2015

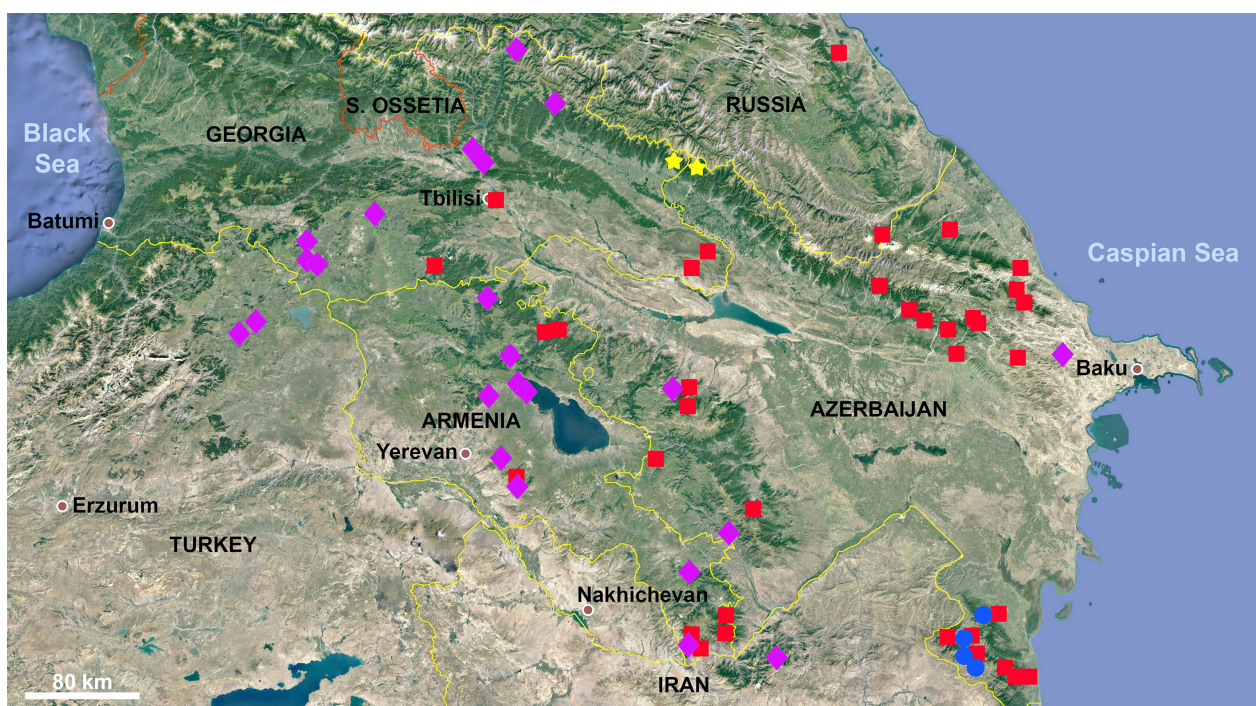
*Leptoiulus trilineatus* (C.L. Koch, 1847)

*Leptoiulus meskhii* sp. nov.

*Leptoiulus gonopodialis* sp. nov.

and numerous other species (<https://fauna-eu.org/content/diplopoda-0>)

(Koch 1847; Attems 1901; Lohmander, 1932, 1936; Mikhaljova *et al.* 2015; and hereafter)



**MAP 2.** Distribution of *Leptoiulus* species in the Caucasus: *Leptoiulus hastatus* Lohmander, 1932 (purple diamond), *Leptoiulus tanymorphus* (Attems, 1901) (red square), *Leptoiulus meskhii* sp. nov. (blue circle), *Leptoiulus gonopodialis* sp. nov. (yellow star).

### *Leptoiulus hastatus* Lohmander, 1932

Figs 15A, 16, 17, 18, 19, 20, 21, 22, 23, 41D, Map 2

*Leptoiulus hastatus* Lohmander, 1932: 8 (D).

*Leptoiulus hastatus*—Lang, 1959: 1791 (M); Lokšina and Golovatch, 1979: 386 (M); Enghoff and Moravvej, 2005: 66 (M).

*Leptoiulus disparatus* Lohmander, 1936: 60 (D), **syn. n.**

*Leptoiulus disparatus*—Lang, 1959: 1791 (M); Kobakhidze, 1964: 190 (R), 1965: 392 (M); Lokšina and Golovatch, 1979: 386 (M); Bababekova, 1996: 91 (M); Enghoff, 2006: 181 (R); Kokhia and Golovatch, 2018: 40 (M).

### Material examined.

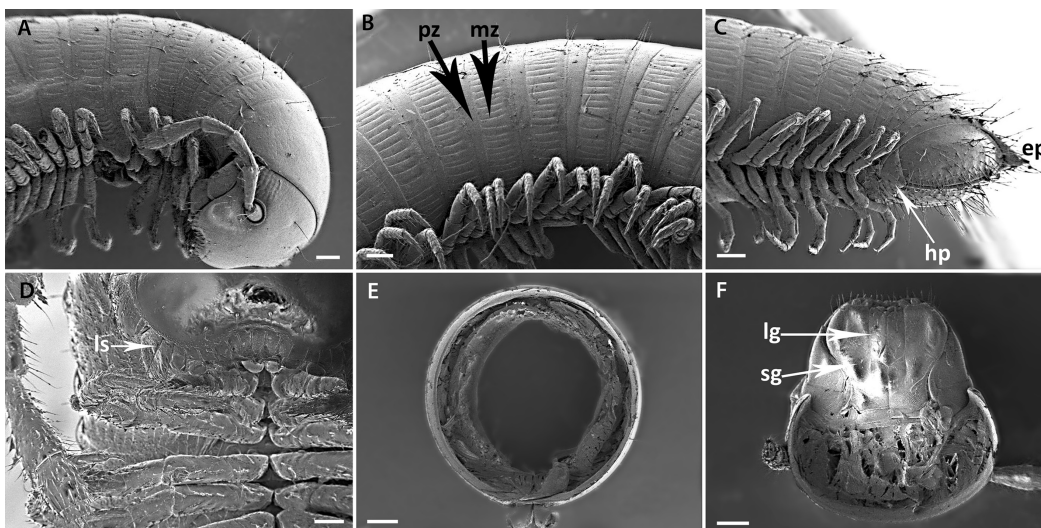
**Azerbaijan:** 6 males, 4 females, 2 juv. (ZMUM), Mountainous Karabakh, Aganos S of Lachin, 1100 m a.s.l., *Quercus*, *Fagus*, *Carpinus* forest, litter, 30.IV.1983, leg. S. Golovatch. 1 male (SMNG), 1 male (IZB), Göygöl Distr., Tođanalý towards Çýraqdərə, *Quercus*, *Carpinus* with *Cornus*, low trees, litter, 1220 m a.s.l., 40.4509°N, 46.3355°E, 29.III.2015. 6 males, 9 females, 1 juv. (SMNG), 6 males, 9 females, 1 juv. (IZB), Qobustan distr., Ceyrankeçməz, Pamaxý-Baku highway at bridge over Ceyrankeçməz River, steppe, strong loamy, under stones, 490 m a.s.l., 40.4980°N, 49.0427°E, 30.III.2015, all leg. H.S. Reip and D.Ž. Antić.

**Armenia:** 2 females (ZMUM), Tsakhkadzor, dry *Quercus* forest, 14.V.1972. 2 females (ZMUM), Khosrov Nature Reserve, *Quercus*, *Juniperus* etc. woodland, 7.V.1972. 4 males, 16 females (ZMUM), same locality, 1450–1550 m a.s.l., *Juniperus* with *Quercus* and *Crataegus*, along river, litter and under stones, 19–20.IV.1983, leg. S. Golovatch. 1 female (ZMUM), Tsakhkadzor, humid *Quercus* forest, 14.V.1972. 3 males, 4 females (ZMUM), Pam-bag (Sevan), *Juniperus* and *Quercus* woodland, 17.V.1972. 2 females, 3 juv. (ZMUM), Dilizhan Nature Reserve, dry *Quercus* and *Carpinus* forest, 19.V.1972. 8 females (ZMUM), same locality, *Taxus* grove, 18.V.1972. 3 juv. (ZMUM), same locality, Lake Parzlich, *Carpinus* and *Fagus* forest, 15.V.1972. 1 female (ZMUM), Gegart, arid

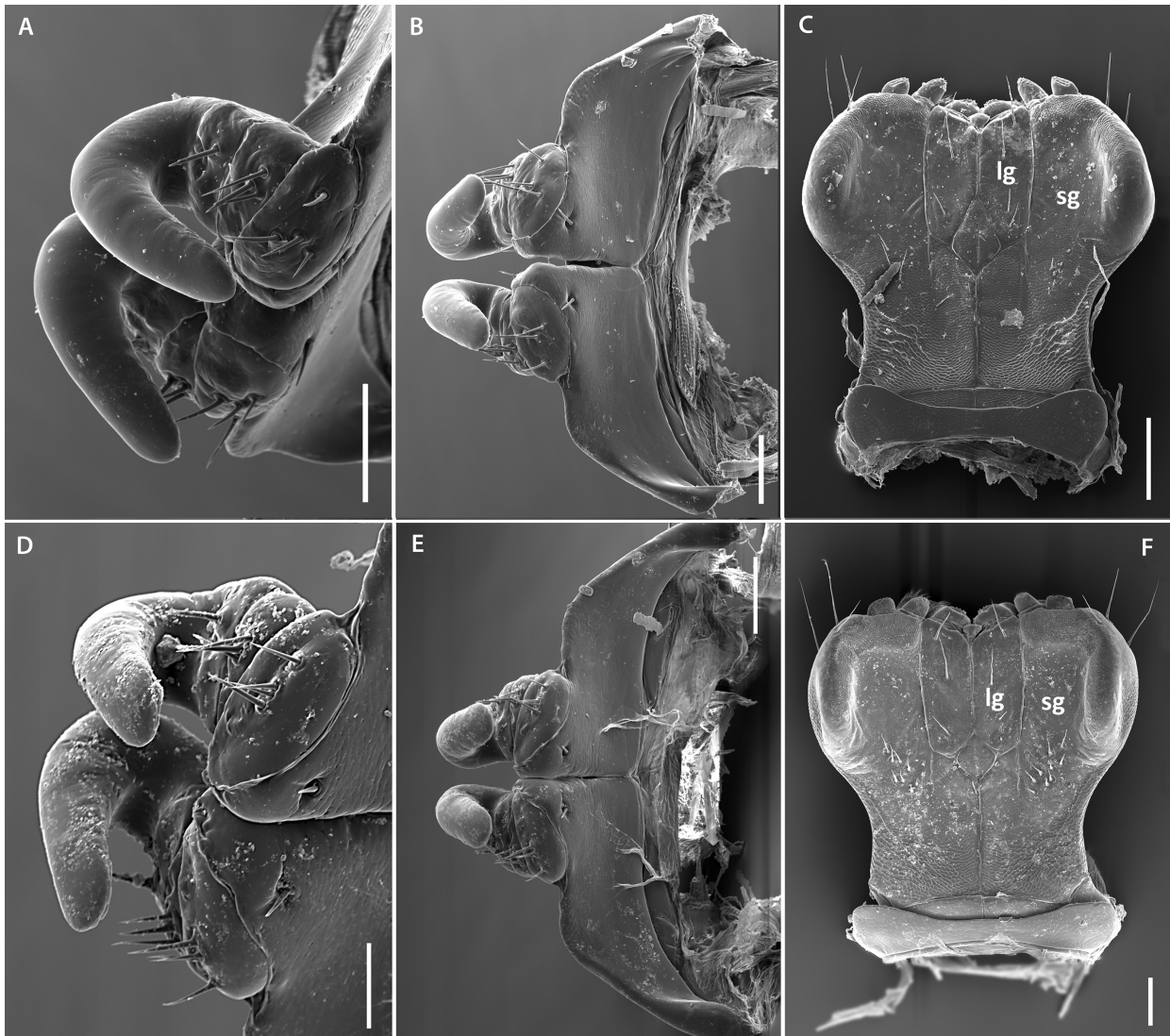
woodland, 4.V.1972, all leg. M. Ghilarov. 2 males, 4 females, 4 juv. (ZMUM), SW of Shnokh halfway between Alaverdi and Bagratashen, *Carpinus* forest, litter, 24.V.1987, leg. S. Golovatch and K. Eskov. 17 males, 27 females, 2 juv. (ZMUM), Megri Distr., SSE of Lichk, Megri River valley, *Quercus* forest, 1530 m a.s.l., litter, under stones and bark, 25.IV.1983, leg. S. Golovatch. 1 male, 10 females (ZMUM), Sevanavank Monastery, under stones, 4.V.2019. 1 male, 2 females (ZMUM), Totev, 3.V.2019, all leg. O. Makarova.



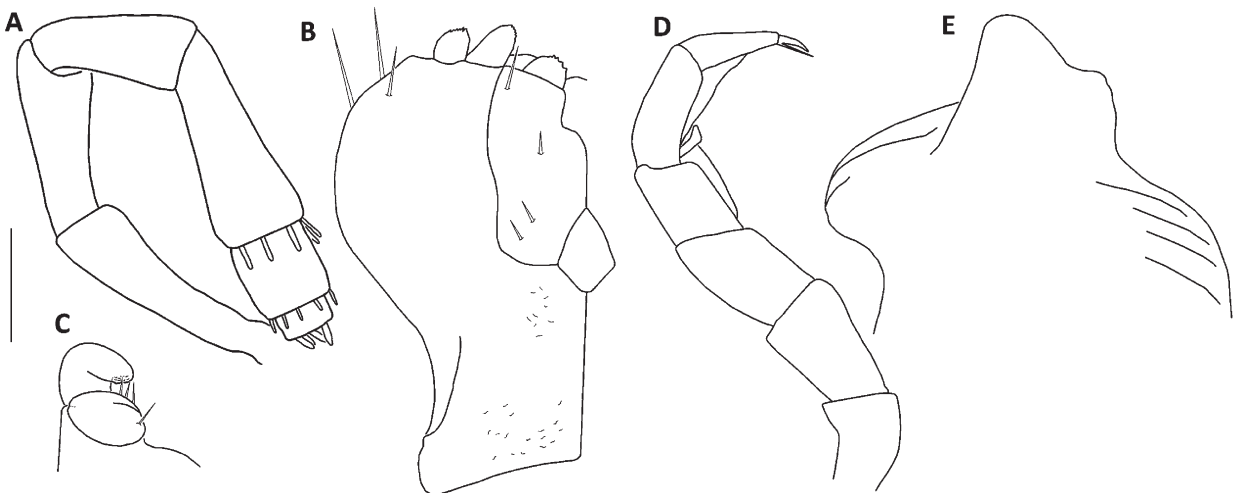
**FIGURE 15.** Habitus pictures of some species of Leptoiulini from the Caucasus, lateral views. **A:** *Leptoiulus hastatus* Lohmander, 1932, male from near Shnokh, Armenia. **B:** *Leptoiulus tanymorphus* (Attems, 1901), male from Ajikent, Azerbaijan. **C:** *Leptoiulus meskhii* sp. nov., male paratype from Galabyn, Azerbaijan. **D:** *Leptoiulus gonopodialis* sp. nov., male paratype from Lagodekhi Nature Reserve, Georgia. Scale bar: 1 mm.



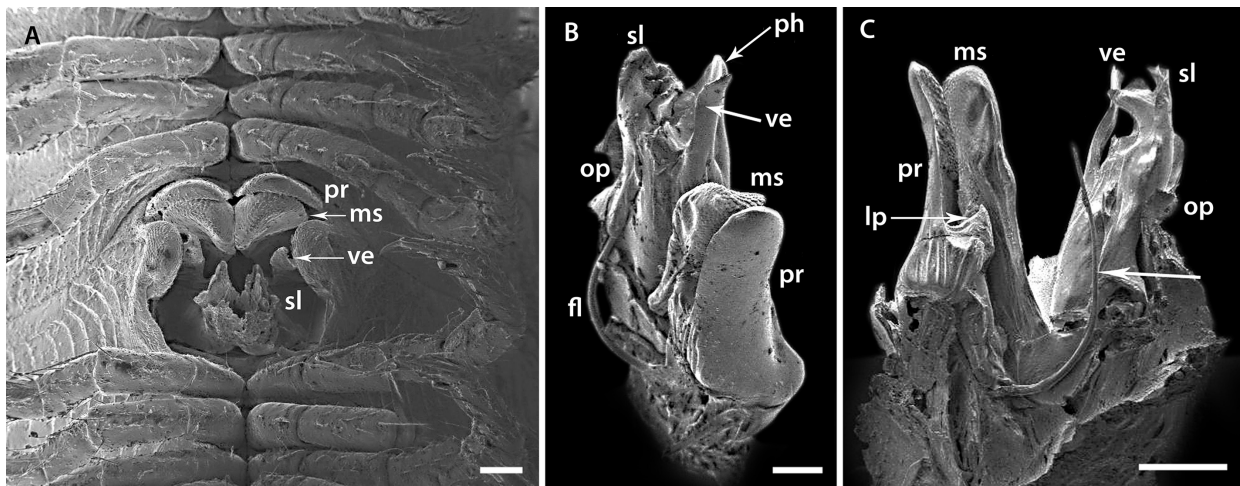
**FIGURE 16.** *Leptoiulus hastatus* Lohmander, 1932, male from near Lichk, Armenia. **A:** anterior part of body, lateral view. **B:** middle part of body, lateral view. **C:** posterior part of body, dorsolateral view. **D:** anterior part of body, ventral view. **E:** midbody ring, frontal view. **F:** head, ventral view. **Abbreviations:** ep, epiproct; hp, hypoproct; lg, lamella lingualis of gnathochilarium; ls, labral seta; mz, metazona; pz, prozona; sg, stipes of gnathochilarium. Scale bars: 0.2 mm (A–C, E, F) or 0.1 (D).



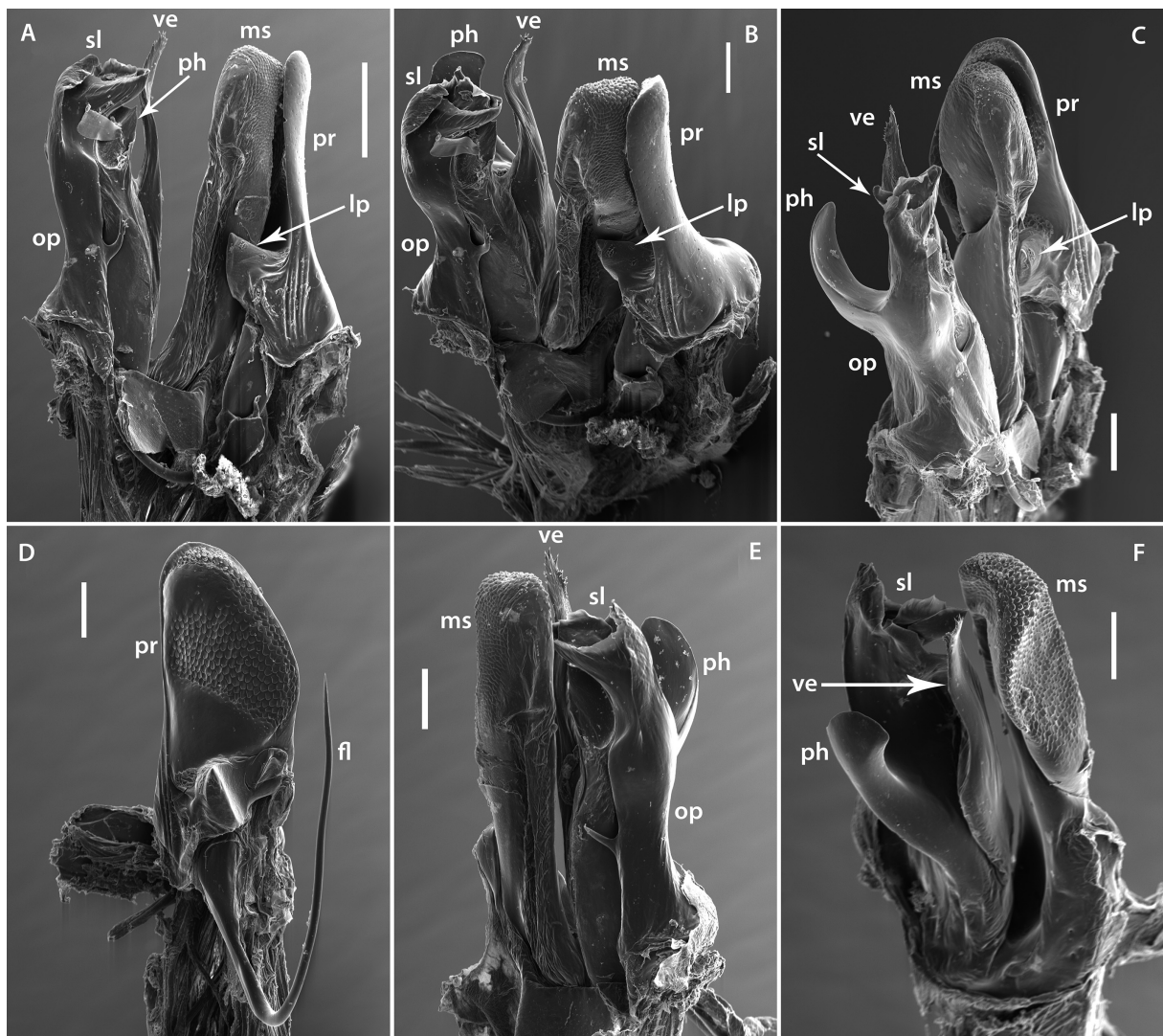
**FIGURE 17.** *Leptoiulus hastatus* Lohmander, 1932. **A–C:** male from Tođanalý, Azerbaijan. **D–F:** Morph B, male from Ceyrankeçməz, Qobustan, Azerbaijan. **A:** leg pair 1, anterolateral view. **B:** leg pair 1, anterior view. **C:** gnathochilarium, ventral view. **Abbreviations:** **lg**, lamella lingualis of gnathochilarium; **sg**, stipes of gnathochilarium. Scale bars: 0.1 mm (**A–C**, **E**, **F**) or 0.05 mm (**D**).



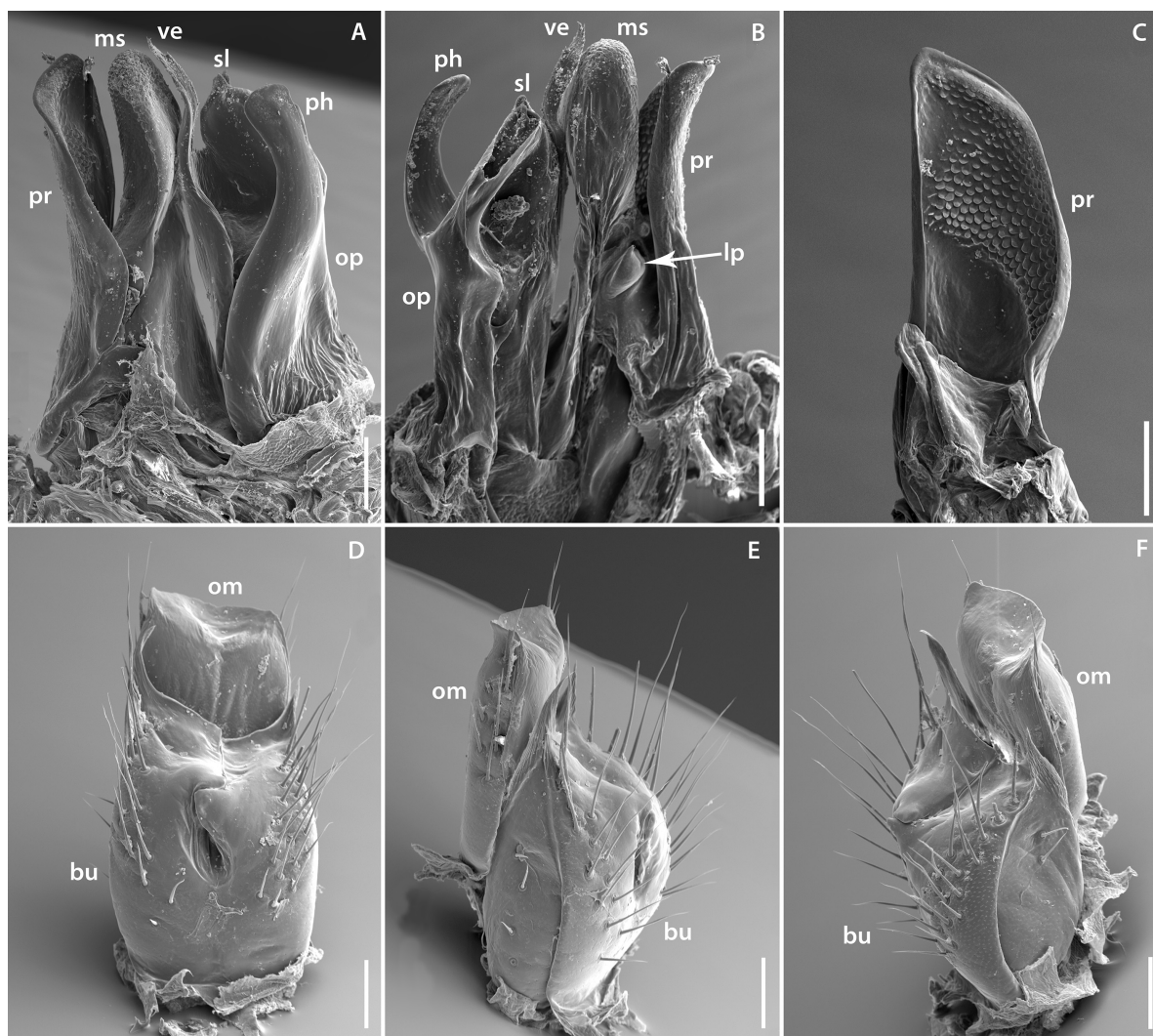
**FIGURE 18.** *Leptoiulus hastatus* Lohmander, 1932, male from Aganos, Azerbaijan. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.



**FIGURE 19.** *Leptoiulus hastatus* Lohmander, 1932, male from near Lichk, Armenia. **A:** segment 7, ventral view. **B-C:** gonopod, frontoventral and mesal views, respectively. **Abbreviations:** **fl**, flagellum; **lp**, lamella of promere; **ms**, mesomere; **op**, opisthomere; **ph**, phylacum; **pr**, promere; **sl**, solenomere; **ve**, velum. Scale bars: 0.5 mm (A), 0.2 mm (B, C).



**FIGURE 20.** *Leptoiulus hastatus* Lohmander, 1932, male from Tođanalý, Azerbaijan. **A:** gonopods, mesal view. **B:** gonopods, mesodistal view. **C:** gonopods, posterodistal view. **D:** promere of gonopod, posterior view. **E:** gonopods without promere, mesal view. **F:** gonopods without promere, lateral view. **Abbreviations:** **fl**, flagellum; **lp**, lamella of promere; **ms**, mesomere; **op**, opisthomere; **ph**, phylacum; **pr**, promere; **sl**, solenomere; **ve**, velum. Scale bars: **A:** 0.2 mm, rest: 0.1 mm.



**FIGURE 21.** *Leptoiulus hastatus* Lohmander, 1932, aberrant male from Ceyrankeçməz, Qobustan, Azerbaijan. **A:** gonopods, lateral view. **B:** gonopods, mesal view. **C:** promere of gonopod, posterior view. Female from same place as male. **D:** vulva, posterior view, **E:** vulva, lateral view. **F:** vulva, mesal view. **Abbreviations:** **bu**, bursa; **lp**, lamella of promere; **ms**, mesomere; **om**, operculum; **op**, opisthomere; **ph**, phylacum; **pr**, promere; **sl**, solenomere; **ve**, velum. Scale bars: 0.1 mm.

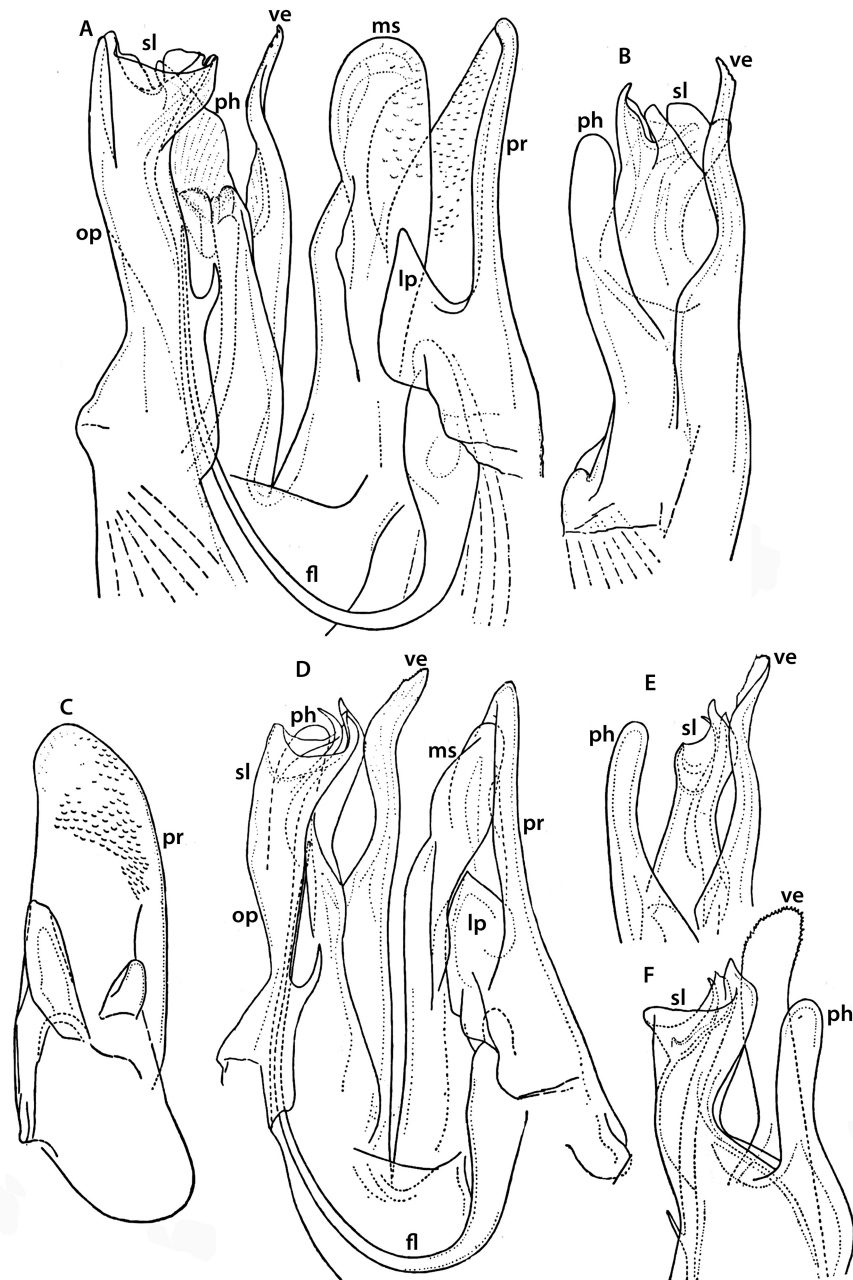
**Georgia:** 1 male (SMNG), Kakhetia, valley of Stori river shortly after Lechuri, *Fagus* forest on a steep hillside, 600 m a.s.l., 42°09'41"N, 45°25'20"E, 02.IX.2009. 1 male (SMNG), Mtskheta-Mtianeti, forest SW of Lake Tba Bazaleti, 42.0308°N, 44.6653°E, 04.X.2011. 1 male, 1 female (SMNG), Kistani, 1970 m a.s.l., 42.5792°N, 45.1025°E, 09.VIII.2014. 1 male (ZMUM), Samtskhe-Javakheti, castle Khert'visi, 1160 m a.s.l., 41.4794°N, 43.2853°E, 04.X.2012. 1 male (SMNG), from bridge 2 km towards Tmogvi, Vardzia, 1240 m a.s.l., 41.3822°N, 43.2975°E, 19.IX.2011. 1 male, 2 females (ZMUM), 11 females (SMNG), same locality and date. 2 males, 1 female (SMNG), same locality, 41.3823°N, 43.2982°E, 25.VIII.2014, all leg. F. Walther.

**Diagnosis.** Differs from other regional congeners by the strongly developed phylacum which is bent backwards and by the wavy long velum. Solenomere with three apical lamellae.

**Descriptive notes.** Length of adults 19–34 mm, width 1.35–1.9 mm. Number of segments in adults from 44+5+T to 61+3+T. Body subcylindrical (Fig. 16E), marbled brown to brownish grey, legs and antennae yellow (Fig. 15A). Eye patches subtriangular, each composed of 18–45 ommatidia. Striations on metazonae regular, deep, not reaching the caudal margin (Figs 16A–C). Collum and metazonae with a row of setae at posterior margin (Figs 16A–C).

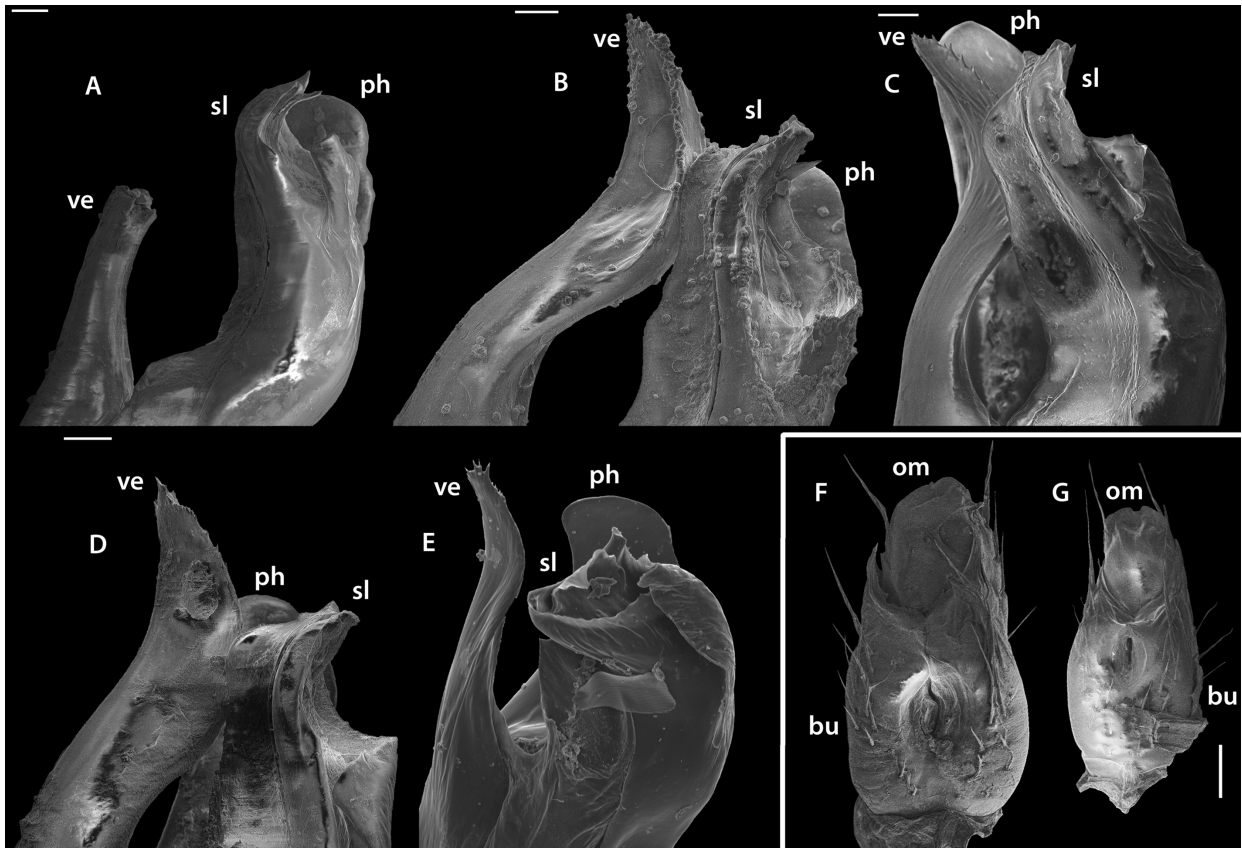
Antennae relatively long, *in situ* reaching segment 5; a complete corolla of sparse, long, bacilliform sensilla on antennomeres 5 and 6 (Figs 16A, 18A). Head with 7+7–8+8 labral setae, 2+2 supralabral setae, and 4+4–5+5 at base of antennae (Figs 16A, 16D). Gnathochilarium with 3 or 4 short setae on each lamella lingualis; groups of 3–6

short setae on stipites (Figs 16F, 17C, F, 18B). Distal half of stipites with a very strong, lateral, lengthwise elongated swelling. Apical claw short and not sharpened on tip (Fig. 18D). Anal valves strongly setose. Epiproct rather long, subtriangular, straight (Fig. 16C). Hypoproct subtriangular and with 4+4 setae.



**FIGURE 22.** **A-B:** *Leptoiulus hastatus* Lohmander, 1932, male holotype, after Lohmander, 1932 (A-B). **A:** gonopod, mesal view. **B:** opisthomere of gonopod, lateral view. **C-F:** male holotype of *L. disparatus* Lohmander, 1936, after Lohmander, 1936. **C:** promere of gonopod, caudal view. **D:** gonopod, mesal view. **E:** end of opisthomere, frontolateral view. **F:** end of opisthomere, caudal view. **Abbreviations:** fl, flagellum; lp, lamella of promere; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Drawn not to scale.





**FIGURE 23.** *Leptoiulus hastatus* Lohmander, 1932. **A-E:** end of gonopod opisthomere, mesal views. **A:** male from Vardzia, Georgia. **B:** male from Tba Bazaleti Lake. **C:** male from Vardzia, Georgia. **D:** male from Vardzia, Georgia. **E:** male from Tođanalý, Azerbaijan. **F-G:** vulvae, posterior view. **F:** female from Sevanavank Monastery, Armenia. **G:** female from Tba Bazaleti Lake. **Abbreviations:** bu, bursa; om, operculum; ph, phylacum; sl, solenomere; ve, velum. Scale bars: 0.02 mm (**A-D**), 0.1 mm (**F-G**) or not to scale (**E**).

**MALE.** Leg-pair 1 small and unciform, with a group of setae on coxa; telopodite with a field of papillae in apical part (Figs 17A, B, D, E, 18B). Leg-pair 2 with pads on postfemur and tibia (Fig. 18D); a very long accessory claw slightly longer than claw itself. Penes short, bifurcated on top.

All three parts of gonopods (Figs 19B, C, 20A–C, E, F, 21A, B, 22A, 22D) forming a tight block. Promere (**pr**) triangular, sagittally relatively flat, covered with small tubercles in middle part, with a tooth- or leaf-like lamella (**lp**) in basal part (Figs 19C, 20A–D, 21A–C, 22A, C–B, 22E). Flagella (**fl**) relatively short (Figs 19B, C, 20D, 22A, D). Mesomere (**ms**) simple, a little lower/shorter than promere, in apical part with small tubercles (Figs 19B, C, 20A–C, 22A, D). Velum (**ve**) of opisthomere (**op**) narrow, attenuating distad, about as high/long as or slightly higher/longer than **pr** (Figs 19B, C, 20A–C, 20E, F, 21A, B, 22A, B, 22D–F). Solenomere (**sl**) apically with three lamellae (Figs 19B, C, 20A–C, 20E, F, 21A, B, 22A, B, 22D–F). Phylacum (**ph**) slender, about as high/long as or lower/shorter than **sl**.

Ventral edge of male segment 7 with small curved lamellae bordering the gonopodal aperture (Figs 16A, 18E, 19A).

**FEMALE.** First two leg-pairs unmodified. Vulva covered with relatively short setae (Figs 21D–F, 23F–G, 42D). Operculum (**om**) suboval, densely setose. Median field (**mf**) of bursa (**bu**) short, emargination (**em**) of **mf** rounded. Receptaculum seminis (**rs**) consisting of two tubes located at base of vulva, devoid of ampullae.

**Remarks.** This species was described from Mount Kara-Dag, NW Iran (Lohmander 1932, Enghoff and Moravvej 2005). In the Caucasus, it has been recorded from Azerbaijan, Georgia and Armenia, inhabiting deciduous forests and steppe environments. This species is thus new to the faunas of Azerbaijan and Armenia.

*Leptoiulus disparatus* was described, based on a single male (holotype) from near Borjomi, Georgia (Lohmander 1936), and it was initially stated as being very similar to *L. hastatus*.

Since our collections are very large and densely blanket the entire region in question, we believe that these two “species” actually represent one, *L. hastatus* by priority. Evidence to support this conclusion is brought below and it mostly comes from certain details of gonopodal structure. *L. hastatus* gonopods show only minor individual variations in the shape of the medio-parabasal lamella on the promere (**lp**), as well as of the velum. The height of the velum relative to the other parts of the opisthomere, as well as velum width, vary in individual males, including syntopic ones (Figs 19C, 20A–C, 21A, B, 22B–F, 23A–E). In contrast, the solenomere varies to only some extent. The posterior edge can be either the highest point of the solenomere, with the opening of the solenomere facing forward (Figs 20A, B, E, 22A, 23E), or the apical structure can be complete and tilted back (Fig. 22E or Fig. 23A–D, the latter in specimens from Vardzia, Georgia). An aberrant structure of the solenomere was found in a male from Qobustan, Azerbaijan, where the opening of the solenomere is based in the middle of the apical part of the opisthomere (Figs 21A, B). Because of the similarly structured velum and phylacum, we identify this specimen as belonging to *L. hastatus*.

No meaningful variations in the shapes and setation of the gnathochilarium, male leg-pair 1 and female vulvae have been traced (Fig. 17, 23F, G). The size differences noted for *L. hastatus* and *L. disparatus* by Lohmander (1936) are likewise fictitious, since the males and females tend to be similar in size, forming a continuous cloud in the number of podous body rings and body diameter (Figs 43, 44). *Leptoiulus hastatus* is the diplopod species with the largest North-South span across the Caucasus region (Map 2). It inhabits various, mostly midmontane environments, both woodland and relatively xerophilous ones, and shows slight polymorphism in a few morphological traits, especially gonopodal ones.

### ***Leptoiulus tanymorphus* (Attems, 1901)**

**Figs 15B, 25, 26, 27, 28, 29, 30, 41E, Map 2**

*Julus tanymorphus* Attems, 1901: 288 (D).

*Leptoiulus tanymorphus*—Lohmander, 1936: 57 (D, R); Lokšina and Golovatch, 1979: 386 (M); Lang, 1959: 1791 (M); Kobakhidze, 1965: 392 (M); Bababekova, 1996: 90 (M); Kokhia and Golovatch, 2018: 40 (M).

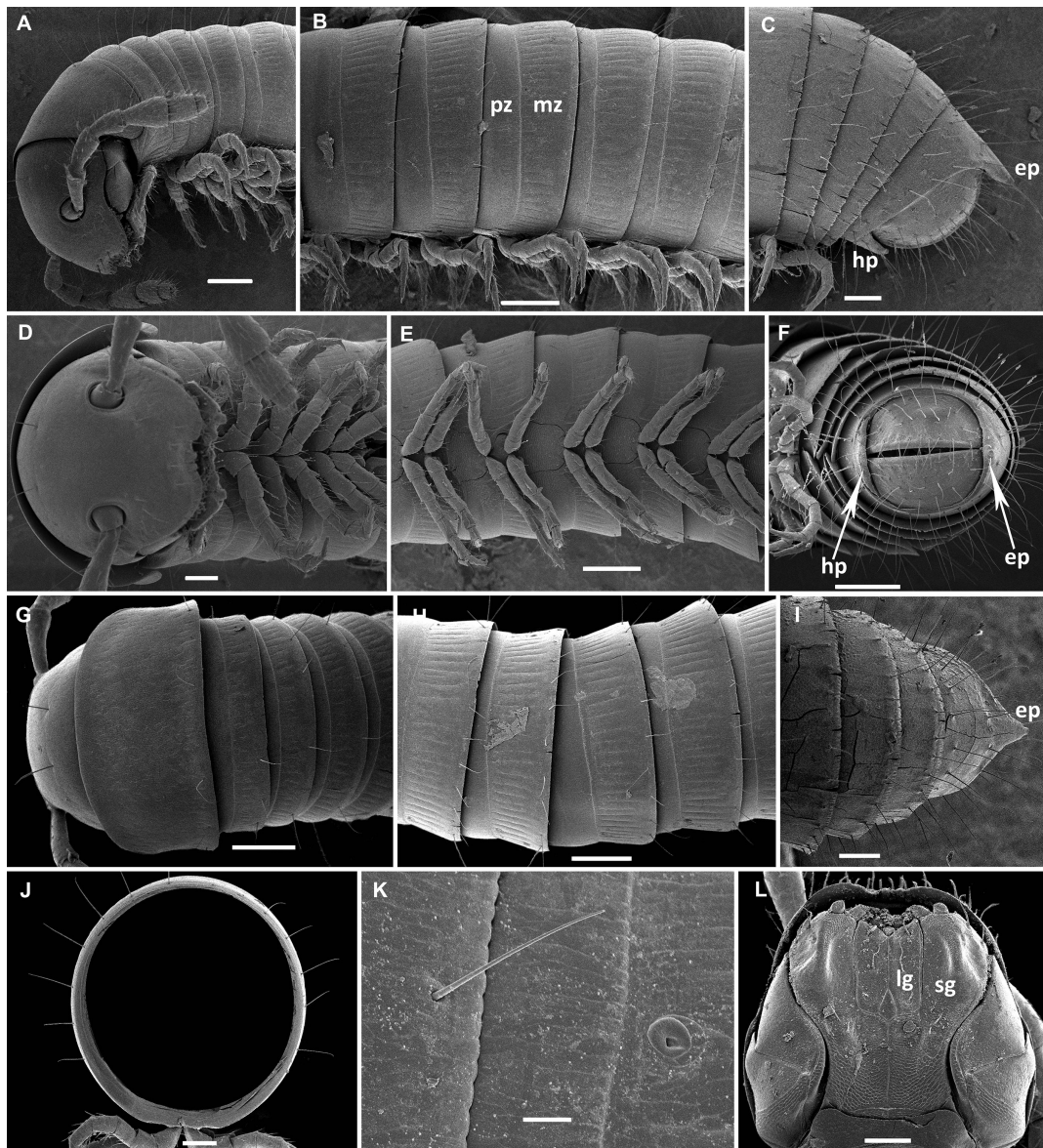
*Leptoiulus tiflisianus* Jawłowski, 1929: 51 (D); synonymized by Lohmander (1936).

*Leptoiulus tiflisianus*—Lohmander, 1936: 57 (M); Lang, 1959: 1791 (M).

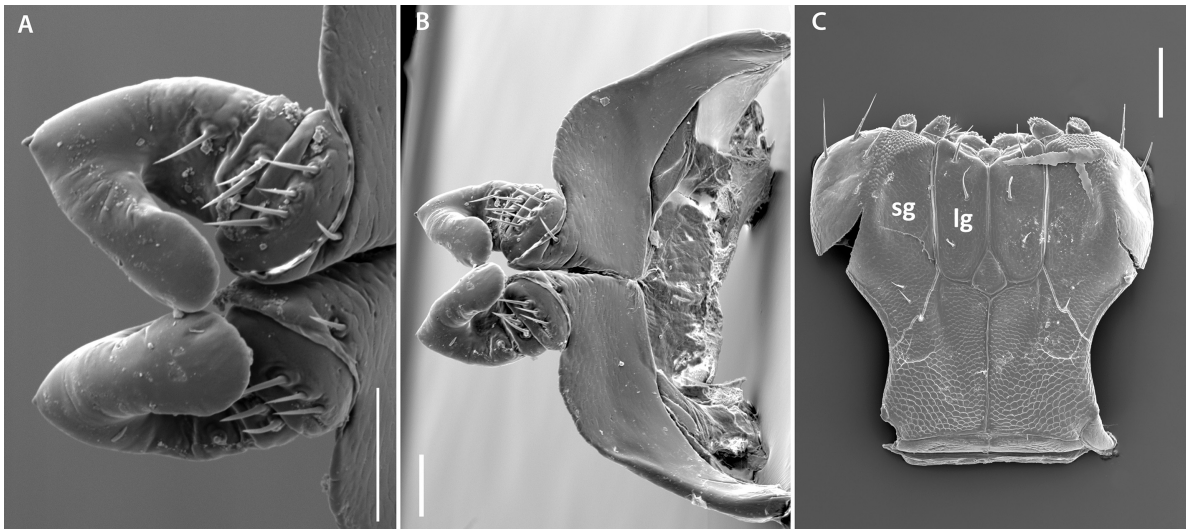
### **Material examined.**

**Azerbaijan:** 44 males, 64 females, 12 juv. (ZMUM), Shemakha Distr., Pirkuli, near Observatorium, 1200–1250 m a.s.l., *Quercus*, *Acer*, *Taxus* etc. forest, litter, 30.IV.1987. 24 males, 68 females, 14 juv. (ZMUM), Yarymja SE of Alty-Agach, 1320–1350 m a.s.l., *Fagus*, *Quercus*, *Carpinus* etc. forest, litter and under bark, 20, 24 and 25.IV.1987. 1 male, 3 females, 1 juv. (ZMUM), ca. 5 km N of Kutkashen, 1150–1200 m a.s.l., *Fagus* and *Carpinus* forest, litter and rotten wood, 2.V.1987. 41 males, 48 females, 6 juv. (ZMUM), SW of Kuba, 750 m a.s.l., *Fagus*, *Quercus*, *Carpinus* etc. forest, litter and under bark, 23.IV.1987. 1 male (ZMUM), same locality and date. 1 male, 1 female (ZMUM), Alty-Agach, 1050–1100 m a.s.l., *Quercus*, *Fagus*, *Carpinus* etc. forest, litter, 20 and 26.IV.1987. 3 males, 15 females, 2 juv. (ZMUM), ca. 12 km E of Ismailly, Girdyman-Chay River valley, 850–880 m a.s.l., *Fagus*, *Quercus*, *Carpinus*, *Acer* forest, litter and under bark, 1.V.1987. 7 males (ZMUM), Lesser Istisu halfway between Kelbajar and Istisu, 1550 m a.s.l., *Quercus* and *Acer* scrub on slope, litter, 31.V.1987, all leg. S. Golovatch and K. Eskov. 3 males, 6 females (ZMUM), above Akhsu, 120 km W of Baku, 900 m a.s.l., *Quercus* shrub, 22.V.1981, leg. S. Golovatch and J. Martens. 2 males, 6 females, 1 juv. (ZMUM), farm Azerbaijan ca. 10 km SE of Lerik, 550 m a.s.l., *Quercus*, *Carpinus*, *Acer* etc. forest along stream, litter, wood, 12.X.1983. 15 males, 22 females, 14 juv. (ZMUM), Istisu ca. 5 km SW of Masally, *Quercus*, *Acer*, *Carpinus* etc. forest, 80–140 m a.s.l., litter, under bark and stones, 19–20.X.1983. 25 males, 29 females (ZMUM), above Ajikend S of Ganja (former Kirovabad), 1400 m a.s.l., anthropogenous meadow, under stones, 3.V.1983. 8 males, 14 females, 2 juv. (ZMUM), Lenkoran, Apo below Bilasar, 350 m a.s.l., 8–9.VI.1996. 3 males, 4 females (ZMUM), Lenkoran Distr., Apo ca. 8 km SW of Alekseevka, *Quercus*, *Acer*, *Carpinus*, *Parrotia* etc. forest, litter, under stones and bark, 14 and 16.X.1983. 3 males, 13 females, 2 juv. (ZMUM), Divichi Distr., Kala-Alty ca. 20 km W of Siazan, 600 m a.s.l., *Quercus*, *Carpinus*, *Acer* etc. forest, litter, 12.VI.1983. 1 male (ZMUM), Yardymly, Avash, 1200–1500 m a.s.l., 14–17.VI.1996. 1 male, 1 female, Mountainous Karabakh, Dashalty near Shusha, 1100–1300 m a.s.l., *Quercus* and *Carpinus* forest, litter, logs, under stones, 1.V.1983, all leg. S. Golovatch. 1 male, 1 female (ZMUM), Shemakha Distr., farm Guseinzade, foothills,

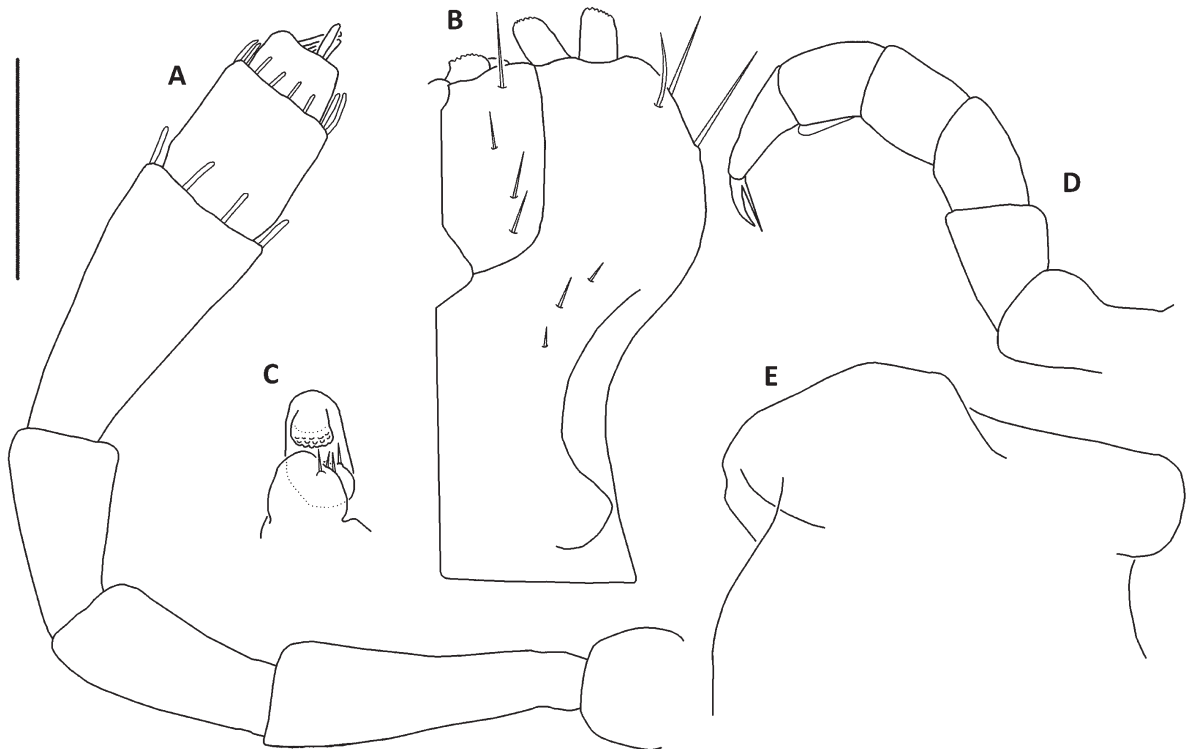
summer 1982, leg. A. Ismailov. 1 male, 1 female (ZMUM), Shemakha, Pirkuli, 24.VI.1988, leg. N. Loginova. 2 males (IZB), 1 male, 2 females (SMNG), Lerik Distr., Hyrcan Nature Reserve, Günəşli 2 km towards Lerik, *Quercus* forest in a small valley between pastures, 710 m a.s.l., 38.7975°N, 48.4644°E, 26.III.2015. 1 male (SMNG), Göygöl Distr., Çýraqdərə, *Quercus*, *Carpinus* with *Cornus* and *Acer*, low trees, litter, 1380 m a.s.l., 40.4596°N, 46.3297°E, 29.III.2015. 2 males, 1 female (SMNG), 1 male, 2 females (IZB), Yevlax Distr., N of Xanabad, sandy badlands, degraded steppe with deep-incised water channels, with scarce vegetation, various herbaceous plants, under stones and sheep dung, 110 m a.s.l., 40.8117°N, 47.1876°E, 29.III.2015. 1 male, 2 females (SMNG), 1 male, 1 female (IZB), Qəbələ Distr., Qəbələ towards Lake Nohur, slope of a small brook, mixed forest, *Fagus*, *Carpinus*, *Quercus*, *Castanea*, litter, 800 m a.s.l., 40.9682°N, 47.8639°E, 30.III.2015. 1 female, 1 juv. (IZB), Ýsmayýllý Distr., Xanəgah 2 km towards Ýsmayýllý, flat area with old *Fagus* forest, with channels, litter, 650 m a.s.l., 40.8233°N, 48.1518°E, 30.III.2015. 1 male, 5 females (SMNG), 6 females (IZB), S of Zərgəran, slope with *Corylus*, *Clematis* and some *Prunus* trees, stone heaps overgrown by moss, litter and under stones, 880 m a.s.l., 40.7310°N, 48.3680°E, 30.III.2015, all leg. H.S. Reip and D.Ž. Antić.



**FIGURE 24.** *Leptoiulus tanymorphus* (Attems, 1901) male from near Kuba, Azerbaijan. **A–C:** anterior, middle and posterior parts of body, respectively, lateral views. **D:** same, respectively, ventral views. **E:** middle part of body, ventral view. **F:** posterior part of body, ventrocaudal view. **G–I:** anterior, middle and posterior parts of body, respectively, dorsal view. **J:** midbody ring, frontal view. **K:** seta and ozopore on body ring, lateral view. **L:** head, ventral view. **Abbreviations:** ep, epiproct; hp, hypoproct; lg, lamella lingualis of gnathochilarium; mz, metazona; pz, prozona; sg, stipes of gnathochilarium. Scale bars: 0.2 mm (A, B, E–H), 0.1 mm (C, D, I, J, L) or 0.05 mm (K).



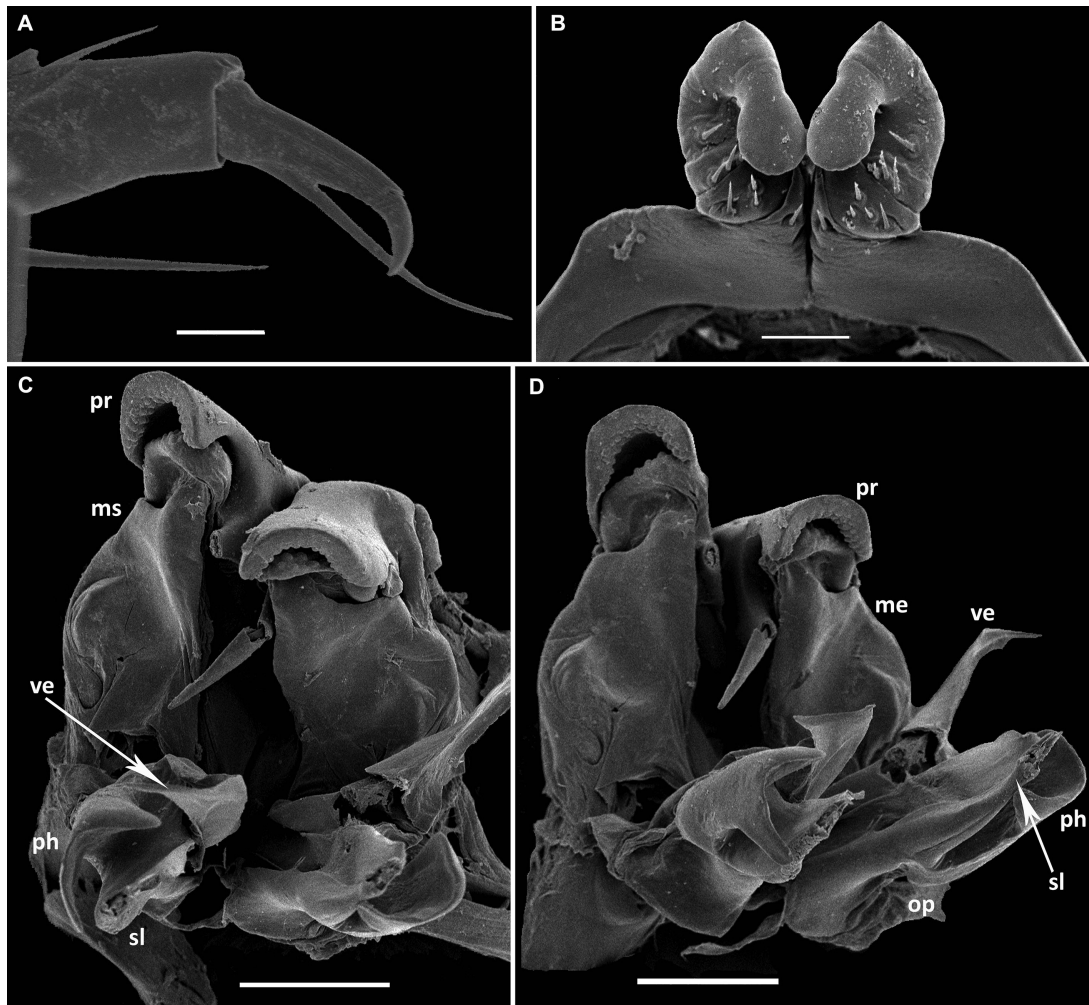
**FIGURE 25.** *Leptoiulus tanymorphus*, male from Zərgəran, Ýsmayýllý, Azerbaijan. **A:** leg pair 1, anteriolateral view. **B:** leg pair 1, anterior view. **C:** gnathochilarium, lateral view. **Abbreviations:** **lg**, lamella lingualis of gnathochilarium; **sg**, stipes of gnathochilarium. Scale bars: A, B: 0.05 mm, C: 0.1 mm.



**FIGURE 26.** *Leptoiulus tanymorphus* (Attems, 1901), male from Ismailly, Azerbaijan. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.

**Armenia:** 4 males, 10 females (ZMUM), Dilizhan Nature Reserve, Akhnabat valley near Salakh, 1400–1500 m a.s.l., *Fagus*, *Taxus*, *Carpinus* etc. forest, litter, under bark and stones, 17.IV.1983. 1 male (ZMUM), environs of Megri, xerophytous bare canyon, under stones, sparse *Juniperus* and *Paliurus*, ca. 1000 m a.s.l., 24.IV.1983. 1 male, 6 females (ZMUM), ca. 4 km NNW of Megri, Legvaz, *Juglans* and *Quercus* shrub with *Paliurus* and *Rosa*, 1000 m a.s.l., litter and under stones, 24–25.IV.1983. 11 males, 33 females (ZMUM), Megri Distr., SSE of Lichk, Megri River valley, *Quercus* forest, 1530 m a.s.l., litter, under stones and bark, 25.IV.1983. 1 male (ZMUM), same locality and date. 3 males, 7 females, 1 juv. (ZMUM), Kafan Distr., Shikahoh Nature Reserve, Shikahoh, 900–950 m a.s.l., *Quercus*, *Fagus*, *Carpinus* forest near spring, litter, logs and under stones, 28.IV.1983. 9 females (ZMUM),

same locality and date. 2 males, 2 females (ZMUM), same locality, Tsav, 1000 m a.s.l., *Quercus*, *Fagus*, *Carpinus* forest, litter, 29.IV.1983. 2 males, 2 females, 1 juv. (ZMUM), same locality, Shishkert, 1700–1800 m a.s.l., *Quercus*, *Fagus* and *Carpinus* forest, litter and under stones, 29.IV.1983. 7 males, 10 females (ZMUM), W of Shamshadyn halfway between Ijevan and Berd, 1500–1600 m a.s.l., *Fagus*, *Carpinus*, *Acer* etc. forest, litter and under bark, 26–27.V.1987, all leg. S. Golovatch. 13 males, 8 females, 10 juv. (ZMUM), Khosrov Nature Reserve, 1700–1900 m a.s.l., forest, slope, 12.V.1984. 1 male (ZMUM), same locality and date. 1 female (ZMUM), Megri, 25.IV.1983, 1 male, 3 females (ZMUM), Megri Distr., Nyuvadi, xerophytous gorge, under stones, 25.IV.1983, all leg. V. Yanushev.

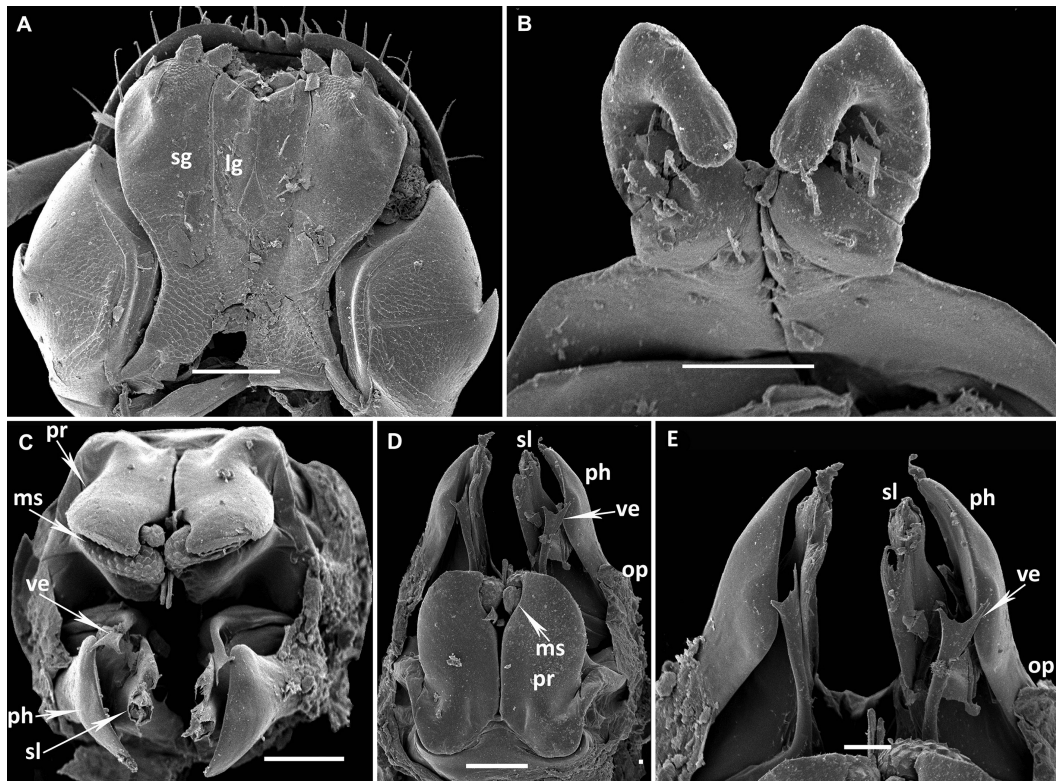


**FIGURE 27.** *Leptoiulus tanymorphus* (Attems, 1901), male from near Kuba, Azerbaijan. **A:** tip of leg 2, caudal view. **B:** leg-pair 1, caudal view. **C & D:** gonopods, ventral and ventrolateral views, respectively. **Abbreviations:** fl, flagellum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.01 mm (A), 0.05 mm (B), 0.1 mm (C, D).

**Georgia:** 1 male, 2 females (ZMUM), Vashlovani Nature Reserve, *Pistacia* forest, 29.IV.1972. 2 males, 1 female (ZMUM), same locality and date. 1 male (ZMUM), same locality and date, all leg. M. Ghilarov. 7 males, 25 females (ZMUM), same locality, sparse *Juniperus* and *Pistacia* forest, 500–580 m a.s.l., litter, under stones, 7–9.V.1983, leg. S. Golovatch. 2 males, 4 females (ZMUM), Bolnisi Distr., Safarloo SSW of Patara Dmanisi, 1000–1050 m a.s.l., *Quercus*, *Fagus*, *Acer* etc. forest, litter, 21.V.1987, leg. S. Golovatch and K. Eskov. 4 females (ZMUM), E of Kasristskali, salt swamp, *Scirpus*, 7.V.1983, leg. V. Yanushev. 1 male, 1 female (SMNG), Tbilisi, Botanical Garden, 450 m a.s.l., 41°41'14"N, 44°48'30"E, 01.XI.2009, leg. F. Walther.

**Russia, Dagestan:** 2 males, 3 females, 3 juv. (ZMUM), Akhty Distr., above Mirakh ca. 15 km SSW of Usukhchay, 1800 m a.s.l., *Betula* forest with *Salix* and *Alnus* at timberline, 10.VII.1989. 2 females (ZMUM), N Kurush ca 30 km SSW of Usukhchay, 2500–2800 m a.s.l., alpine meadow, 7–13.VII.1989. 17 males, 44 females, 2 juv. (ZMUM), 4

km E of Sergokala, *Quercus* and *Crataegus* scrub, litter and under stones, 7.VI.1982. 1 female (ZMUM), Sergokala Distr., near Degva, *Quercus* forest on slope, litter, 9.VI.1982, all leg. S. Golovatch.



**FIGURE 28.** *Leptoiulus tanymorphus* (Attems, 1901), male from Khosrov Nature Reserve, Armenia. **A:** head, ventral view. **B:** leg-pair 1, caudal view. **C & D:** gonopods, ventral and frontoventral views, respectively. **E:** opisthomere of gonopod, frontal view. **Abbreviations:** **fl**, flagellum; **lg**, lamella lingualis of gnathochilarium; **ms**, mesomere; **op**, opisthomere; **ph**, phylacum; **pr**, promere; **sg**, stipes of gnathochilarium; **sl**, solenomere; **ve**, velum. Scale bars: 0.1 mm (A), 0.05 mm (B–D), 0.02 mm (E).

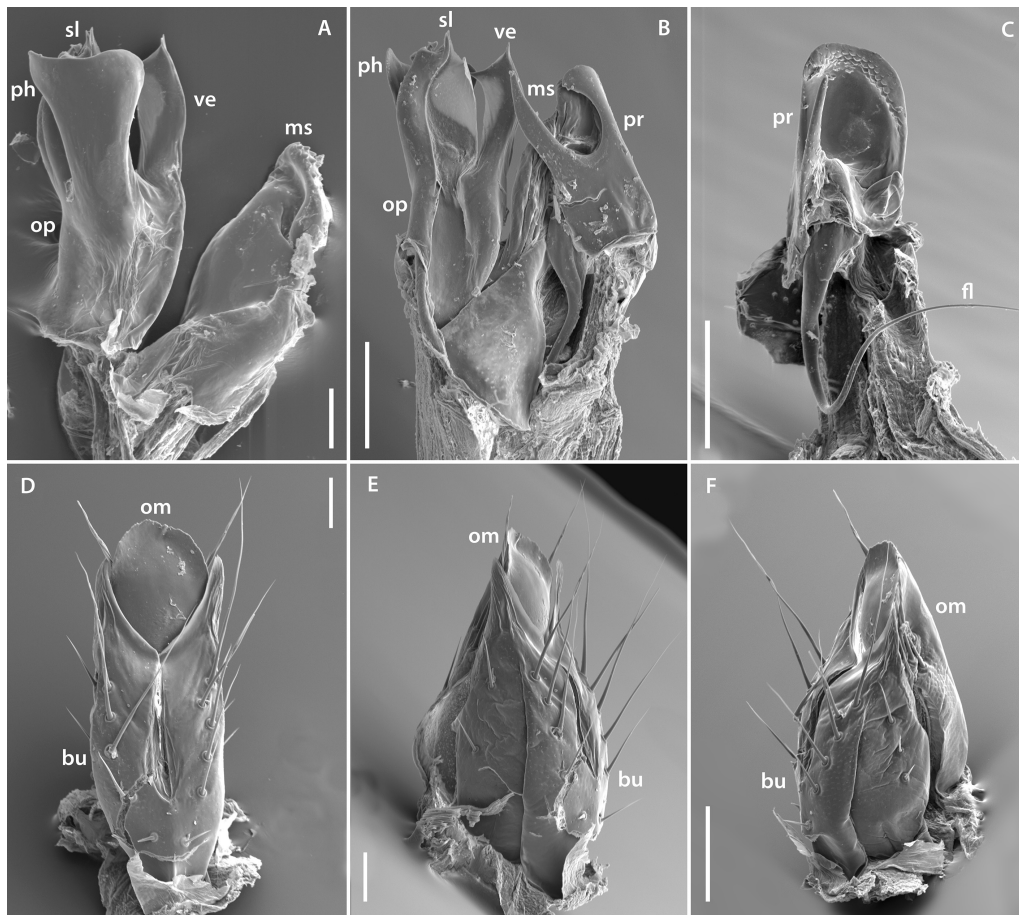
**Diagnosis.** Differs from congeners by a combination of the following gonopodal characteristics: promere and its mesal spike subequal in length/height; velum long, flattened and angular apically; phylacum broad.

**Descriptive notes.** Length of adults 10–18 mm, width 0.6–1.0 mm. Number of segments in adults from 38+4+T to 59+2+T. Males collected at Lesser Istisu (Azerbaijan) were larger than those from other samples: length 21–28 mm, width 0.8–1.1 mm, body segment formula from 66+2+T to 75+3+T (Fig. 43, blue square with dots). Body subcylindrical (Fig. 24J), from brown to brownish grey, legs and antennae yellow (Fig. 15B). Eye patches suboval, each composed of 15–20 ommatidia. Striations on metazonae regular, deep, striae not reaching the caudal margin (Figs 24A–C, 24G–H). Collum and metazonae with a row of setae at posterior margin (Figs 24A–24I).

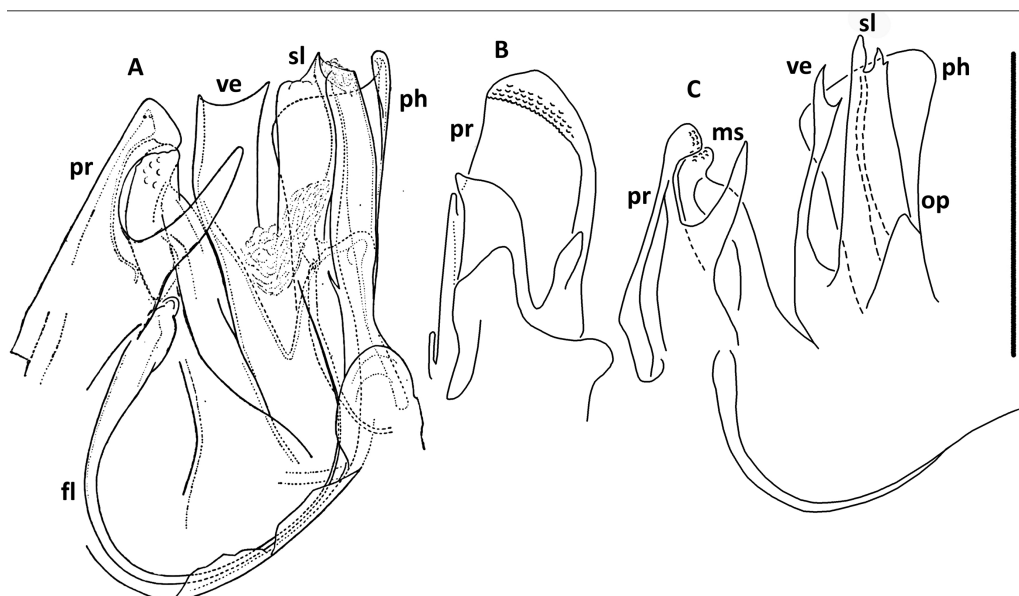
Antennae relatively long, *in situ* reaching segment 4; a complete corolla of bacilliform sensilla on antennomeres 5 and 6: sparse and longer bacilli on 5<sup>th</sup>, denser and shorter bacilli on 6<sup>th</sup> (Figs 24A, 26A). Head with 5+5–6+6 labral setae, 2+2 supralabral setae, and 4+4–6+6 at base of antennae (Fig. 24A, D). Gnathochilarium with 3 or 4 long setae on each lamella lingualis; groups of 2 or 3 short setae on stipites (Figs 24L, 25C, 26B). Epiproct subtriangular, straight, with a short claw (Fig. 24C, I). Hypoproct subtriangular, with 3+3 setae (Fig. 24F).

**MALE.** Leg-pair 1 small, unciform, with a group of setae on each coxa; telopodite with a field of papillae in apical part (Figs 25A, B, 26C, 27B, 28B). Leg-pair 2 with a pad on each tibia (Fig. 26D); an accessory claw clearly longer than claw itself (Figs 26D, 27A). Penes short, bifurcated on top.

All three parts of gonopods (Figs 27C, D, 28C–E, 29B, 30A, C) forming a tight block. Promere (**pr**) spoon-shaped, with lamellae and a long spike at mesal margin, with small tubercles in distomesal part (Figs 27C, D, 28C, D, 29A–C, 30A–C). Flagella (**fl**) relatively short (Figs 29C, 30A, C). Mesomere (**ms**) simple, lower/shorter than **pr**, in apical part with small tubercles (Figs 27C, D, 28C, D, 29A, B, 20A, C). Velum (**ve**) of opisthomere (**op**) concave at apical part, higher/longer than **pr**, variable in width: relatively broad (Figs 29A, B, 30A) to narrow (Figs 27C, D, 28C–E, 30C). Solenomere (**sl**) elongate, narrow, with spines in apical part, higher/longer than both **pr** and **ve** (Figs 27C, D, 28C–E, 29A, B, 30A, C). Phylacum (**ph**) broad and curved, higher/longer than both **pr** and **ve**.



**FIGURE 29.** *Leptoiulus tanymorphus*, male from Zərgəran, Ýsmayýllý, Azerbaijan. **A:** gonopods without promere, lateral view. **B:** gonopods, mesal view. **C:** promere of gonopod, posterior view. Female from same place as male. **D:** vulva, posterior view, **E:** vulva, lateral view. **F:** vulva, mesal view. **Abbreviations:** bu, bursa; fl, flagellum; om, operculum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.05 mm (A, D, E) or 0.1 mm (B, C, F).

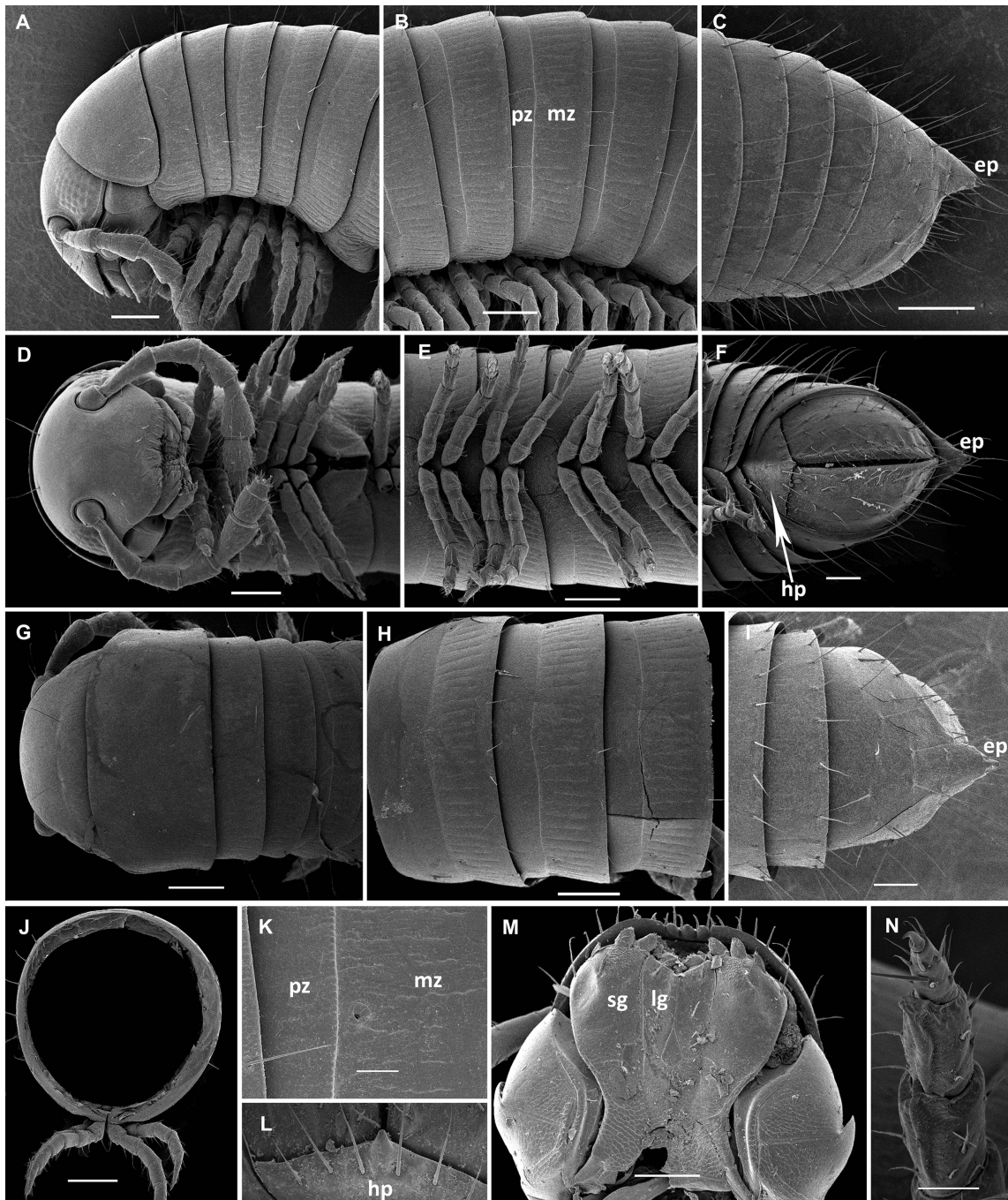


**FIGURE 30.** *Leptoiulus tanymorphus* (Attems, 1901) (**A**, male, after Lohmander (1936), **B** and **C**, male from near Shamshadyn, Armenia). **A:** gonopods, mesal view. **B:** promere of gonopod, caudal view. **C:** gonopod, mesal view. **Abbreviations:** fl, flagellum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bar 0.2 mm (B) or drawn not to scale (A, C).

Ventral edge of male segment 7 with small curved lamellae bordering the gonopodal aperture (Fig. 26E).

**FEMALE.** First two leg-pairs unmodified. Vulva elongated, covered with long setae (Figs 29D–F, 42E). Operculum (**om**) subtriangular apically. Median field (**mf**) of bursa (**bu**) long, emargination (**em**) of **mf** suboval. Receptaculum seminis (**rs**) consisting of two tubes. One tube short with a rounded ampulla (**a**), the second tube long and coiled, with a similarly rounded ampulla (**a**).

**Remarks.** *Leptoiulus tanymorphus* is the most widespread Leptoiulini species in the eastern half of the Caucasus, recorded from both the Caucasus Major and Caucasus Minor: Georgia, Armenia, Azerbaijan and Dagestan, Russia.



**FIGURE 31.** *Leptoiulus meskhii* sp. nov., male paratype from Galabyn, Azerbaijan. **A–C:** anterior, middle and posterior parts of body, respectively, lateral views. **D–F:** anterior, middle and posterior parts of body, respectively, ventral views. **G–I:** same, respectively, dorsal views. **J:** midbody ring, frontal view. **K:** ozopore, lateral view. **L** hypoproct, ventral view. **M:** head, ventral view. **N:** tip of leg 2, ventrocaudal view. **Abbreviations:** **ep**, epiproct; **hp**, hypoproct; **lg**, lamella lingualis of gnathochilarium; **mz**, metazona; **pz**, prozona; **sg**, stipes of gnathochilarium. Scale bars: 0.2 mm (**A–E**), 0.1 mm (**F**, **I**, **M**) or 0.05 mm (**K**, **L**, **N**).



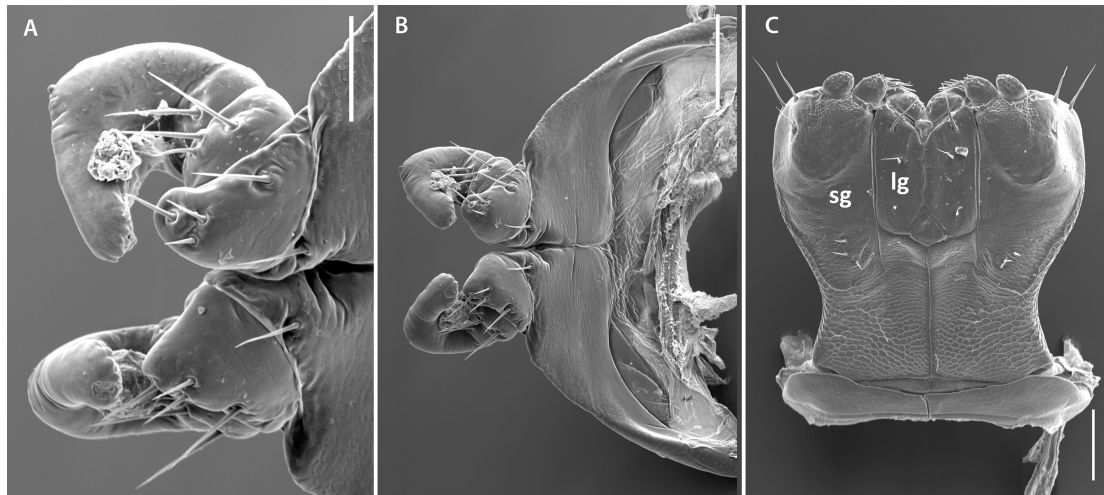
*Leptoiulus meskhii* sp. nov.

Figs 15C, 31, 32, 33, 34, 35, 36, 41F, Map 2

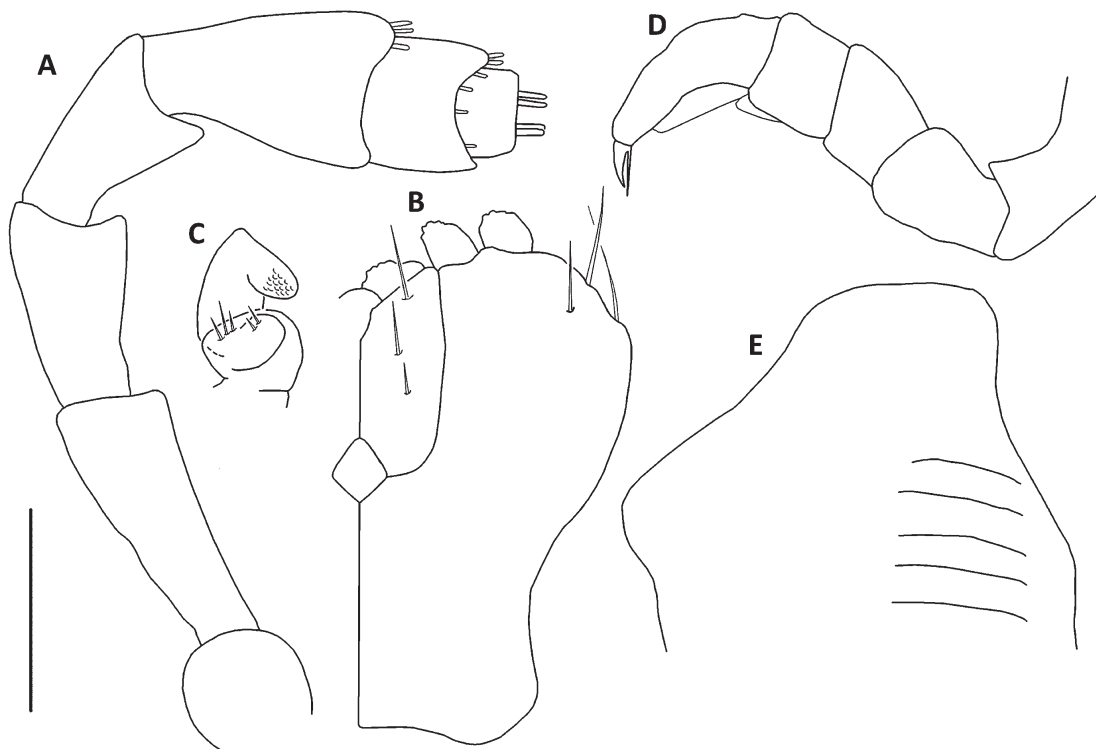
**Type material.**

**Holotype male** (ZMUM), **Azerbaijan**, Talysh Mts, Lerik Distr., Zuvand, Galabyn, 1700–2000 m a.s.l., under stones on slopes, 10–11.X.1983, leg. S. Golovatch.

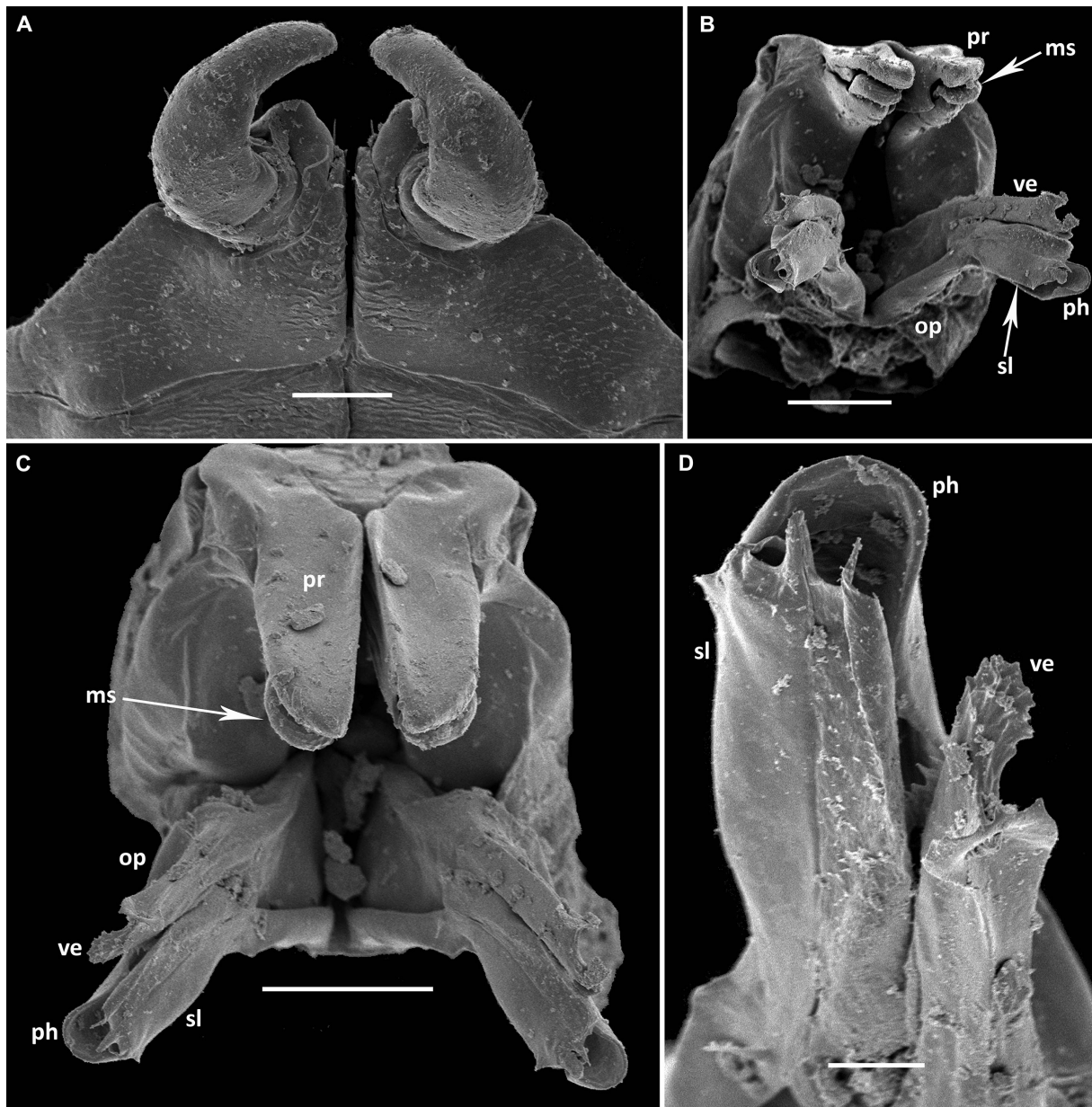
**Paratypes.** 18 males, 16 females (ZMUM), same locality and date, together with holotype. 1 male (ZMUM), same locality and date. 10 males, 5 females (ZMUM), same locality, but near Gosmalyan, 2.V.1996, 1 male (ZMUM), same locality and date, all leg. O. Gorbunov. 6 males, 7 females (SMNG), 4 males, 6 females (IZB), Talysh Mts, Lerik Distr., northern part of gorge between Blaband and Hoveri, exposed rock, 1160 m a.s.l., 38.7250°N, 48.4319°E, 26.III.2015, all leg. H.S. Reip and D.Ž. Antić.



**FIGURE 32.** *Leptoiulus meskhii* sp. nov., male from Hoveri, Lerik, Azerbaijan. **A:** leg pair 1, anterolateral view. **B:** leg pair 1, anterior view. **C:** gnathochilarium, ventral view. **Abbreviations:** **lg**, lamella lingualis of gnathochilarium; **sg**, stipes of gnathochilarium. Scale bars: **A:** 0.05 mm (**A**) or 0,1 mm (**B, C**).



**FIGURE 33.** *Leptoiulus meskhii* sp. nov., male paratype from Galabyn, Azerbaijan. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.



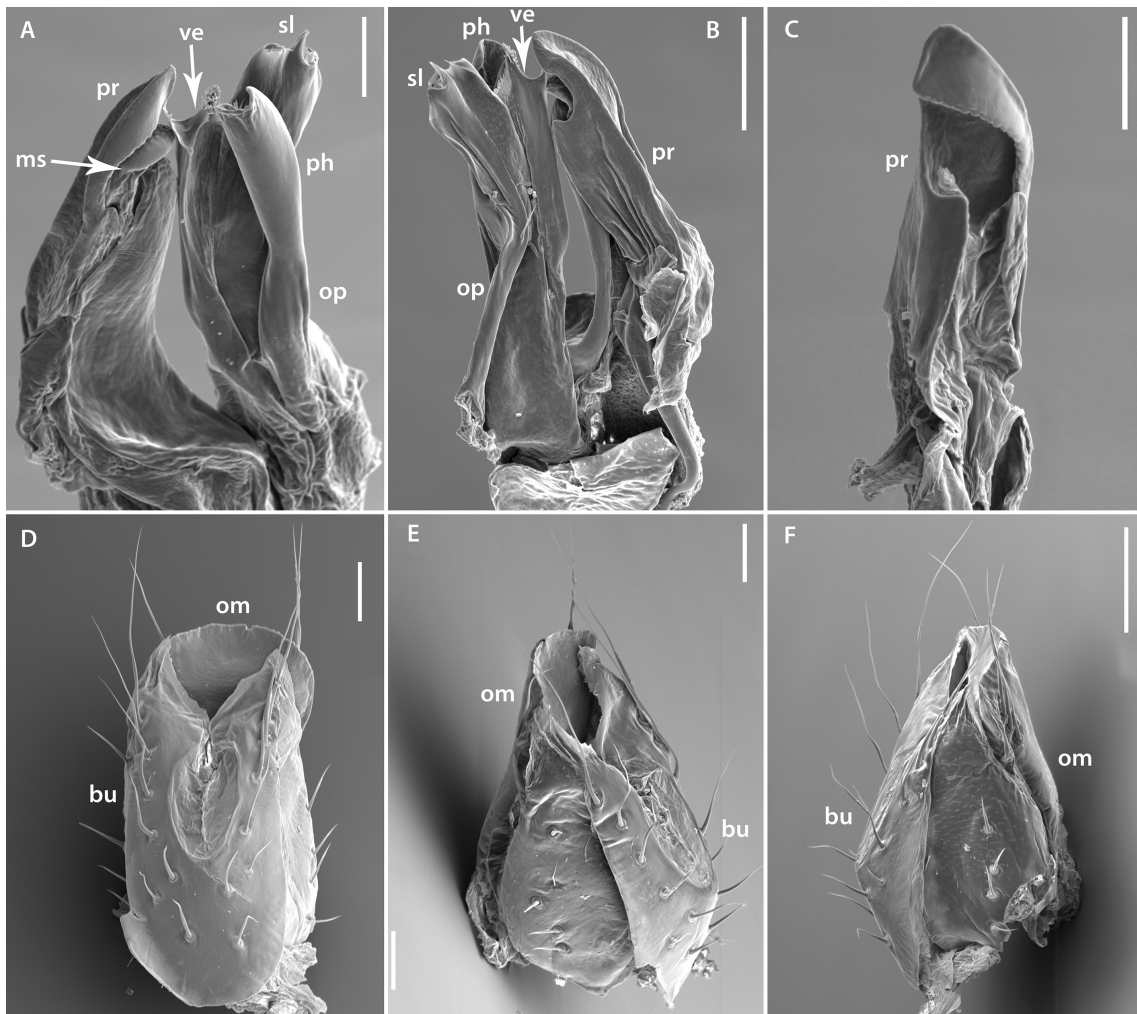
**FIGURE 34.** *Leptoionulus meshkii* sp. nov., male paratype from Galabyn, Azerbaijan. **A:** leg-pair 1, frontoventral view. **B & C:** gonopods, ventrolateral and ventrocaudal views, respectively. **D:** opisthomere of gonopod, mesal view. **Abbreviations:** fl, flagellum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.05 mm (A), 0.1 mm (B, C) or 0.02 mm (D).

#### Non-type material examined.

**Azerbaijan:** 2 males, 2 females, 1 juv. (SMNG), 1 male, 1 female (IZB), Talysh Mts, Lerik Distr., southern entrance of gorge between Blaband and Hoveri, north-facing slope, 1260 m a.s.l., 38.7094°N, 48.4226°E, 26.III.2015. 5 males, 6 females, 1 juv. (SMNG), 5 males, 5 females, 1 juv. (IZB), large side valley of gorge between Blaband and Hoveri, stone on pasture, 1240 m a.s.l., 38.7229°N, 48.4230°E, 26.III.2015. 4 males, 3 females, 1 juv. (SMNG), 3 males, 2 females, 1 juv. (IZB), Hoveri 0.75 km towards Qosmalýan, semi-desert, under large stones, 1300 m a.s.l., 38.6966°N, 48.4100°E, 26.III.2015, all leg. H.S. Reip and D.Ž. Antić.

**Diagnosis.** Differs from other species of the genus by the following combination of gonopodal characters: promere relatively narrow and flat, velum with a dentate lamella in anterior part and a dentate field in apical part, solenomere with two spikes at apex.

**Etymology.** To honour Professor Besarion Meskhi, Rector of the Don State Technical University; noun in apposition.



**FIGURE 35.** *Leptoiulus meskhii* sp. nov., male from Hoveri, Lerik, Azerbaijan. **A:** gonopods, lateral view. **B:** gonopods, mesal view. **C:** promere of gonopod, posterior view. Female from same place as male. **D:** vulva, posterior view, **E:** vulva, lateral view. **F:** vulva, mesal view. **Abbreviations:** bu, bursa; om, operculum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.05 mm (A, C, D, E) or 0.1 mm (B, F).

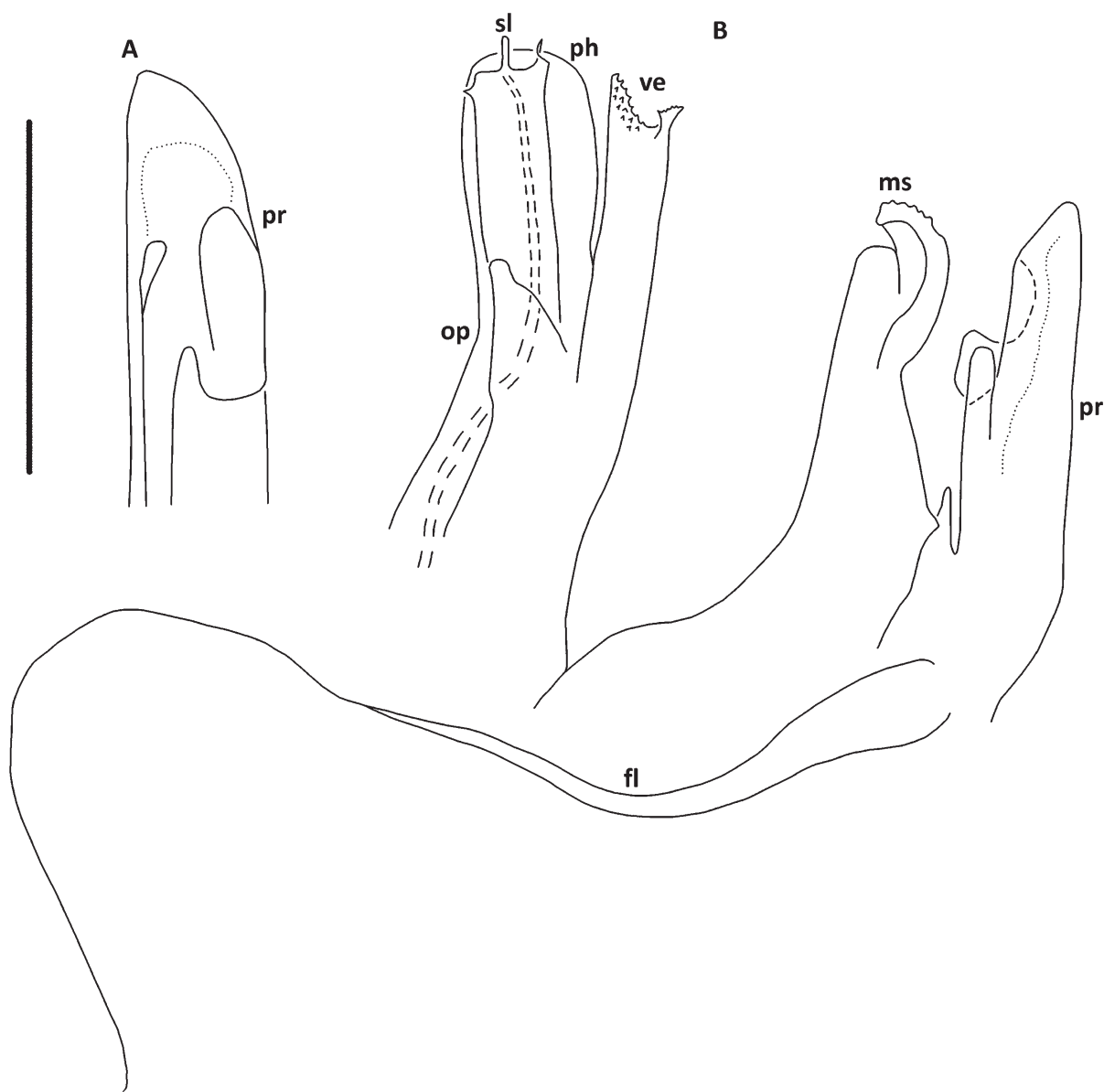
**Description.** Length 13–18 mm, width 0.8–1.1 mm (female), or length 12–18 mm, width 0.8–1.0 mm (male). Body segment formula: from 43+3+T to 59+2+T (male) or from 47+3+T to 53+2+T (female). Body, head and collum marbled brownish grey, legs yellow, antennae brown (Fig. 15D).

Eye patches subtriangular, each composed of 13–20 ommatidia. Epicranial setae 1+1, supralabral setae 2+2, labral setae 4+4–5+5, and 3+3–4+4 at base of antennae (Figs 31A, D). Genae unmodified. Antennae relatively long, *in situ* reaching segment 4; an incomplete corolla bacilliform sensilla on antennomere 5, a complete one of shorter bacilli on antennomere 6 (Figs 31D, 33A).

Each lamella lingualis of gnathochilarium with three long setae. Stipites with 0–3 setae in central part (Figs 31M, 32C, 33B).

Body subcylindrical (Fig. 31J). Male segment 7 thicker than others. Suture dividing pro- and metazonae distinctly constricting both. Ozopores small, lying behind suture without touching it (Fig. 31K). Metazonae with regular striations reaching the caudal margin, the latter with a relatively dense row of setae (Fig. 31A–E). Epiproct subtriangular, short, with long setae (Figs 31C, 31F). Anal valves convex, densely setose (Fig. 31F). Hypoproct broadly triangular, with 3+3 setae.

**MALE.** Ventral edge of segment 7 with small and curved lamellae bordering the gonopodal aperture (Figs 31D, 33E). Leg-pair 1 unciform; a group of short setae in basal part, telopodite with small tubercles at apex (Figs 32A, B, 33C, 34A). Leg-pair 2 with pads on tibia and tarsus, an accessory claw slightly longer than claw itself (Figs 31N, 33D). Penes bifurcated at apex.



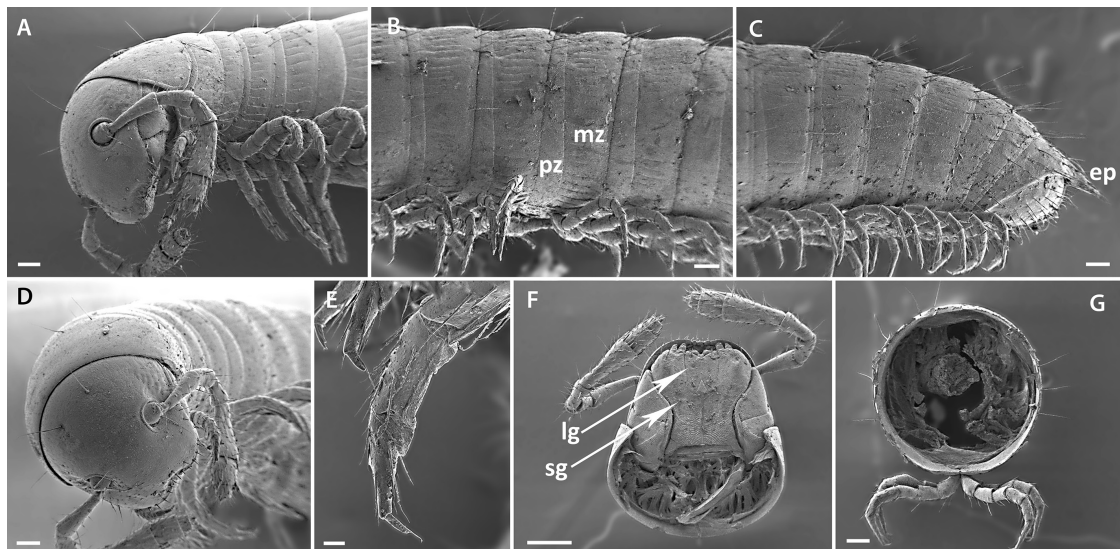
**FIGURE 36.** *Leptoiulus meskhii* sp. nov., male paratype from Galabyn, Azerbaijan. **A:** promere of gonopod, caudal view. **B:** gonopod, mesal view. **Abbreviations:** **fl**, flagellum; **ms**, mesomere; **op**, opisthomere; **ph**, phylacum; **pr**, promere; **sl**, solenomere; **ve**, velum. Scale bar: 0.2 mm.

All three parts of gonopods (Figs 34B, C, 35A, B, 36B) forming a tight block. Promere (**pr**) flat and rather narrow, with a square rounded process in the middle along mesal margin and a lamella at external edge (Figs 34B, C, 35B, C, 36A, B). Flagella (**fl**) very long (Fig. 36B). Mesomere (**ms**) lower/shorter than **pr**, in apical part with a curved lobe covered with small tubercles (Figs 34B, C, 35A, B, 36B). Velum (**ve**) of opisthomere (**op**) narrow, with a dentate lamella in anterior part and a dentate field in apical part, higher/longer than both **pr** and **ms**, but lower/shorter than both **sl** and **ph**. Solenomere (**sl**) relatively broad, with two spikes at apex and another one at posterior margin, higher/longer than **pr**, **ms** and **ve**. Phylacum (**ph**) slightly curved, about as high as **sl** (Figs 34B, D, 35A, B, 36B).

**FEMALE.** First two leg-pairs unmodified.

Vulva relatively broad, covered with long setae (Figs 35D–F, 42F). Operculum (**om**) weakly M-shaped. Median field (**mf**) of bursa (**bu**) broad, with a small tubercle. Emargination (**em**) of **mf** suboval. Receptaculum seminis (**rs**) with two tubes, only one of which bearing a rounded ampulla (**a**).

**Remark.** This species seems to be narrowly endemic to the Talysh Mountains in the Republic of Azerbaijan (Map 2), but it is most likely to occur also in the adjacent parts of NW Iran.



**FIGURE 37.** *Leptoiulus gonopodialis* sp. nov., male paratype from Lagodekhi Nature Reserve, Georgia. **A–C:** anterior, middle and posterior parts of body, respectively, lateral views. **D:** anterior part of body, frontolateral view. **E:** tip of leg 2, frontal view. **F:** head, ventral view. **G:** midbody ring, frontal view. **Abbreviations:** ep, epiproct; lg, lamella lingualis of gnathochilarium; mz, metazona; pz, prozona; sg, stipes of gnathochilarium. Scale bars: 0.1 mm (A–D, G), 0.02 (E) or 0.2 (F).

***Leptoiulus gonopodialis* sp. nov.**

**Figs 15D, 37, 38, 39, 40, 41, 41G, Map 2**

**Type material.**

**Holotype male** (ZMUM), **Georgia**, Lagodekhi Nature Reserve, *Fagus*, *Fraxinus*, *Acer* etc. forest, 600–700 m a.s.l., litter, under bark and stones, 5–6.V.1983, leg. S. Golovatch.

**Paratypes.** 18 males, 44 females (ZMUM), same locality and date, together with holotype. 1 male, 1 female (ZMUM), same locality as holotype, but along trail to meteorological station, *Carpinus* forest, 41°51'38"N, 46°20'27"E, 1830 m a.s.l., 27.VII.2012, leg. Y. Marusik. 1 male (ZMUM), **Azerbaijan**, Zakatali Nature Reserve, Katekh-Chai River valley, 800–1200 m a.s.l., 23.V.1981, leg. S. Golovatch and J. Martens.

**Diagnosis.** Differs from congeners in its gonopodal structure: promere with a very long spike, velum with fine teeth on top, solenomere with a posterior lobe-shaped part.

**Etymology.** To emphasize the complex gonopodal structure; adjective.

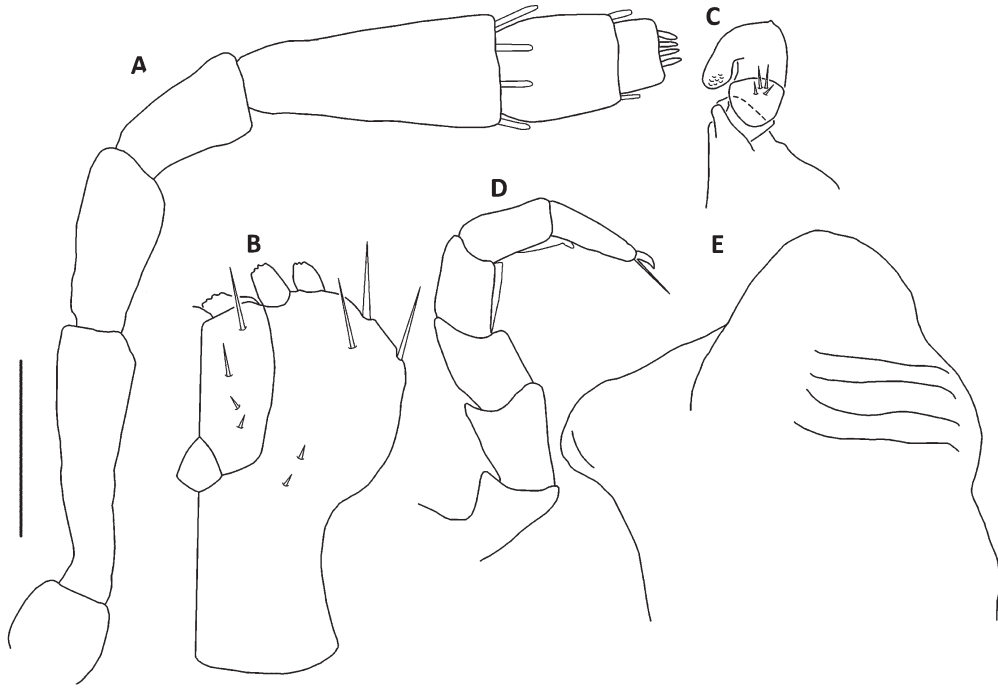
**Description.** Length 8–14 mm, width 0.6–1.1 mm (female), or length 10–12 mm, width 0.7–0.9 mm (male). Body segment formula: from 33+4+T to 41+3+T (male) and from 32+2+T to 44+4+T (female). Body, head and collum marbled greyish yellow, legs and antennae yellow (Fig. 15D).

Eye patches suboval, each composed of 13–15 ommatidia. Epicranial setae 1+1, supralabral setae 2+2, labral setae 5+5–6+6, and 3+3–4+4 at base of antennae (Figs 37A, 37D). Genae unmodified. Antennae long, *in situ* reaching segment 5; a corolla of bacilliform sensilla on antennomeres 5 and 6, complete on 5<sup>th</sup>, incomplete and of shorter bacilli on 6<sup>th</sup> (Figs 37A, 37A).

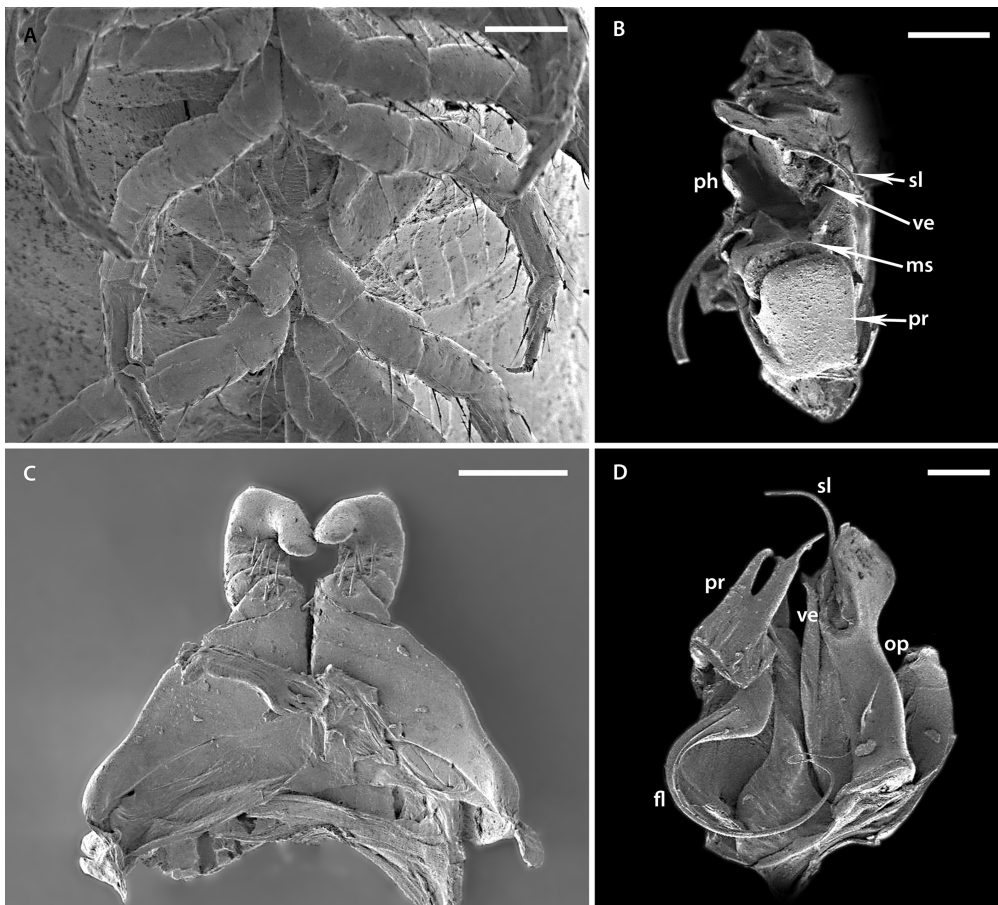
Each lamella lingualis of gnathochilarium with two short and two long setae. Stipites with a group of 2 or 3 short setae in central part (Figs 37F, 38B).

Body subcylindrical (Fig. 37G). Male segment 7 thicker than others. Suture dividing pro- and metazonae distinctly constricting both. Ozopores small, lying behind suture without touching it. Metazonae with regular striations reaching the caudal margin, the latter with relatively dense rows of setae (Figs 37A–C). Epiproct subtriangular, with long setae. Anal valves convex, densely setose (Fig. 37C). Hypoproct broadly triangular, with 2+2 setae.

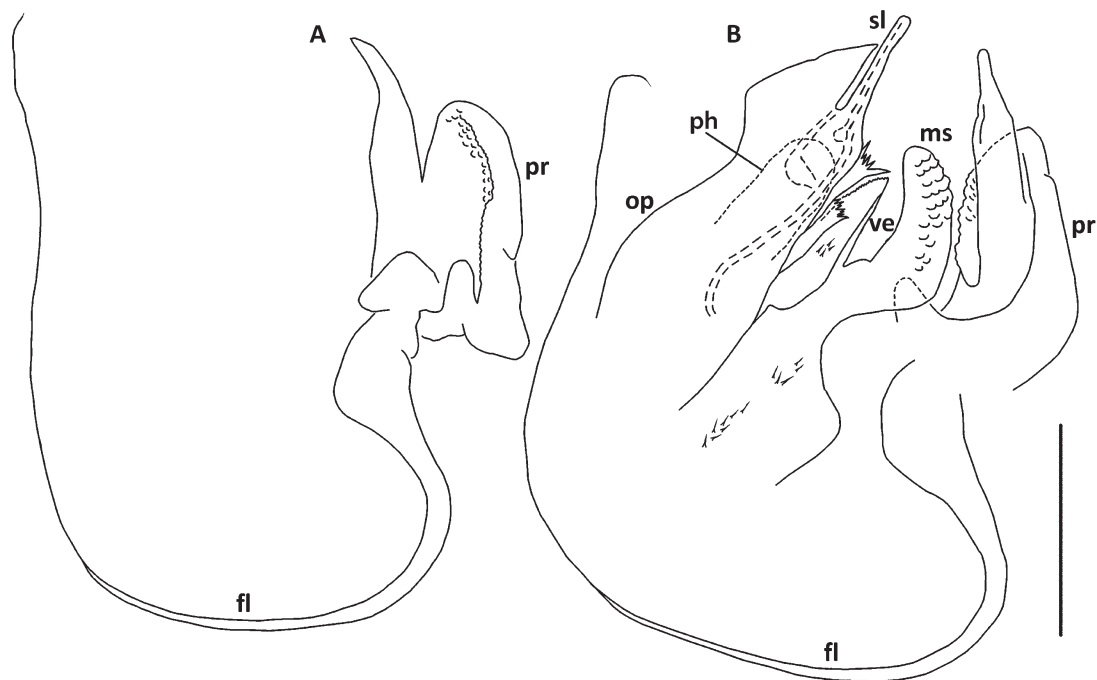
**MALE.** Ventral edge of segment 7 with small curved lamellae bordering the gonopodal aperture (Figs 38E, 39A). Leg-pair 1 uniform; a group of short setae in basal part; telopodite with small tubercles at apex (Figs 38C, 39B). Leg-pair 2 with pads on postfemur and tibia, an accessory claw longer than claw itself (Figs 37E, 38D). Penes bifurcated at apex.



**FIGURE 38.** *Leptoiulus gonopodialis* sp. nov., male paratype from Lagodekhi Nature Reserve, Georgia. **A:** antenna, lateral view. **B:** gnathochilarium, ventral view. **C:** leg 1, caudal view. **D:** leg 2, caudal view. **E:** ventral edge of segment 7, lateral view. Scale bar: 0.2 mm.



**FIGURE 39.** *Leptoiulus gonopodialis* sp. nov., male paratype from Lagodekhi Nature Reserve, Georgia. **A:** segment 7, fronto-ventral view. **B:** leg-pair 2, caudal view. **C & D:** gonopod, ventral and mesal views, respectively. **Abbreviations:** fl, flagellum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bars: 0.1 mm.



**FIGURE 40.** *Leptoiulus gonopodialis* sp. nov., male paratype from Lagodekhi Nature Reserve, Georgia. **A:** promere of gonopod with flagellum, caudal view **B:** gonopod, mesal view. **Abbreviations:** fl, flagellum; ms, mesomere; op, opisthomere; ph, phylacum; pr, promere; sl, solenomere; ve, velum. Scale bar: 0.2 mm.

All three parts of gonopods (Figs 39C, D, 40B) forming a tight block. Promere (**pr**) spoon-shaped, with small tubercles in distal part and along mesal edge; external margin with a very large, long and thick spike exceeding **pr** in height; basal part with a lamella (Figs 39D, 40A, B). Flagella (**fl**) relatively long (Figs 39D, 40A, B) Mesomere (**ms**) simple, lower/shorter than **pr**, both apical and anterior parts with small tubercles (Figs 39C, 40B). Velum (**ve**) of opisthomere (**op**) short, attenuating distad, finely denticulate on top, lower, shorter than other gonopodal parts (Figs 39D, 40B). Solenomere (**sl**) high/long, with ampules, additional channels and a posterior lobe-like part. Phylacum (**ph**) flat, rounded at apex, lower/shorter than **sl**.

FEMALE. First two leg-pairs unmodified.

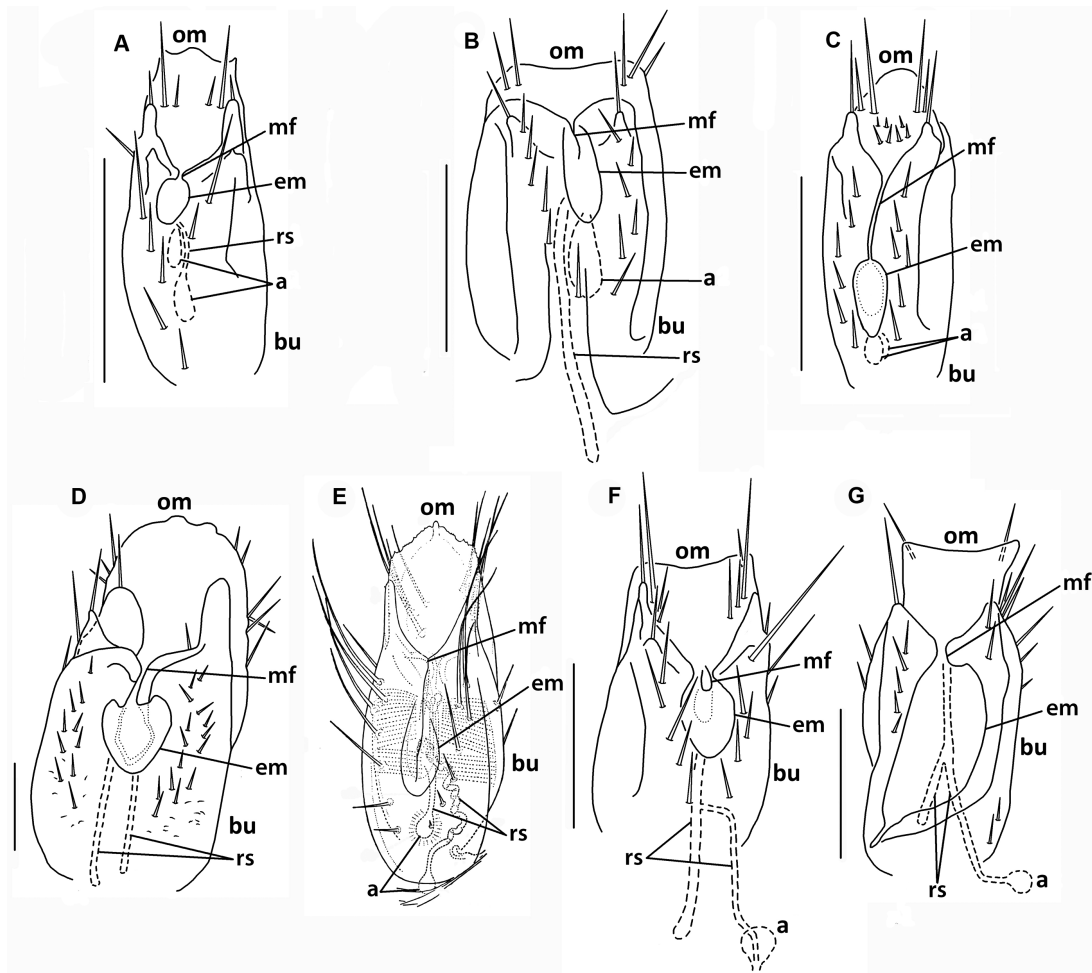
Vulva relatively broad (Fig. 42G). Operculum (**om**) with fairly sharp apical corners. Median field (**mf**) of bursa (**bu**) short and broad, emargination (**em**) of **mf** large and asymmetric. Receptaculum seminis (**rs**) consisting of two tubes, one short and the other long. Long tube with a rounded ampulla (**a**) located at base of vulva.

**Remark.** This species seems to be narrowly endemic to the Caucasus Major within NE Georgia and NW Azerbaijan (Map 2), a mid- to high-montane forest-dweller.

### Key to Leptoiulini species occurring in the Caucasus (based on males)

1. Promeres of gonopods without flagella, phylacum of opisthomere absent ..... 2
- Promeres of gonopods with flagella, phylacum of opisthomere more or less clearly developed ..... (genus *Leptoiulus*) 4
2. Promere slender; solenomere narrow, higher than promere, but shorter than velum; apical part with a tooth, connected to velum through thin plate with folds in basal part (Figs 4C, 4D, 5A, 5D) ..... *Chaetolephophyllum flexum*
- Promere subtriangular. Velum deeply separated from solenomere ..... (genus *Kubaniulus*) 3
3. Velum rounded towards top, separated from solenomere only by a shallow notch with a finely denticulate margin (Figs 13C, D, 14B) ..... *K. lativelatus* sp. nov.
- Velum expanded towards apical part, deeply and widely separated from solenomere, without a denticulate margin (Figs 8B, 8C, 9B) ..... *K. gracilis*
4. Promere with a leaf- or tooth-shaped lamella (**lp**) in basal part. Solenomere with three lamellae at apex (Figs 19B, C, 20A–C, E, F, 21A, B, 22B, E) ..... *L. hastatus*
- Promere without a lamella in basal part. Solenomere without three apical lamellae ..... 6
6. Promere without spike (Figs 34B, C, 35A, B, 36B) ..... *L. meshkii* sp. nov.
- Promere with a spike at inner margin ..... 7

7. Solenomere with a posterior lobe-like part. Spike on promere higher/longer than promere itself (Figs 39D, 40A, B) . . . . . *L. gonopodialis* sp. nov.  
 – Solenomere elongate, narrow. Spike lower/shorter than promere (Figs 27C, D, 28C–E, 29A–C, 30A–C) . . . . . *L. tanymorphus*



**FIGURE 41.** Female vulvae of Leptoiulini from the Caucasus, caudolateral views. **A:** *Chaetoleptophyllum flexum* Golovatch, 1979 (female from Algeti Nature Reserve, Georgia). **B:** *Kubaniulus gracilis* Lohmander, 1936 (female from Pasture Abago, Krasnodar Prov.). **C:** *Kubaniulus lativelatus* sp. nov. (paratype from near Gelenjik, Krasnodar Prov.). **D:** *Leptoiulus hastatus* Lohmander, 1936 (female from Totev, Armenia). **E:** *Leptoiulus tanymorphus* (Attems, 1901) (paratype, after Lohmander, 1936). **F:** *Leptoiulus meskhii* sp. nov. (paratype from Galabyn, Azerbaijan). **G:** *Leptoiulus gonopodialis* sp. nov. (paratype from Lagodekhi Nature Reserve, Georgia). **Abbreviations:** a, ampulla/ -ae; bu, bursa; em, emargination of median field; mf, median field; om, operculum; rs, receptaculum seminis. Scale bar: 0.2 mm (A–E, G), drawn not to scale (H, F).

## Conclusions

All seven species of the tribe Leptoiulini described here are endemic or subendemic to the Caucasus. Endemism is partly expressed at the generic level with *Kubaniulus* being confined to the Caucasus Major (Map 1). While *Chaetoleptophyllum* and *Kubaniulus* species are restricted to the western and central parts of the Caucasus Major, *Leptoiulus* spp. occur both in the Caucasus Major and Caucasus Minor (Maps 1 and 2), including the adjacent parts of Turkey and NW Iran. The species of the Leptoiulini most widespread in the region are *Chaetoleptophyllum flexum*, *Leptoiulus tanymorphus* and *L. hastatus*. A few more *Leptoiulus* species are known from Iran alone (Lohmander 1932), and the two new species described here are narrowly endemic: one (*L. meskhii* sp. nov.) to the Talysh Mountains of the Republic of Azerbaijan, while the other (*L. gonopodialis* sp. nov.) is endemic to the central Caucasus Major within NE Georgia and NW Azerbaijan (Map 2). This alone suggests that further narrowly endemic Leptoiulini may well be found to occur in the Caucasus.



As regards the vertical distributions, most Leptoiulini in the Caucasus are confined to montane forests. Only *Leptoiulus meskhii* **sp. nov.** seems to be restricted to the xerophytous montane steppes of the Talysh Mountains at 1800–2000 m a.s.l. On the other hand, at least *L. tanymorphus* is also capable of inhabiting some xerophytic foothill to montane woodlands, e.g. in the Vashlovani Nature Reserve, 500–580 m a.s.l., Georgia or the Khosrov Nature Reserve, 1700–1900 m a.s.l., Armenia. The same seems to apply to *L. hastatus* as well.

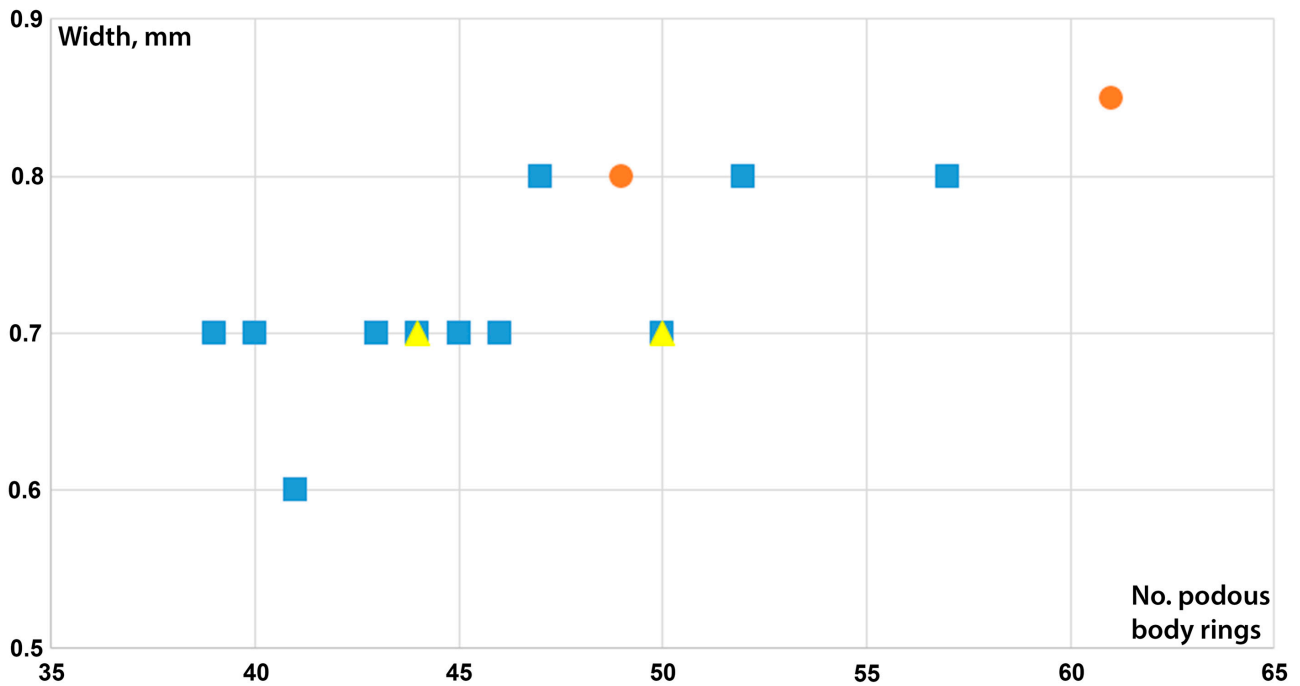


FIGURE 42. Relationship between the number of podous body rings and body diameter in males of some Leptoiulini species in the Caucasus: *Chatoleptophyllum flexum* Golovatch, 1979 (blue square); *Kubaniulus gracilis* Lohmander, 1936 (orange circle); *Kubaniulus laticellatus* **sp. nov.** (yellow triangle).

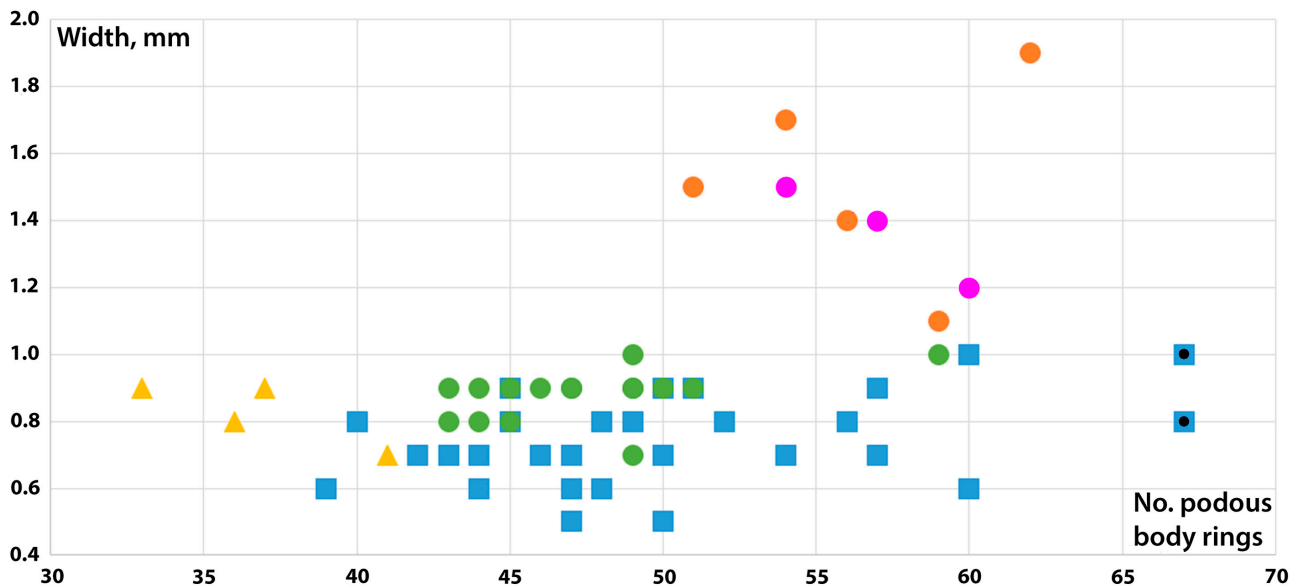
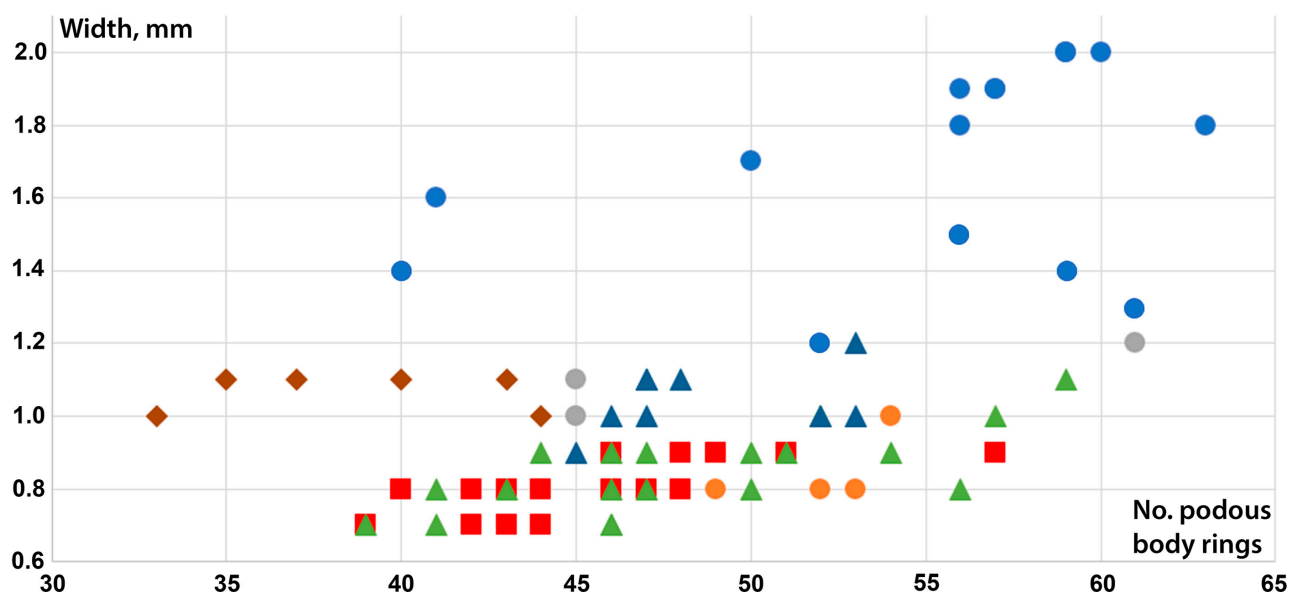


FIGURE 43. Relationship between the number of podous body rings and body diameter in males of *Leptoiulus* species in the Caucasus: *Leptoiulus hastatus* Lohmander, 1932 (orange circle), “*Leptoiulus disparatus*” Lohmander, 1936 (purple circle), *Leptoiulus tanymorphus* (Attems, 1901) (blue square), *Leptoiulus meskhii* **sp. nov.** (green circle), *Leptoiulus gonopodialis* **sp. nov.** (yellow triangle).

Both species of *Kubaniulus* are allopatric and endemic to the Colchis: *K. gracilis* has been recorded from the northern macro slopes of the Caucasus Major, while *K. laticellatus* **sp. nov.** occurs mostly on its southern slopes and

along the Black Sea coast. Within *Leptoiulus*, only *L. tanymorphus* and *L. hastatus* have been recorded sympatrically, but both tend to differ in body size. Both new species of *Leptoiulus* appear to show very narrow distributions: *L. gonopodialis* sp. nov. from the southern slopes of the Caucasus Major at the border between Georgia and Azerbaijan, and *L. meskhii* sp. nov. from the Talysh Mountains, Hyrcania, Azerbaijan (most likely to occur also in the adjacent parts of northwestern Iran).



**FIGURE 44.** Relationship between the number of podous body rings and body diameter in females of all Leptoiulini species in the Caucasus: *Chaetoleptophyllum flexum* Golovatch, 1979 (red square); *Kubaniulus gracilis* Lohmander, 1936 (orange circle); *Kubaniulus laticelatus* sp. nov. (grey circle); *Leptoiulus hastatus* Lohmander, 1932 (blue circle), *Leptoiulus tanymorphus* (Attems, 1901) (green triangle), *Leptoiulus meskhii* sp. nov. (blue triangle), *Leptoiulus gonopodialis* sp. nov. (brown diamond)

Males of *Chaetoleptophyllum flexum* and *Kubaniulus* species are usually similar in size (Fig. 42). Only one species, *K. gracilis*, can be relatively larger both in the number of segments and in body width. Species of *Leptoiulus* show greater variations in their body size (Fig. 43). For example, *L. hastatus* is the largest species of the tribe to occur in the Caucasus and both sexes differ well from other species in their size (Figs 43, 44). At the same time, *L. gonopodialis* sp. nov. is the smallest species, being comparable in size to *C. flexum*. Males of two species, *L. tanymorphus* and *L. hastatus* sp. nov., are very similar in size, but samples of the former species from Lesser Istisu, Azerbaijan are the largest in the number of segments and fail to vary in width (Fig. 43, blue squares with dots). The same general pattern is observed in females (Fig. 44), these typically being expectedly larger and less slender than males (cf. Read 1990).

Based on morphological characteristics of the gonopods, the Caucasian species of *Leptoiulus* show similarities to European and Asian congeners. For example, the solenomere and phylacum of *L. hastatus* are similar to those in the widespread European *L. trilineatus* (C.L. Koch, 1847) and the Siberian *L. tigirek* Mikhaljova *et al.*, 2015. The gonopod promere carrying a long spike and the shapes of the phylacum and velum in *L. gonopodialis* sp. nov. strongly resemble those of *L. arabistanus* Lohmander, 1932, from Iran (Lohmander 1932).

The ancestral species of the genus *Kubaniulus* might have separated from a *Leptoiulus* stem through the loss of flagella on the promeres and evolved *in situ* within the Caucasus. Generally, reduction or loss of flagella appears to have happened many times within the Julida (e.g., Read 1992; Enghoff *et al.* 2011). As noted above, the question concerning the phylogeny of *Chaetoleptophyllum flexum* and its relationship with the European *C. montanum* still remains open.

The morphological structures of the females, including the vulvae, seem to be unsuitable for a solid phylogenetic analysis, since they largely fail to show significant differences even between species, let alone genera. Still sometimes they can be used for species identification.

The present taxonomy and distributions as outlined above must be clarified and refined through future research, both morphology- and molecular-based.

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