



Research article

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## A new genus of mongoliulid millipedes from the Far East of Russia, with a list of species in the family (Diplopoda, Julida, Mongoliulidae)

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**Abstract.** The genus *Koiulus* gen. nov. and its type-species, *Koiulus interruptus* gen. et sp. nov., are described from the Russian Far East. The new genus is compared with other genera of Mongoliulidae, in particular with *Ussuriulus* Golovatch, 1980, also from the Russian Far East, with which it shares the absence of ozopores from individual body rings distributed along the body, a condition so far otherwise unknown in the superorder Juliformia. A synoptic table of genera and a list of species of Mongoliulidae are presented.

**Keywords.** Taxonomy, new species.

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### Introduction

The Mongoliulidae is a small family of small to medium-sized julidan millipedes, geographically confined to East Asia (Russian Far East, Korea, China, Japan). Up to now, seven genera of the family have been described: *Ansiulus* Takakuwa, 1940a (Korea, Russian Far East, 4 species), *Ikahoiulus* Takakuwa, 1941 (Japan, monotypic), *Kopidoiulus* Attems, 1909 (Japan, Russian Far East, 7 species), *Senbutudoiulus* Miyosi, 1957 (Japan, monotypic), *Skleroprotopus* Attems, 1901 (= syn. *Mongoliulus* Pocock, 1903) (Japan, Korea, China, Russian Far East, 20 species), *Uenoiulus* Murakami, 1971 (Japan, monotypic), and *Ussuriulus* Golovatch, 1980 (Russian Far East, monotypic). The family includes cave dwellers as well as surface living species.

Considering the small size of the family, the morphological diversity regarding secondary sexual characters, especially in males, is considerable, and the new genus described here adds significantly to this diversity. Of special interest is that the type and only species of the new genus, instead of having a continuous series of defense gland openings (ozopores) starting on body ring 6 as in virtually all other juliformian millipedes (in some the series starts on ring 5, though, exceptionally on ring 3), has the series interrupted by ozopore-less rings at more or less regular intervals. This trait, which was also reported from *Ussuriulus* by Golovatch (1980), but has otherwise been neglected, adds particular interest to the new genus and its type species. This will be discussed in a separate paper.

## Material and methods

The material treated here has been deposited in the collections of the Zoological Museum, University of Copenhagen, Denmark (ZMUC), Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia (FSCB) and the Zoological Museum of the State University of Moscow, Russia (ZMUM). Paratypes of *Uenoiulus notabilis* Murakami, 1971 were borrowed from the National Museum of Nature and Science, Ibaraki, Japan (NMNS). The material was preserved in 70–75% alcohol and examined in alcohol under a stereo microscope. Gonopods and some other parts were dissected from a limited number of males and females and mounted in Canada balsam or temporarily in glycerine.

The numbers of podous and apodous rings were counted, and body length and midbody vertical diameter were measured on all entire specimens. For females, only maximum values are given because of difficulties in distinguishing juvenile and adult females without dissection.

Specimens for scanning electron microscopy (SEM) were transferred to 96% ethanol, then to acetone, air-dried, mounted on aluminium stubs or on pieces of flexible aluminium tape and in turn mounted on stubs, coated with platinum-palladium and studied in a JEOL JSM-6335F scanning electron microscope. SEM images were processed in PhotoShop and plates were composed in Microsoft Publisher.

## Results

Class Diplopoda de Blainville in Gervais, 1844  
Order Julida Brandt, 1833  
Family Mongoliulidae Pocock, 1903

*Koiulus* gen. nov.

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## Diagnosis

A genus of Mongoliulidae characterized by lacking ozopores on certain body rings (shared with *Ussuriulus*), strongly reduced, three-segmented second male legs, strongly reduced seventh male legs (shared with all other genera except *Ussuriulus*), strongly reduced flagella of anterior gonopods, posterior gonopods deeply split into two equally long processes: a slender anterior and a broad posterior one.

## Etymology

The specific epithet refers to the River Ko where the type locality is situated.

## Type and only known species

*Koiulus interruptus* gen. et sp. nov.

*Koiulus interruptus* gen. et sp. nov.

[urn:lsid:zoobank.org:act:04617A80-8F8D-47E0-A237-F1A5030EBAA8](https://doi.org/10.21203/rs.3.rs-1046171/v1)

Figs 1–9

**Etymology**

The species is named after the interrupted series of ozopores.

**Material examined**

**Holotype**

RUSSIA: ♂, Khabarovskii Krai (southern), Sikhote-Alin (Central) range, upper course of river Ko, 47.074° N, 136.478° E, 700–800 m, fir-birch forest, 23–25 May 2015, wet leaf litter, A. Hansen, M. Justesen and A. Solodovnikov leg., sample RUS 15-7a (ZMUC 00040235).

**Paratypes**

RUSSIA: 4 ♂♂ (incl. 2 used for SEM), 18 ♀♀ (incl. 1 used for SEM), 8 juv. ♂♂, 1 juv. unsex., same data as holotype (ZMUC00040238); 2 ♂♂, 2 ♀♀, 1 juv. ♂, same data as holotype (ZMUM P 3534); 2 ♂♂, 3 ♀♀, same data as holotype, but 47.037° N, 136.396° E, 580 m, mixed forest, 22 May 2015, leaf litter and river bank and flood debris, samples RUS 15-6a and RUS 15-6b (ZMUC00040239, ZMUC00040240); 2 ♂♂, 4 ♀♀, 2 juv. ♂♂, 2 juv. ♀♀, same data as holotype, but 47.0716° N, 136.4572° E, 750 m, fir-birch forest, 26 May 2015, leaf litter, samples RUS 15-8a and RUS 15-8e (ZMUC00040241, ZMUC 00040242); 3 ♂♂, 2 ♀♀, same data as holotype, but 47.04° N, 136.37° E, 400–500 m, mixed forest along the road, sample RUS 15-9 (ZMUC00040243); 1 ♂ (6 trunk fragments + slightly broken head + leg pairs 1, 2 and 7, gnathochilarium and gonopods in Canada balsam), Khabarovskii Krai, ca 75 km SE of Khabarovsk, environs of Zolotoi village, mixed forest, 5 Oct. 1981, G.N. Ganin leg. (FSCB).

**Description**

MEASUREMENTS. See Fig. 2 for a graphical representation of size parameters. Males: length (14)19–20 mm (all males from river Ko site 19–20 mm), diameter 0.94–1.01 mm, 38–44 podous rings + 2–5 apodous rings in front of telson (fewer apodous rings in larger males). Females: length up to 21 mm,



**Fig. 1.** *Koiulus interruptus* gen. et sp. nov., paratype, juvenile male from upper course of river Ko. Notice interrupted series of defense glands. Scale bar: 1 mm.

diameter up to 1.31 mm, up to 46 podous rings + at least one, usually 2–5 apodous rings in front of telson (fewer apodous rings in larger females).

COLOUR (Fig. 1). Marbled brownish, darker dorsally, no pronounced colour pattern. Defense glands visible as dark spots on the body rings on which they occur (see below). Male from environs of Zolotoi village beige (probably faded by preservation). Eye patches black. Antennae brown.

EYE PATCHES. Subtriangular, composed of 30–45 ocelli. A pair of long frontal (epicranial) setae (broken in many specimens), at least some individuals with scattered additional long setae between antennal sockets and labrum. 2+2 supralabral setae, at least 5+5 labral setae.

ANTENNAE. Reaching body ring 3 when folded back. Antennomeres 5, 6 and 7 each with an external subapical group and corolla of sensory bacilli; sensory bacilli of antennomere 7 minute. Antennomere 3 longer than the others:  $3 > 2 \approx 4 \approx 5 > 6 >> 7 > 1$ .

MANDIBLES (Fig. 3A–C). External tooth (odontomere of Hoffman & Howell 1995), with three cusps decreasing in size from posterior to anterior. Internal tooth (dentate lamella of Hoffman & Howell 1983, sectile edge of psectromere of Hoffman & Howell 1996), with ca 5 cusps decreasing in size from posterior to anterior. Eight rows of simple pectinate teeth. Molar plate without grooves, with a row of hand-like processes, each with 3–5 bent ‘fingers’, along anterior margin.

GNATHOCHILARIUM (Fig. 3D–E). Three apical setae on each stipes and four or five setae in a longitudinal row on each lamella lingualis; promentum (modified in male, see below) completely separating lamellae linguales.

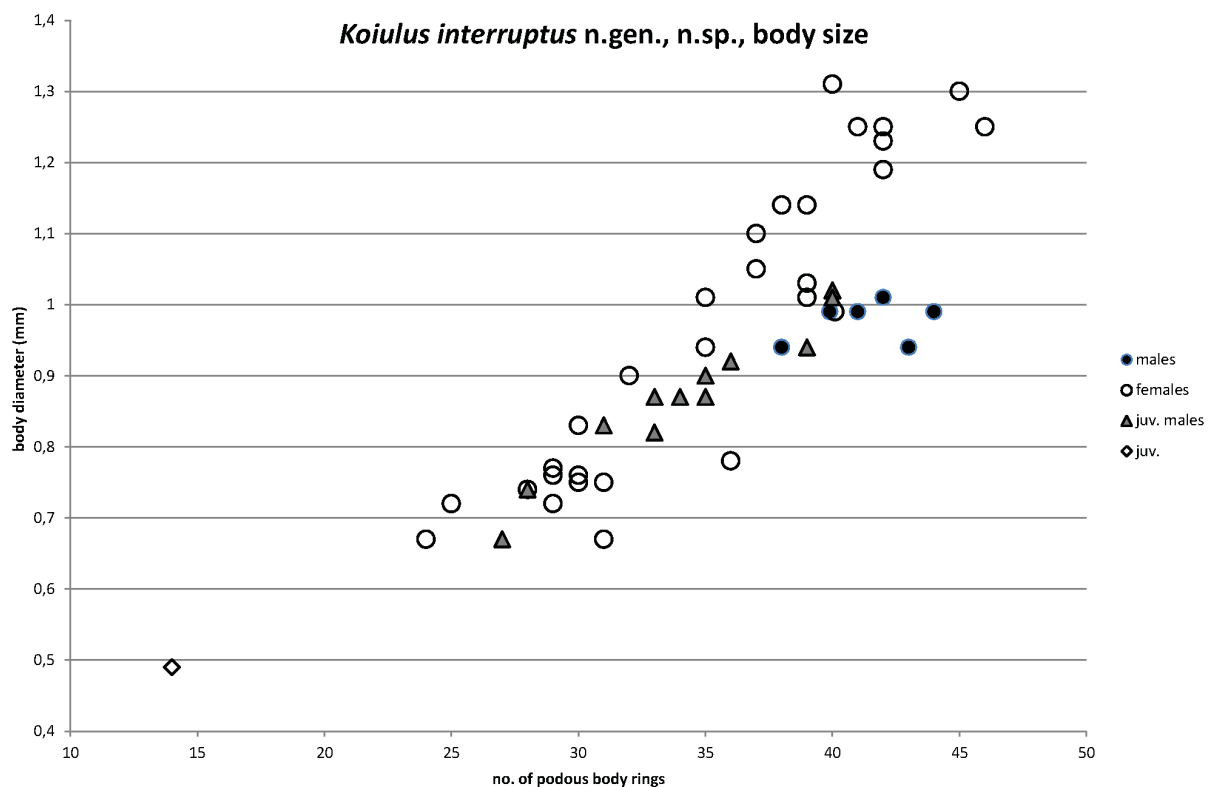
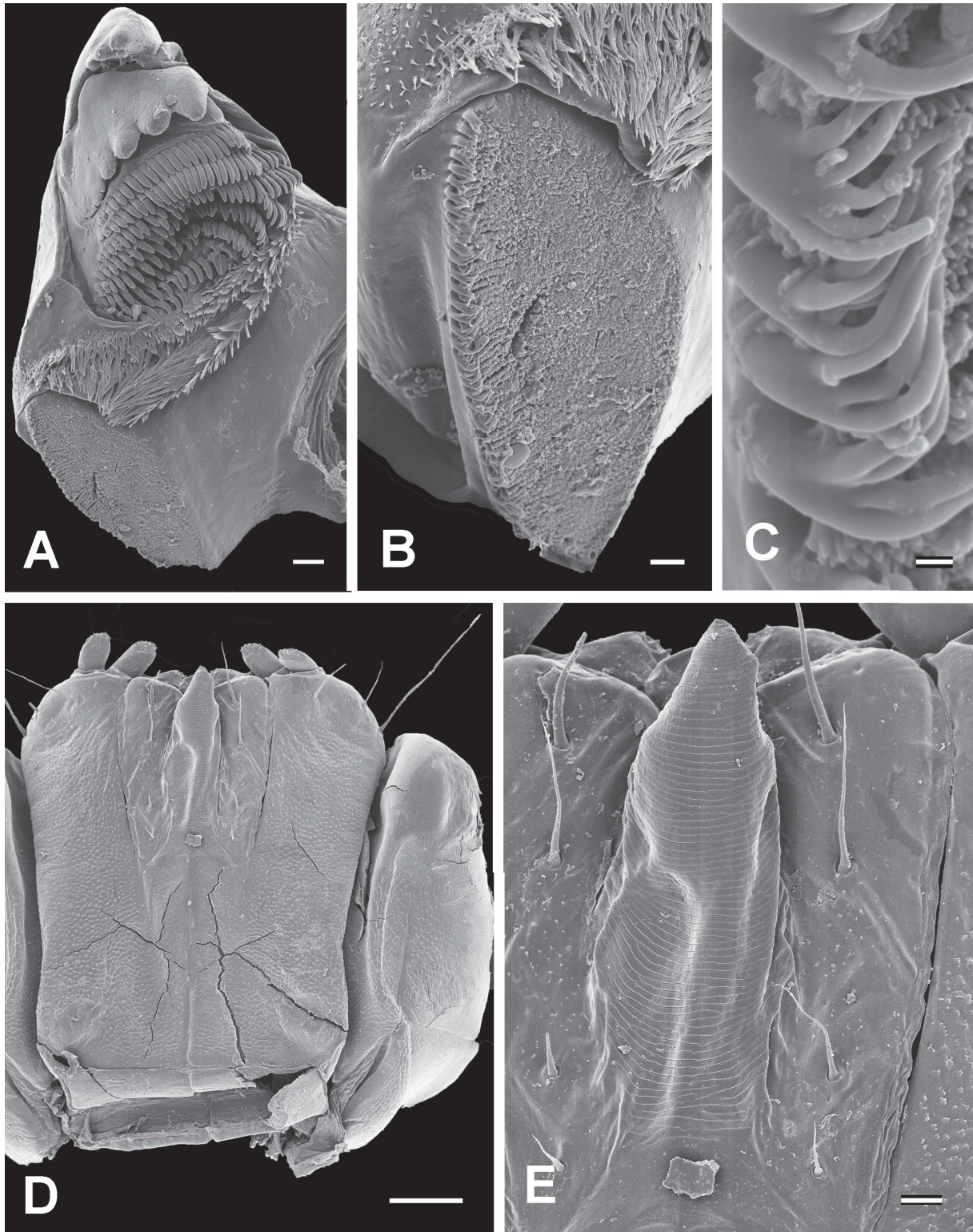


Fig. 2. *Koiulus interruptus* gen. et sp. nov. Body size as expressed by number of podous body rings and midbody diameter.



**Fig. 3.** *Koiulus interruptus* gen. et sp. nov., paratype, ♂, from the upper course of the river Ko. **A.** Left mandible. **B.** Molar plate of left mandible. **C.** Handle-like processes on anterior margin of molar plate. **D.** Gnathochilarium. **E.** Lamellae linguales and modified promentum of gnathochilarium. Scale bars: A, E = 0.02 mm; B = 0.01 mm; C = 0.001 mm; D = 0.1 mm.

COLLUM (Fig. 4B). Smooth, with one or two striae along lower margin.

BODY RINGS (Figs 1, 4A–D). Slightly vaulted, prozonites smooth, metazonites with longitudinal striae in ventral half. A row of short setae on posterior margin, length of setae ca  $0.1 \times$  body diameter. Ozopores present from ring 6 onward, but missing from rings 7, 11, 14 or 15, one of rings 17–20 and several single rings further backward (Fig. 4C).

TELSON (Figs 1, 4A). Preanal ring with a short dorsal process and setae along posterior margin. Anal valves each with two setae. Subanal scale with two setae.

LEGS (Figs 1, 4A–C). Moderately long and slender. Claws long, weakly curved, without modifications.

### **Male sexual characters**

MANDIBLES (Fig. 4B). Stipes with a small, protruding, ventro-posterior lobe.

GNATHOCHILARIUM (Fig. 3D–E). Promentum swollen, transversely microstriate, anteriorly produced in triangular tip overreaching lamellae linguales.

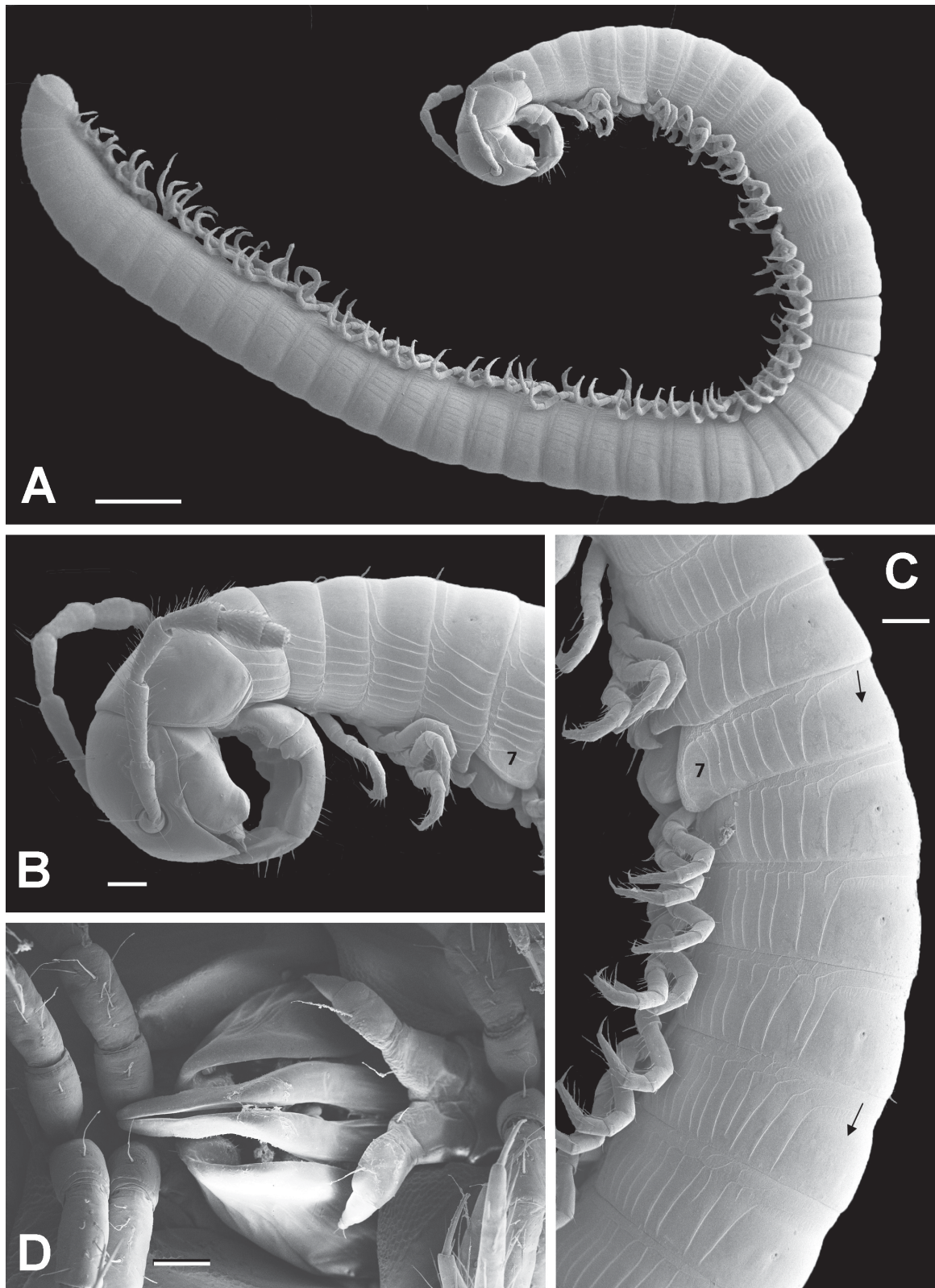
FIRST PAIR OF LEGS (Figs 4A–B, 5A–C). Strongly enlarged, consisting of an unpaired coxosternum and five-segmented telopodites. Interpretation of basal sclerite as a coxosternum supported by narrow ‘trochanters’ (not visible on Fig. 5) situated between unpaired sclerite and each of the telopodites. Third telopodomere longer than the others:  $3 > 4 > 1 > 2 > 5$ . Telopodomere 1 (prefemur?) massive, ca as broad as long, with an area densely covered in short bristles on anterior side (obscured by a secretion-like substance on imaged specimen). Telopodomere 2 (femur?) much broader than long, with a hump on anterior surface, i.e., in inner curvature of telopodite. Telopodomere 3 (postfemur, or postfemur + tibia?) much longer than any of the others, its basal ca 40% flattened, much more slender than distal ca 60%. Telopodomere 4 (tibia, tarsus, or tibia+tarsus?) flattened, of uniform width throughout. Telopodomere 5 (strongly reduced tarsus or claw?) very small, hemispherical. Telopodomeres 1–4 with scattered setae, 5 entirely smooth.

SECOND PAIR OF LEGS (Fig. 5D–F). Strongly reduced, consisting of an unpaired (coxo?)sternum and three-segmented telopodites. Telopodomere 1 cylindrical, gently curved, ca 3 times as long as broad, with scaly microsculpture on posterior surface and a long disto-mesal seta on anterior surface. Telopodomere 2 barrel-shaped, slightly longer than broad, with a long disto-mesal seta on anterior surface and several shorter, scattered setae. Telopodomere 3 contrastingly black, tapering to narrow tip, here with a bunch of ca 7–8 stout setae with irregularly multi-spiked tips (Fig. 5F); several normal setae scattered over telopodomere surface.

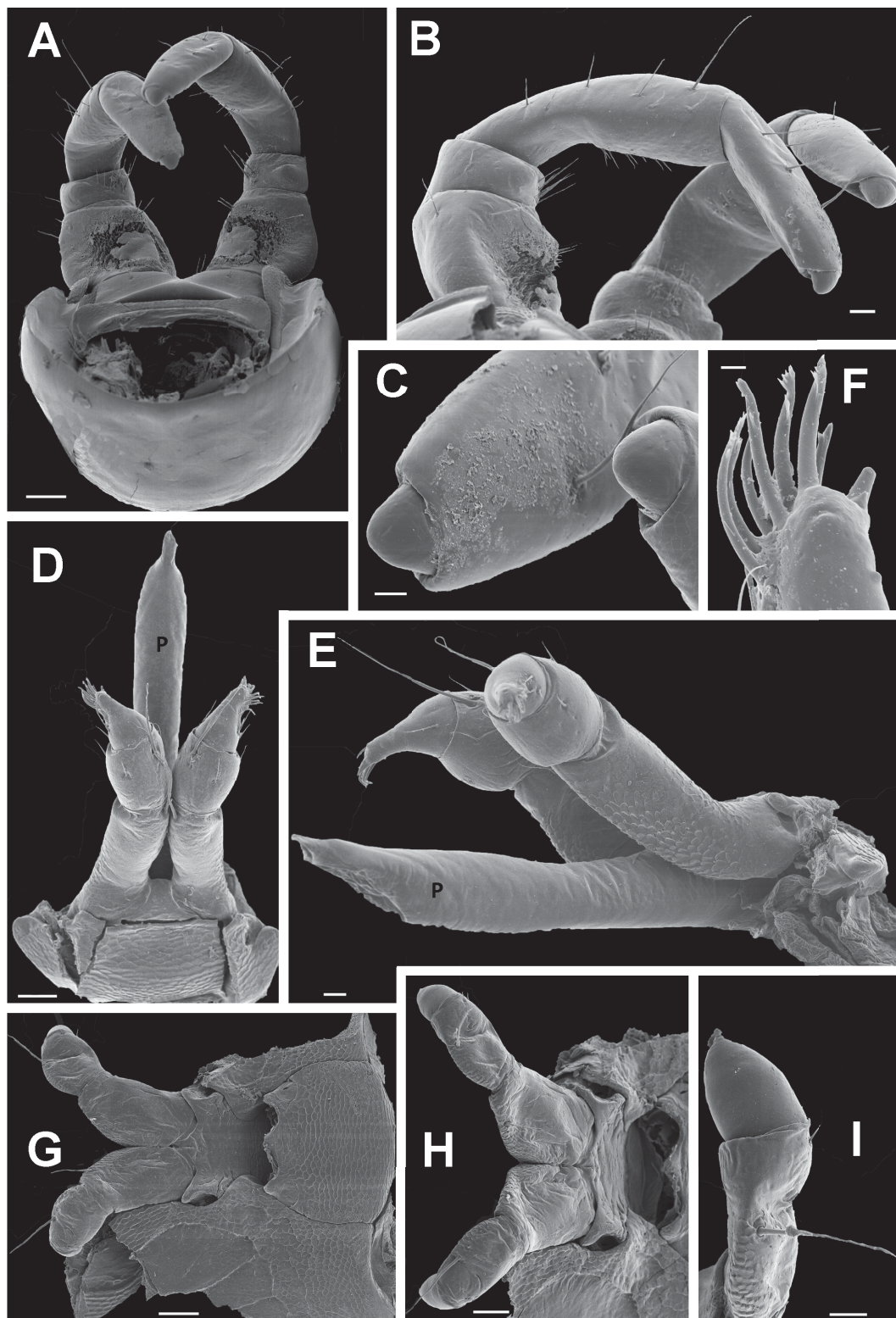
PENIS (Fig. 5D–E). Unpaired, cylindrical, longer than second legs, gradually narrowing towards end or with a slender, parallel-sided tip.

SEVENTH PAIR OF LEGS (Figs 5G–I, 6). Strongly reduced, each leg consisting of three-four podomeres of uncertain homology. Podomere 1 almost twice as long as podomere 2; podomere 1, sometimes also podomeres 2 and 3, with scaly microsculpture on mesal surface and a long (disto-)mesal seta, podomere 2 further with a few short setae. Podomere 3 contrastingly black, pear-shaped or conical, smooth or with a few short setae, sometimes surmounted by a tiny podomere 4 carrying 5 strong setae laterally and a claw apically (Fig. 6).

SEVENTH PLEUROTERGITE (Fig. 4B–C). With triangular-rounded ventral lobes (protecting gonopods).



**Fig. 4.** *Koiulus interruptus* gen. et sp. nov., paratype, ♂, from the upper course of the river Ko. **A.** Entire body, 39 podous + 3 apodous body rings + telson. **B.** Anterior end. **C.** Body rings (5)6–12(13); note absence of ozopores on rings 7 and 11 (arrows). **D.** Leg-pair 7 and gonopods in situ. 7 = seventh body ring with ventral lobes. Scale bars: A=1 mm; B–C = 0.2 mm; D = 0.1 mm.



**Fig. 5.** *Koiulus interruptus* gen. et sp. nov., paratype, ♂, from the upper course of the river Ko. **A–C.** First pair of legs. **A.** Anterior view. **B.** Sublateral view. **C.** Tips. – **D–F.** Second pair of legs, and penis. **D.** Anterior view. **E.** Lateral view. **F.** Modified setae on tip of leg. – **G–I.** Seventh pair of legs. **G.** Ventral view. **H.** Posterior-ventral view. **I.** Tip of one telopodite. P = penis. Scale bars: A, G = 0.1 mm; B, D, H = 0.05 mm; C, E, I = 0.02 mm; F = 0.005 mm.



ANTERIOR GONOPODS (Fig. 7). Coxal processes (CX) separate, long and slender, slightly curved posteriad, laterally excavated for accommodation of telopodites, tips rounded. Flagella (FL) strongly reduced, short, finger-like, projecting perpendicularly from coxal process, with strong scaly microsculpture. Telopodite (TLP) almost as long as coxal process, apically with large mesal lobe; tip of lobe with scaly microsculpture and a group of ca 6 short setae. Remaining surface of telopodite smooth, except for some tiny (~10 µm) sub-circular, densely porose structures (PS, Fig. 7C–D).

POSTERIOR GONOPODS (Fig. 8). Each posterior gonopod divided from the basis into two equally long branches. Anterior branch (AB) slender, almost parallel-sided, mesally excavated, apical  $\frac{1}{3}$  with dense cover of retrorse micro-spicules; tip slender, curved up in densely microspiculate spiral. Posterior branch (PB) broad at base, tapering regularly towards tip and hence with a triangular outline; anterior surface excavated for accommodation of anterior branch; an anterior-lateral row of ca 15 short setae; mesal margin distally with subtriangular, antieriad lobes.

### Female sexual characters

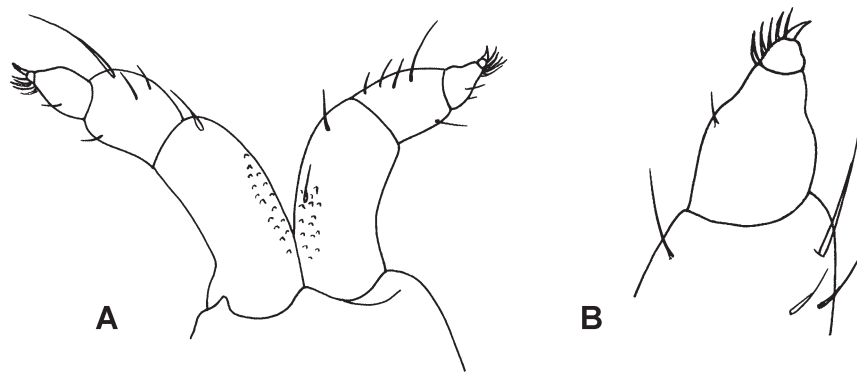
VULVA (Fig. 9). Placed vertically in short vulval sacs behind unmodified second leg-pair, very slender, oblong pyriform. Operculum (OP) slightly longer than bursa, with two parallel rows of short setae on anterior surface and several strong setae on distal half; tip subtriangular. Bursa (BU) consisting of a single sclerite, but with longitudinal sutures in basal  $\frac{3}{4}$  of mesal and lateral sides; four longitudinal rows of setae, one on each side of the two longitudinal sutures. Posterior surface apically divided into two rounded lobes.

A tiny (~15 µm) structure of unknown identity was observed next to one of the apical bursal setae (Fig. 9D (arrow)–E). It is sausage-shaped, has an apical pore and is apparent attached by its basal end to the surface of the bursa as well as laterally attached to the neighbouring seta.

## Discussion

### Comparison of *Koiulus* gen. nov. with other Mongoliulidae

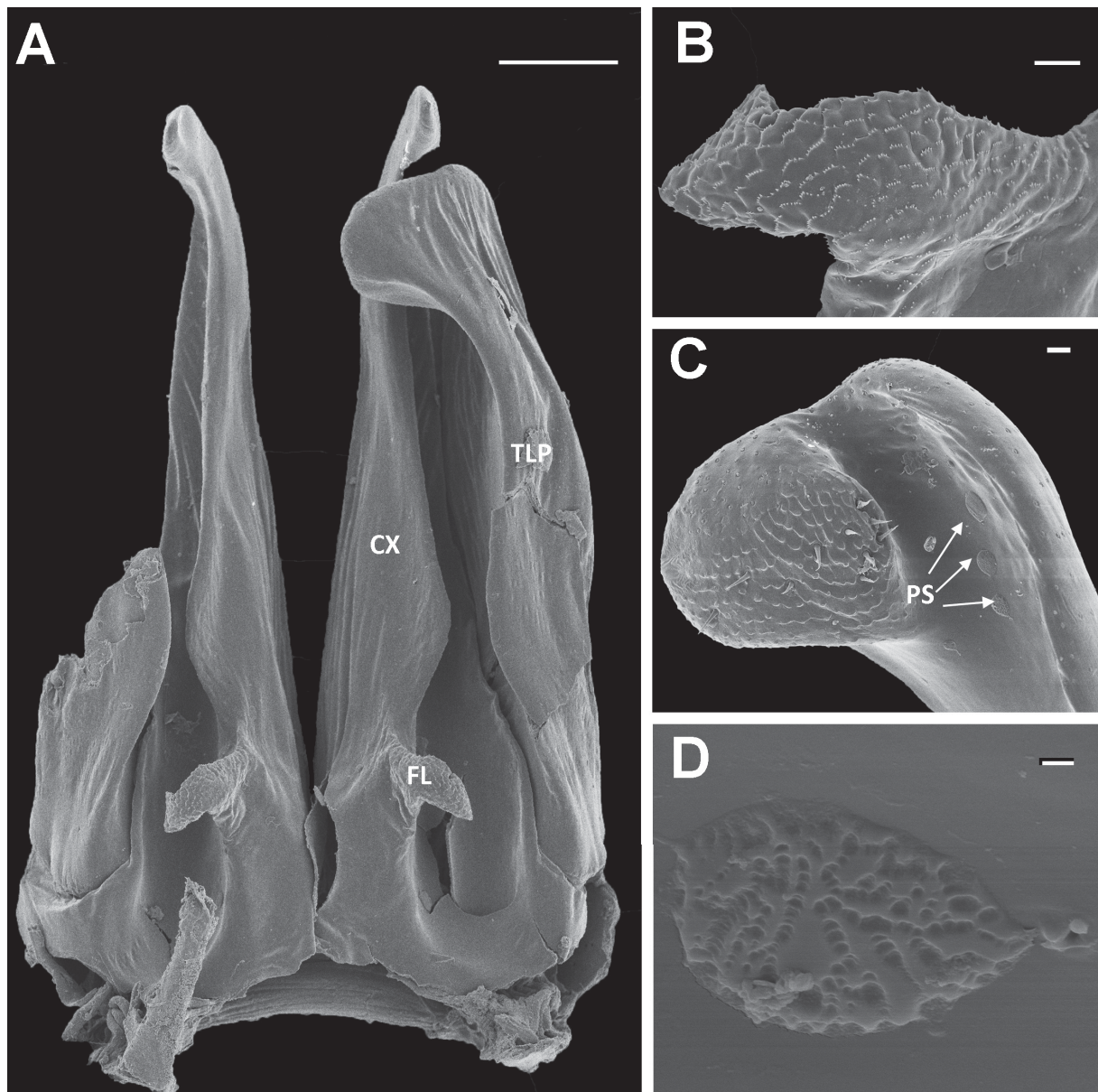
The Mongoliulidae is a small family of julidan millipedes, geographically confined to East Asia (Russian Far East, Korea, China, Japan). The family is closely related to the mainly North American family Parajulidae; the sister-group relationship between the two families is supported by morphological characters (enlarged first male legs, enlarged and soft male promentum; Enghoff 1981) and *Kopidoiulus continentalis* (Mongoliulidae) comes out as sister group to *Uroblaniulus caroliniensis* Causey, 1953 (Parajulidae) in the molecular phylogenies of Enghoff *et al.* (2011, 2013). According to Enghoff *et al.*



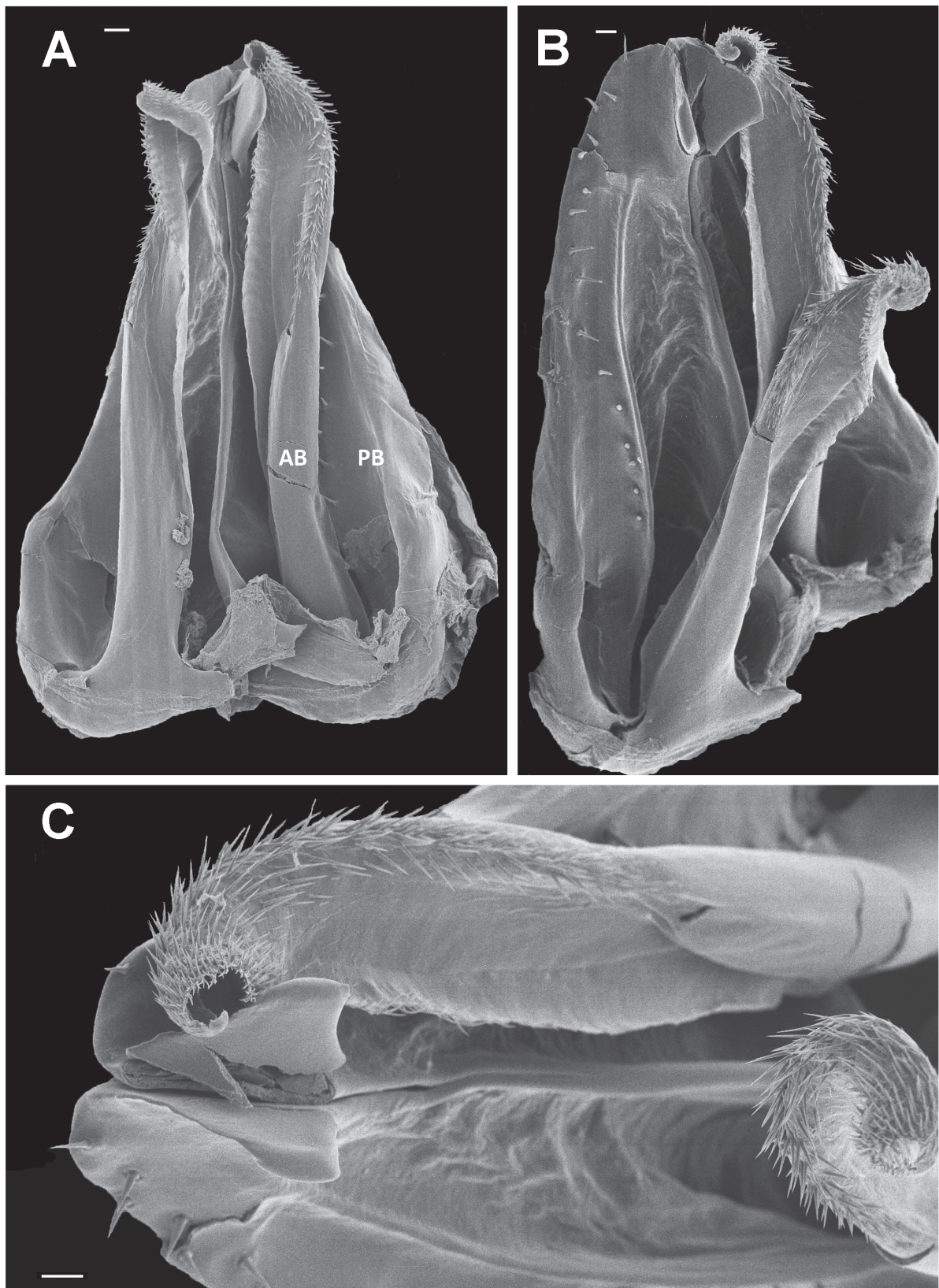
**Fig. 6.** *Koiulus interruptus* gen. et sp. nov., paratype, ♂, from the environs of the village of Zolotoi, seventh pair of legs. **A.** Ventral view. **B.** Tip of the telopodite. Scale bars: A = 0.5 mm; B = 0.1 mm.

(2015) Mongoliulidae differ from Parajulidae by having the claw of the first male legs absent or reduced, the second pair of male legs at most moderately modified, the penis unpaired, the seventh pair of male legs with enlarged coxae and modified and/or size-reduced telopodites (exception: *Ussuriululus*), and the anterior gonopods mostly with flagella (reduced to tiny flaps in *Kopidoiulus*, missing in *Ussuriululus* and (?) *Ikahoiulus*).

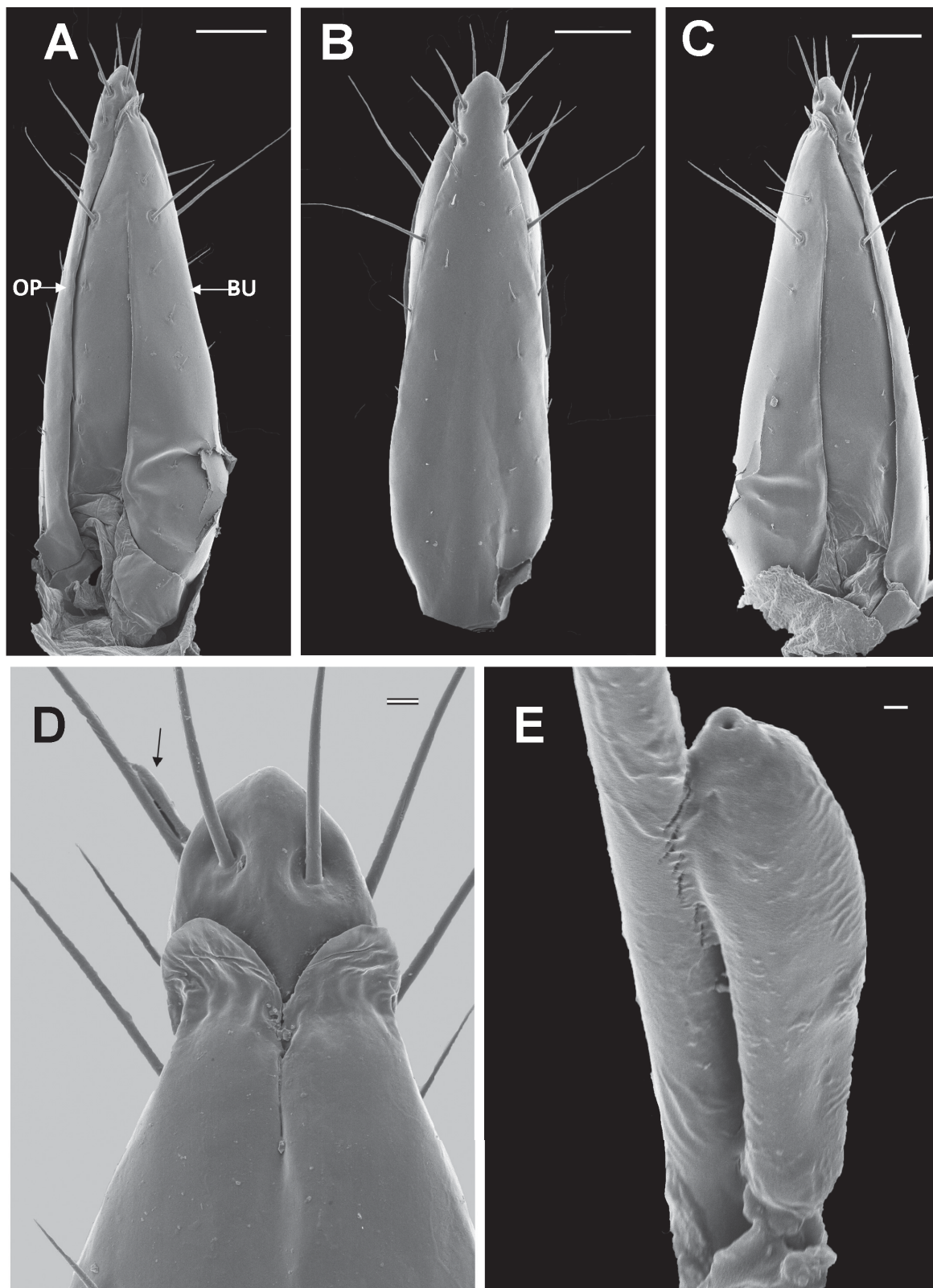
Additional distinguishing characters of Mongoliulidae are: Eyes present or absent. Surface of metazonites clearly striate only below ozopore level. The first pair of male legs enlarged (exception: *Ansiulus deminutus* Mikhaljova, 2001) and modified to a varying degree. The second pair of male legs



**Fig. 7.** *Koiulus interruptus* gen. et sp. nov., paratype, ♂, from the upper course of the river Ko, anterior gonopods. **A.** Posterior view. **B.** Modified flagellum. **C.** Tip of left telopodite. **D.** Porose structure from telopodite. Abbreviations: CX = coxal process; FL = flagellum; PS = porose structure; TLP = telopodite. Scale bars: A = 0.1 mm; B–C = 0.01 mm; D = 0.001 mm.



**Fig. 8.** *Koiulus interruptus* gen. et sp. nov., paratype, ♂, from the upper course of the river Ko, posterior gonopods. **A.** Anterior view. **B.** Posterior-lateral view. **C.** Posterior-apical view. Abbreviations: AB = anterior branch; PB = posterior branch. Scale bars = 0.02 mm.



**Fig. 9.** *Koiulus interruptus* gen. et sp. nov., paratype, ♀, from upper course of river Ko , right vulva. **A.** Lateral view. **B.** Anterior view. **C.** Mesal view. **D.** Tip, posterior view; arrow points to unknown structure. **E.** Unknown structure from opercular seta. Abbreviations: BU = bursa; OP = operculum. Scale bars: A–C = 0.1 mm; D = 0.01 mm; E = 0.001 mm.

normal (exception: *Koiulus* gen. nov.), somewhat reduced in size, coxae prolonged. Anterior gonopods with coxal processes, flagella and reduced telopodites. Posterior gonopod with or without telopodites.

*Koiulus* gen. nov. shares all the diagnostic characters of Mongoliulidae including the reduced claw of the first pair of legs, the unpaired penis, the modified seventh male legs and possibly also the presence of flagella, although these seem to be strongly modified.

Table 1 shows a comparison of *Koiulus* gen. nov. with the seven already described genera of Mongoliulidae.

The new genus seems to be especially similar to the genera known from the Far East of Russia, *Ansiulus*, *Skleroprotopus*, *Kopidoiulus* and *Ussuriulus*, in the structure of the male gnathochilarial promentum, the first and seventh pairs of male legs (however, the latter is unmodified in *Ussuriulus*), separate coxal processes and the relatively long telopodites of the anterior gonopod. With *Kopidoiulus*, *Ikahoiulus* and *Ussuriulus* it shares the reduced to absent flagella, and with *Ussuriulus* it shares the peculiar lack of ozopores on certain body rings, a condition unknown in all other juliformian millipedes. (In the original description of *Uenoiulus notabilis* Murakami, 1971, there is a drawing of the anterior end of the holotype male in which the ozopore seems to be missing from body ring 7. We have examined four male and two female paratypes of *U. notabilis* and have found that ozopores are present in a continuous series starting from ring 6, but in males, where ring 7 is very narrow, the pore is difficult to see.)

On the other hand, the new genus stands out by the strongly modified second pair of male legs.

Species of *Ansiulus*, *Skleroprotopus* and *Kopidoiulus* appear to be morphologically rather variable (Mikhaljova 1997; Mikhaljova & Korsós 2003). The male leg-pair 7 and the gonopods are most often subject to variability. As regards the male leg-pair 7, the number of segments of the telopodite is particularly unstable and variability may even occur between both sides of the same specimen (Mikhaljova & Korsós 2003). In *Koiulus interruptus* gen. et sp. nov. the number of segments of male leg 7 ranges from 3 in the males from the upper course of River Ko to 4 in the male from the environs of Zolotoi village.

The close resemblance, including gonopodal characters, between *Ansiulus* and *Skleroprotopus*, in combination with the high variability in some species, might be evidence for the synonymy of these genera. The same applies to *Kopidoiulus* and *Ikahoiulus*. This will be discussed in a separate article (Mikhaljova in prep.).

### Postembryonic development

Fig. 2 clearly shows that males are thinner than females with similar numbers of podous rings. Interestingly, smaller juvenile males seem to follow the same “growth-pattern”, expressed as “diameter per podous ring” as females, whereas adult males, as well as larger juvenile males, are thinner than females, the difference increasing with increasing numbers of podous rings. It thus seems that the development of a more slender body in adult males is coupled to the onset of maturity. This tendency was also observed in the genus *Cylindroiulus* Verhoeff, 1894, family Julidae by Enghoff (1982).

The implications of the missing defence glands for interpretation of postembryonic growth will be discussed in a separate article.

### Acknowledgements

We are most grateful to Dr Alexey Solodovnikov, Aslak Kappel Hansen and Matthias Justesen who kindly collected millipedes during their expedition to the Russian Far East, as well as to Dr Gennady Ganin (Khabarovsk, Russia) who collected some additional material, to Dr Hirotugo Ono, NMNS, who

**Table 1** (continued on next page). Comparison of mongoliulid genera.

	<i>Koiulus</i> gen. nov.	<i>Ansiulus</i>	<i>Ikahoitulus</i>	<i>Kopidoiulus</i>	<i>Senbutudoiulus</i>	<i>Skleroprotopus</i>	<i>Uenoitulus</i>	<i>Ussuriulus</i>
Ozopores	Lacking on certain body rings	On all body rings (no information for <i>A. mattumotoi</i> )	No information	On all body rings	No information	On all body rings	On all body rings	Lacking on certain body rings
Gnathochilarium: Promentum (male)	Swollen, soft, densely transversely striate	Prominent, swollen	Almost oval, many transverse striae	Broad, not swollen	Oblong oval	Prominent, swollen, soft	Triangular, prominent, swollen, similar to <i>Skleroprotopus</i>	Broad, almost rectangular
1 <sup>st</sup> pair of legs (male)	Prolonged, incrassate, telopodite 5-segmented	Enlarged (exception: <i>A. deminutus</i> ), telopodite 4- or 5-segmented	Incrassate, telopodite 4-segmented	Enlarged, telopodite 4- or 5-segmented	Large, straight, densely setose, broad, flattened, coxa + 4-segmented telopodite	Enlarged, telopodite 4- or 5-segmented	Shortened, incrassate, densely setose on anterior surface, telopodite 5-segmented, prefemur and femur with spherical lateral processes	Prolonged, incrassate, telopodite 5-segmented
1 <sup>st</sup> pair of legs, terminal segment (male)	Sub-hemispherical, glabrous, no setae	Conical, with setae, with or without claw	Swollen, ovoid, setose, no claw	Tiny, swollen or cylindrical, with remnant of claw, with or without setae	Subhemispherical, densely setose, no claw	Subconical or cylindrical, with or without setae, without claw in majority of species	Conoid, glabrous	Very small, glabrous ("claw vestigial")
2 <sup>nd</sup> pair of legs (male)	Reduced, 3-segmented, terminal segment with modified setae	Normal, somewhat reduced in size, coxa prolonged	Normal	Normal, somewhat reduced in size, coxa prolonged	Coxa prolonged, telopodite densely setose, otherwise normal, claw well-developed	Normal, somewhat reduced in size, coxa prolonged	Normal, slightly reduced in size, coxa prolonged, telopodite unmodified	Normal or slightly reduced in size
7 <sup>th</sup> pair of legs (male), coxal process	None	Present or absent	Tooth-shaped	Absent	Well-developed, setose	Present, setose	None	None
7 <sup>th</sup> pair of legs (male), telopodite	Reduced, 2- or 3-segmented	Reduced or not, number of segments varies	Ca ½ as long as other legs, but normal	Normal in shape, but reduced in size	Strongly reduced, 2-segmented	Strongly reduced in size, number of segments varies	Strongly reduced, entire leg consisting of one segment, densely setose	Entire leg unmodified
Anterior gonopods, coxal processes	Separate, apically rounded	Separate	Separate, slender	Separate, slender	Separate, slender	Separate	Separate, 2-branched	Separate, slender

	<b><i>Koiulus</i> gen. nov.</b>	<b><i>Ansiulus</i></b>	<b><i>Ikahoiulus</i></b>	<b><i>Kopidoiulus</i></b>	<b><i>Senbutudoiulus</i></b>	<b><i>Skleroprotopus</i></b>	<b><i>Uenoiulus</i></b>	<b><i>Ussuriulus</i></b>
Anterior gonopods, flagella	Strongly reduced to scaly stump, not articulated with coxa	Well-developed, long or relatively short	Not clear if absent or just strongly reduced	Strongly reduced to basal flap	Well-developed, long, thin, with subterminal side-branch	Well-developed, long, thin	Well-developed, long, thin	Absent
Anterior gonopods, telopodites	Almost as long as coxal processes, 1-segmented, apically expanded	Half as long as coxal processes, 2-segmented (no. of segments unknown for <i>A. matumotoi</i> )	1-segmented, articulated with coxa, ca 0.4 times as long as coxal process	Half or 1/4 as long as coxal processes, 1- or 2-segmented	1-segmented, very short, with several apical setae	Half, 2/3 or 3/4 as long as coxal processes, 1-segmented, except in <i>S. schmidtii</i> (2-segmented)	As long as coxal processes, broad, 1-segmented	Half as long as coxal processes, 1-segmented, sparsely setose
Posterior gonopods, coxal part	Deeply split into two almost equally long processes	2-branched distally	Long, slender, simple, a small mesal process at base (unless the small process is the coxal one and the long process is the telopodite) or with a short process (if the long process is the telopodite)	Long, slender, simple, a small mesal process at base (unless the small process is the coxal one and the long process is the telopodite) or with a short process (if the long process is the telopodite)	Not clear from drawing whether one or two branches, no information in summary	2-branched distally	Short, simple	Complicated
Posterior gonopods, telopodite	Absent	Present, as tiny remnant	Not clear if absent or just strongly reduced	Not clear if absent or just strongly reduced	Absent	Absent	Absent	Not clear if the telopodite is represented
Sources	Pers.obs.	Takakuwa 1940a; Golovatch 1980a; Mikhailjova & Lim 2001; Mikhailjova & Korsós 2003; pers. obs. on FSCB material	Takakuwa 1941	Attems 1909; Golovatch 1979b; Murakami 1990; Mikhailjova 1997; pers. obs. on FSCB material	Miyosi 1957	Attems 1901; Takakuwa 1940b, 1942; Takakuwa & Takashima 1949; Takakuwa 1954; Shinohara 1960; Golovatch 1979a; Zhang 1985; Lim & Mikhailjova 2001; Mikhailjova & Korsós 2003; pers. obs. on FSCB material	Murakami 1971; pers. obs. on paratypes of <i>U. notabilis</i>	Golovatch 1980b; Mikhailjova 1998; pers. obs. on FSCB material

kindly arranged a loan of *Uenoiolus notabilis* paratypes, to Anders Illum who assisted with photography and scanning electron micrography, to Mrs Galina Sinelnikova (Vladivostok, Russia) who kindly inked Fig. 6, and to Dragan Antić and Sergei Golovatch for careful reviews of the manuscript.

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## Appendix

### Species of Mongoliulidae

#### *Ansiulus* Takakuwa, 1940

- A. aberrans* Mikhaljova & Korsós, 2003 (Korea, Russian Far East)
- A. deminutus* Mikhaljova, 2001 (Korea)
- A. legitimus* Golovatch, 1980 (Korea)
- A. matumotoi* Takakuwa, 1940 (Korea)

#### *Ikahoiulus* Takakuwa, 1941

- I. leucosoma* Takakuwa, 1941 (Japan)

#### *Koiulus* gen. nov.

- K. interruptus* gen. et sp. nov. (Russian Far East)

#### *Kopidoiulus* Attems, 1909 (overview: Murakami 1990)

- K. albulus* Haga, 1956 (Japan)
- K. caecus* Attems, 1909 (Japan)
- K. continentalis* Golovatch, 1979 (Russian Far East, NE China)
- K. khasanicus* Mikhaljova, 1997 (Russian Far East)
- K. longus* Shinohara, 1963 (Japan)
- K. ocellatus* Takakuwa, 1940 (Japan)
- K. truncatus* Murakami, 1990 (Japan)

#### *Senbutudoiulus* Miyosi, 1957

- S. platypodus* Miyosi, 1957 (Japan)

#### *Skleroprotopus* Attems, 1901

##### Synonymy

#### *Mongoliulus* Pocock, 1903

#### *Paraprotopus* Verhoeff, 1939

#### *Nesoprotopus* Verhoeff, 1939

- S. chichibuensis* Shinohara, 1960 (Japan)
- S. chollus* Mikhaljova & Korsós, 2003 (Korea)
- S. confucius* Attems, 1901 (China)
- S. coreanus* (Pocock, 1895) (Korea, Russian Far East) (syn.: *S. simileserratus* Golovatch, 1980)
- S. costatus* Mikhaljova & Korsós, 2003 (Korea)
- S. hakui* Takakuwa, 1940 (Korea)
- S. ikedai* Takakuwa, 1940 (Japan)
- S. inferus* Verhoeff, 1939 (Japan)
- S. insularum* Verhoeff, 1939 (Japan)
- S. laticoxalis laticoxalis* Takakuwa, 1942 (China, North Korea)
- S. laticoxalis longus* Murakami & Paik, 1968 (Korea)
- S. membranipedalis* Zhang, 1985 (China)
- S. montanus* Takakuwa, 1942 (Japan)
- S. okiensis* Takakuwa, 1940 (Japan)
- S. osedoensis* Miyosi, 1957 (Japan)
- S. ramuliferus* Lim & Mikhaljova, 2000 (Korea)
- S. schmidtii* Golovatch, 1979 (Russian Far East)
- S. serratus* Takakuwa & Takashima, 1949 (China)

*S. sidegatakedensis* Miyosi, 1957 (Japan)

*S. simplex* Takakuwa, 1940 (Japan)

*S. torii* Takakuwa, 1940 (Japan)

*Uenoiulus* Murakami, 1971

*U. notabilis* Murakami, 1971 (Japan)

*Ussuriulus* Golovatch, 1980

*U. pilifer* Golovatch, 1980 (Russian Far East)