

## Nine new Paradoxosomatidae millipedes from Peru, with an infrageneric reclassification of *Iulidesmus* Silvestri, 1895 (Diplopoda: Polydesmida)

### Девять новых многоножек-диплопод семейства Paradoxosomatidae из Перу с новой внутривидовой классификацией *Iulidesmus* Silvestri, 1895 (Diplopoda: Polydesmida)

S.I. Golovatch<sup>1</sup>, A.M. Korotaeva<sup>2</sup>  
С.И. Головач<sup>1</sup>, А.М. Коротаева<sup>2</sup>

<sup>1</sup> Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospekt 33, 119071 Moscow, Russia.

<sup>1</sup> Институт проблем экологии и эволюции РАН, Ленинский проспект, 33, Москва 119071 Россия.

<sup>2</sup> Institute of Biology and Chemistry, Moscow State Pedagogical University, Zoology and Ecology Department, Moscow 129164 Russia.

<sup>2</sup> Институт биологии и химии МПГУ, кафедра зоологии и экологии, Москва 129164 Россия.

Sergei I. Golovatch sgolovatch@yandex.ru; <https://orcid.org/0000-0001-7159-5484>

Alena M. Korotaeva alenakorotaeva2017@mail.ru; <https://orcid.org/0009-0009-2716-5140>

KEY WORDS: taxonomy, new genus, new species, species group, species subgroup, key, gonopod, evolution, iconography.

КЛЮЧЕВЫЕ СЛОВА: таксономия, новый род, новый вид, группа видов, подгруппа видов, ключ, гонопод, эволюция, иконография.

**ABSTRACT.** The following nine new Paradoxosomatidae are described from Peru: *Graphisternum gracile* sp.n. (Graphisternini), *Incamorpha eskovi* gen.n., sp.n., *Iulidesmus maculatus* sp.n., *I. cingulatus* sp.n., *I. satipo* sp.n., *I. pubescens* sp.n., *I. semicingulatus* sp.n., *I. asulcatus* sp.n., and *I. carpish* sp.n. (all Catharosomatini). *Incamorpha* gen.n. is characterized within the tribe Catharosomatini by a subgeniculate gonopodal telopodite with a normal, not hypertrophied prefemorite, a distinct distofemoral process, but neither traces of a usual long and flagelliform solenomere nor an evident postfemoral sulcus to delimit a postfemorite proper. *Iulidesmus* Silvestri, 1895, by far the largest Neotropical genus of Paradoxosomatidae that presently comprises 85 species, all listed and supplied with brief descriptive notes, is rediagnosed and, based on the gonopodal conformation alone, split into a number of presumably natural species groups and subgroups: the *hylaeicus* group, the *alacer* group, the *differens* group, the *marthae* group, the *golovatchi* group, and the *salvadorii* group, the latter with the *junki* subgroup and the *isthmianus* subgroup. The newly outlined species groups and subgroups are all keyed and delimited in an evolutionary context, as a succession of stages from presumably simple and primitive to increasingly complex and advanced, this being largely related to the development of a postfemorite proper. The following new synonymy is advanced: *Catharosoma* Silvestri, 1897 = *Montesecaria* Kraus, 1956, syn.n. *Catharosoma nitidum* Kraus, 1954, from Peru, is returned back to *Catharosoma* where it was originally described. The following new combination is also proposed: *Iulidesmus golovatchi* (Jeekel, 2002), from Venezuela, comb.n. ex *Montesecaria*.

How to cite this paper: Golovatch S.I., Korotaeva A.M. 2024. Nine new Paradoxosomatidae millipedes from Peru, with an infrageneric reclassification of *Iulidesmus* Silvestri, 1895 (Diplopoda: Polydesmida) // Arthropoda Selecta. Vol.33. No.3. P.293–327, Suppl. Table. doi: 10.15298/arthsel.33.3.01

**РЕЗЮМЕ.** Из Перу описаны следующие девять новых Paradoxosomatidae: *Graphisternum gracile* sp.n. (Graphisternini), *Incamorpha eskovi* gen.n., sp.n., *Iulidesmus maculatus* sp.n., *I. cingulatus* sp.n., *I. satipo* sp.n., *I. pubescens* sp.n., *I. semicingulatus* sp.n., *I. asulcatus* sp.n. и *I. carpish* sp.n. (все Catharosomatini). *Incamorpha* gen.n. характеризуется в пределах трибы Catharosomatini почти коленчатым телоподитом гонопода с нормальным, негипертрофированным префеморитом, явственным дистофеморальным отростком и отсутствием следов как обычно длинного и жгутиковидного соленомера, так и различимой постфеморальной бороздки, отделяющей собственно постфеморит. Для *Iulidesmus* Silvestri, 1895, явно самого большого неотропического рода Paradoxosomatidae, который ныне включает 85 видов, все представленные списком и все снабженные краткими описаниями, дан новый диагноз и на основе лишь строения гоноподов представлены новое деление на ряд предположительно естественных групп и подгрупп видов и ключи: группы видов *hylaeicus*, *alacer*, *differens*, *marthae*, *golovatchi* и *salvadorii*, последняя с подгруппами *junki* и *isthmianus*. Вновь очерченные группы и подгруппы видов выделены в эволюционном контексте, как последовательный ряд стадий от предположительно простых и примитивных до все более сложных и про-

двинутых, что в основном связано с развитием собственно постфеморита. Предложена следующая новая синонимия: *Catharosoma* Silvestri, 1897 = *Montesecaria* Kraus, 1956, syn.n. Вид *Catharosoma nitidum* Kraus, 1954, из Перу, возвращен в состав рода *Catharosoma*, где он и был изначально описан. Также предложена следующая новая комбинация: *Iulidesmus golovatchi* (Jeekel, 2002), из Венесуэлы, comb.n. ex *Montesecaria*.

## Introduction

The Paradoxosomatidae is the largest family in the entire millipede class Diplopoda, presently counting 1000+ species from 200+ genera, 22 tribes and three subfamilies [Nguyen, Sierwald 2013; Enghoff *et al.*, 2015] and being especially diverse in and even dominating the diplopod faunas of Indo-Australia [Golovatch, Liu, 2020]. Surprisingly, indigenous paradoxosomatids are absent not only from Antarctica, which is self-evident, but conspicuously also from North America. This group appears to only marginally populate Central and North America north of Panama [Jeekel, 1963; Hoffman, 1977, 1999]. The anthropochorous introductions concern four species only: the more temperate and subcosmopolitan *Oxidus gracilis* (C.L. Koch, 1847) (Orthomorphini, Paradoxosomatinae), of East rather than Southeast Asian origin, ranging from Canada to Mexico; the pantropical *Asiomorpha coarctata* (de Saussure, 1860) (Orthomorphini, Paradoxosomatinae), of Southeast Asian stock, in America mostly encountered around the Gulf of Mexico and along Mexico's Pacific coast; the similarly almost pantropical, but more sporadic *Chondromorpha xanthotricha* (Attems, 1898) (Sulciferini, Paradoxosomatinae), of South Asian origin, in America recorded from numerous places ranging from southern Texas and several Caribbean islands in the north to a few scattered localities in Mexico in the south; and the basically Australian *Akamptogonus novarae* (Humbert et de Saussure, 1869) (Australiosomatini, Australiosomatinae), introduced from its native Australia not only to New Zealand, whence it was originally described, but also to the Hawaiian Islands, along the coast of California, both U.S.A., and a few places in Mexico [Recuero, García-Paris, 2016]. Only three indigenous species are known to occur in entire Central America, all congeners in *Iulidesmus* Silvestri, 1895 (Catharosomatini, Paradoxosomatinae) and all presently considered as narrow endemics: *I. isthmianus* (Loomis, 1961), from Panama, *I. moorei* (Hoffman, 1977), from Costa Rica, and *I. semirugosus* (Pocock, 1888), from Dominica, Lesser Antilles [Hoffman, 1977, 1999, 2012; Recuero, García-Paris, 2016], whereas both Catharosomatini and *Iulidesmus* are subendemic to and especially diverse across South America [Golovatch, 2005; Golovatch *et al.*, 2022].

In contrast, the indigenous paradoxosomatid fauna of South America south of Panama is quite rich, highly peculiar and diverse (ca 150 species), yet, still being sufficiently impressive, it is larger than that of the Euro-Mediterranean realm, but subordinate in relation to the Afrotropical (together with southern Africa) and, especially, Indo-Australian ones. Two major diversification

centres of Paradoxosomatidae are distinguishable in South America, one in the area of southern Brazil, northern and central Chile, Paraguay and northern Argentina, the other in Peru, northern Bolivia and possibly Ecuador. Until recently, the vast regions of northern Brazil, Guiana, Venezuela and Colombia were thought to support surprisingly few species [Jeekel, 1968, 2002; Golovatch, 2005], but this observation appears to be false at least as regards the faunas of Colombia and Venezuela [Bueno-Villegas *et al.*, 2019; Romero-Rincon, Golovatch, 2024].

The Neotropical fauna itself is strongly dominated by relatively few (about a dozen) genera of the endemic tribe Catharosomatini Brolemann, 1929. Of these genera, *Iulidesmus* is by far the largest, presently encompassing 85 species (Suppl. Table). This genus is particularly widespread, ranging from the island of Dominica in the Caribbean and Costa Rica in the north (see above), through Panama and the Andes of Venezuela, Colombia, Ecuador, Peru, Paraguay and Bolivia, to Uruguay, southern and eastern Brazil, and northern Argentina in the south [Golovatch, 2005; Golovatch *et al.*, 2022; Romero-Rincon, Golovatch, 2024]. *Catharosoma* Silvestri, 1897, the second largest genus, is more restricted in distribution, as its 18 currently recognized species range from Bolivia and Paraguay in the north, through Brazil, to northern Argentina in the south [Rodrigues *et al.*, 2020]. All other contribal genera are mono- or oligotypic. Rather recently, the entire paradoxosomatid fauna of the southern diversification centre of South America was reviewed, and largely keyed [Golovatch, 2005], only slightly updated or corrected since [Rodrigues *et al.*, 2020; Parra-Gómez, 2022].

In addition to Catharosomatini, the indigenous Neotropical fauna comprises further two tribes of the subfamily Paradoxosomatinae: Eviulisomatini Brölemann, 1916, with the sole Neotropical genus *Onciurossoma* Silvestri, 1932 (eight species ranging from Venezuela, Guiana and Suriname in the north to central Amazonia of Brazil in the south, and to Bahia state, Brazil in the east [Golovatch *et al.*, 2022]) and Graphisternini Verhoeff, 1941 (two genera, *Ergethus* Chamberlin, 1949 and *Graphisternum* Verhoeff, 1941, altogether ten species, all in Peru [Nguyen, Sierwald, 2013]). Because the Eviulisomatini also includes several genera and numerous species in tropical eastern Africa, the disjunct, amphi-Atlantic distribution pattern of the tribe, i.e. West Africa and northern South America, invites speculations that, in the geological past, when both continents were united within the supercontinent Gondwana, the Eviulisomatini already existed and split following the continental drift [Jeekel, 1968, 2002].

The present paper puts on record nine new Paradoxosomatidae from Peru, mostly taken in 2017 during a single collecting trip by Kirill Yu. Eskov, a prominent Russian arachnologist, palaeontologist and biogeographer. One more sample from Peru was collected in 2016 by Ilya Melnik, an amateur biologist from Moscow whose material has partly been treated elsewhere [Golovatch, Korotaeva, 2023a, b]. The new samples appear to contain nine new species in three genera: two from the tribe Catharosomatini (eight species, including one representing a new monospecific genus) and one from the Graphisternini.

## Materials and Methods

The material treated in this paper was generously handed to us on loan by Arkady A. Schileyko, the Keeper of Myriapoda collections at the Zoological Museum of the Moscow State University (ZMUM). The samples, still preserved in 75% ethanol, have been fully returned to the ZMUM collection.

The pictures of fixed samples were taken with a Canon EOS 5D digital camera and stacked using Zerene Stacker software. SEM micrographs were obtained using a Tescan Vega 2 electron scanning microscope (Brno, Czech Republic) at the Palaeontological Institute, Russian Academy of Sciences, Moscow. SEM samples were coated with gold and returned back to alcohol upon examination. Final image processing was performed with Adobe Photoshop CC.

Abbreviations used to denote particular structures of the specimens are explained both in the text and in figure captions.

## Taxonomy

### Tribe Graphisternini

Genus *Graphisternum* Verhoeff, 1941

Type species: *Graphisternum pallidum* Verhoeff, 1941, by monotypy [Verhoeff, 1941], from southern Peru.

Other species included: *G. bordoni* Tabacaru, 1981 and *G. ornatum* Kraus, 1959 [Kraus, 1959a, Tabacaru, 1981], both also from Peru.

DIAGNOSIS. The tribe can be characterized by the extremely poorly developed to usually totally missing paraterga, the suberect and distally pointing gonopodal telopodites at most only gently curved cephalad, a drastically shortened and twisted gonopodal femorite supporting a laterad shifted seminal groove, with an elaborate solenophore and an elongate and hypertrophied gonopodal prefemorite, both subequal in length. *Graphisternum* differs from *Ergethus* Chamberlin, 1949, the only other genus of the tribe, with seven species from Peru [Nguyen, Sierwald, 2013], by the solenophore usually being more compact (*vs* rather elongate, typically with a distinct lobe on the mesal side of the femorite), and with a shorter and fully concealed free solenomere (*vs* clearly longer, flagelliform and better exposed at least near the base) [Shear, 1971; Kraus, 1954, 1955, 1959b, 1960]. ♂ sternal and leg modifications usually present and varied.

### *Graphisternum gracile* sp.n.

Figs 1–12.

HOLOTYPE ♂ (ZMUM), Peru, Huanuco Region, Carpish Pass, 2400 m a.s.l., S 09°41'34", W 76°05'06", cloud forest, in epiphytes, 9.IX.2017, K. Eskov leg.

NAME. To reflect the highly gracious appearance.

DIAGNOSIS. Differs from congeners by the peculiar, stripy colour pattern, coupled with the particularly complex structure of the gonopodal telopodite, this being represented distally by four main elements: three lamellar and mostly irregularly rounded lobes and a plate, plus a short free solenomere sheathed by one of the lobes.

DESCRIPTION. Length 18 mm, width on midbody pro- and metazona 0.9 and 1.1 mm, respectively (♂). Body moniliform, colouration generally light beige with a clear pattern of brown paramedian stripes on sides of terga, both pro- and metaterga, above ozopore level. Sides below ozopores similarly, but lighter brownish. Antennae brown, tip pallid, legs light brown (Figs 1–6).

Tegument generally smooth and shining, but metazona, both metaterga and sides, in places faintly rugulose longitudinally down to pleurosternal carinae, caudal margins of metaterga and sides finely striolate. Clypeolabral region sparsely setose, vertex bare, epicranial suture rather faint; interantennal isthmus as wide as diameter of antennal socket. Antennae long and slender, *in situ* extending past ring 4 dorsally (♂); in length, antennomeres 2–5>6>1=7. Genae rounded in dorsal or ventral view.

In width, head = ring 5=15 > collum > 3=4 > 2. Starting with ring 16, trunk gradually tapering towards telson. Paraterga on collum broadly rounded anteriorly, but subrectangular and rather narrowly rounded caudally. Paraterga totally absent, in their stead only faint and regularly rounded lateral swellings on following metazona, each delimited by a wide, lateral, light beige to ivory stripe beneath a similarly wide, brown, dorsolateral stripe (Figs 1–6). Pore formula normal; ozopores lateral, invisible from above, well visible in lateral view, mostly lying at nearly midheight of and about rear 1/4 off caudal margin on poriferous metaterga. Pleurosternal carinae low, simple, mostly arcuate ridges present on rings 2–18, smooth and devoid of caudal spines. Setation pattern 2+2 in a transverse anterior row on all postcollum rings, tergal setae being short, 1/4–1/5 metatergal length. Axial line absent. Transverse metatergal sulci very faint, traceable on rings 5–18. Stricture between pro- and metazona rather shallow, broad and almost smooth. Limbus simple, narrow and entire. Epiproct as usual, long, slender, subtruncate apically, with two very small pre-apical lateral papillae. Hypoproct roundly subtriangular, with 1+1 small rounded tubercles behind a broadly rounded caudal margin.

Sterna densely setose, with faint cross-impressions, transverse impressions being considerably weaker than axial ones. Sternal cones absent. A prominent, finger-shaped, high, suberect, densely setose process each between coxae 4 and 5 (♂). Each coxa 2 with a prominent, rounded, erect, thick and finger-shaped gonapophysis (♂). Legs very long and slender, ca 2.5 times as long as midbody height (♂). Brushes present on tarsi and, distally, on tibiae 1–11 (♂). Adenostyles absent.

Gonopods (Figs 7–12) very complex, each with a rather short, stout, subcylindrical coxite (**cx**) carrying a usual cannula (**ca**) and several distoventral setae on a small, but evident hump (**h**). Telopodite only a little longer than coxite, suberect, also rather short and stout. Prefemorite (**pf**) as usual, densely setose and delimited by a distinct cingulum from a very short and small femorite (**fe**). Postfemorite only very slightly bent forward, consisting of four main, irregularly shaped parts: three lamellar and mostly irregularly rounded lobes (**a**, **b** and **c**), and a plate (**d**) located basal to **c**. Lobe **a** broadly rounded, the dorsalmost and the largest, about twice as long as either **b** and **c**. Lobe **b** sheathing much of a short free solenomere (**sl**), thus representing a solenophore and this being additionally protected by lobes **a** and **c**. Lobe **c** the ventralmost, about as long as **b** or **d**, separated from **d** by a distinct ventral sulcus. Seminal groove (**sg**) shifted laterad on a twisted **fe** to move further onto **sl**.

### Tribe Catharosomatini

Genus *Incamorpha* gen.n.

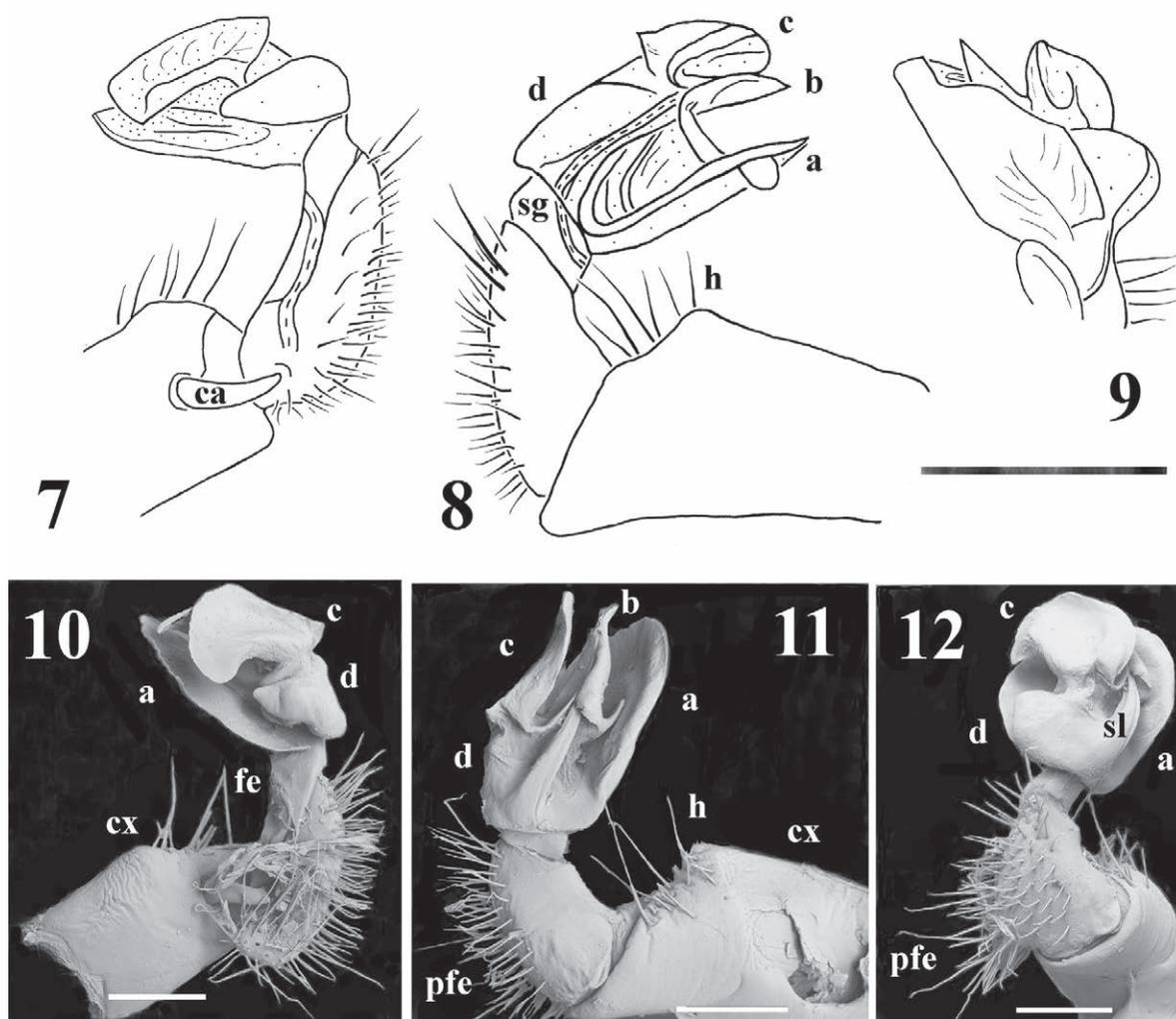
Type species: *Incamorpha eskovi* sp.n.

DIAGNOSIS. A monospecific genus of Catharosomatini with 20 body rings, poorly developed paraterga and evident sternal cones, distinct from the other genera by a clearly subgeniculate gonopodal telopodite, bent at a usual demarcation cingulum dividing a long and slender femorite from a similarly long and slender postfemoral region, or solenophore (**sph**), coupled with both cannula and gonoprefemoral portion being normal (the latter densely setose, as usual, but not hypertrophied); gonofemorite (**fe**) supplied with both a distinct distoventral process (**p**)



Figs 1–6. *Graphisternum gracile* sp.n., ♂ holotype. 1–3 — anterior part of body, dorsal, lateral and ventral views, respectively; 4–6 — middle and posterior parts of body, dorsal, lateral and ventral views, respectively. Photographs taken not to scale.

Рис. 1–6. *Graphisternum gracile* sp.n., голотип ♂. 1–3 — передняя часть тела, соответственно сверху, сбоку и снизу; 4–6 — средняя и задняя части тела, соответственно сверху, сбоку и снизу. Фотографии сняты без масштаба.



Figs 7–12. *Graphisternum gracile* sp.n., ♂ holotype, left gonopod, mesal, lateral, ventral, mesal, lateral and subventral views, respectively. Scale bars: 0.5 mm (7–9) and 0.2 mm (10–12, SEM).

Рис. 7–12. *Graphisternum gracile* sp.n., голотип ♂, левый гонопод, соответственно изнутри, сбоку, снизу, изнутри, сбоку и почти снизу. Масштаб: 0,5 мм (7–9) и 0,2 мм (10–12, SEM).

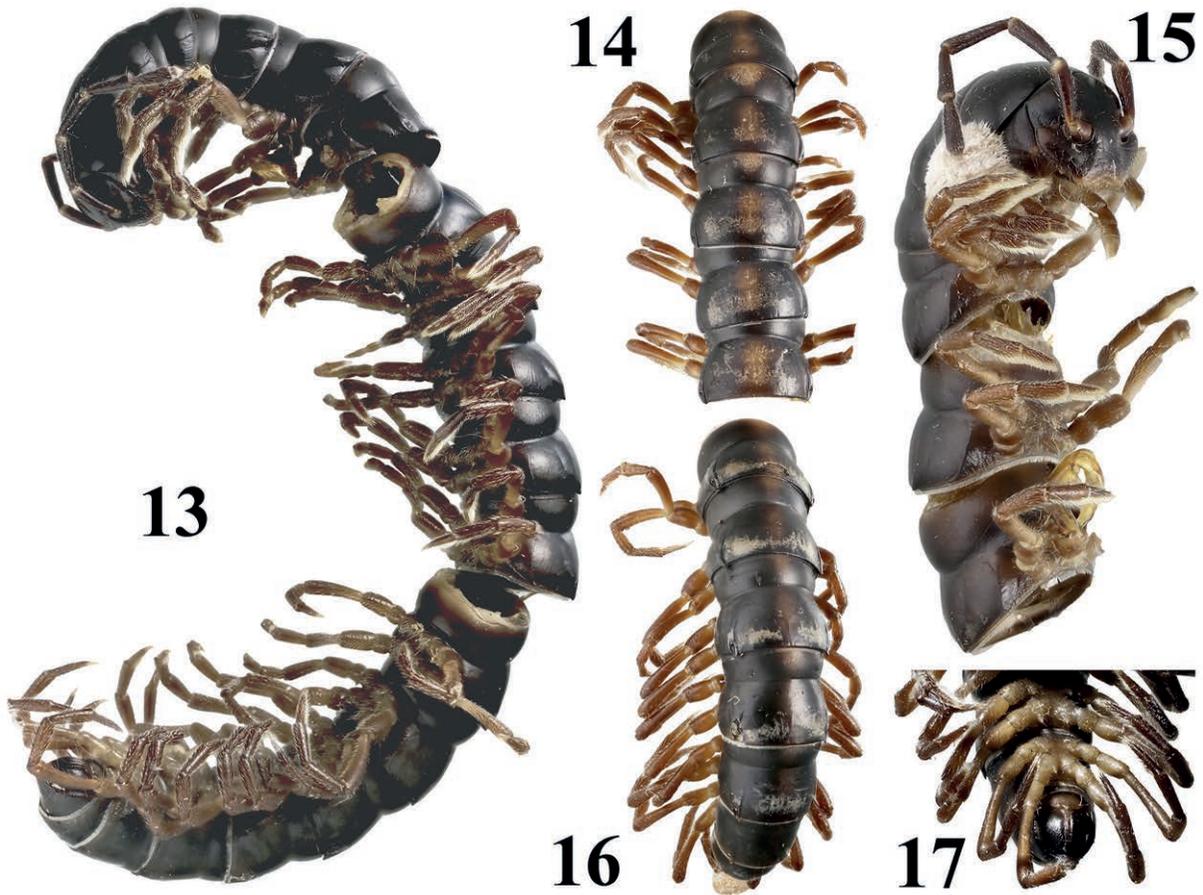
and a ventral fold/bulge (**k**) at the very base of **sph**; telopodite with a superficially virtually invisible free solenomere, only the latter's basalmost part probably traceable on **k** immediately distal to gonofemoral process (**p**) at base of **sph**. Seminal groove first running entirely on mesal side of femorite, only near the geniculation cingulum recurved distally, via bulge **k**, to move ventrad onto the longer branch of a distally bilobed and lamellar **sph** (Figs 22–30). Neither visible traces of a usual long and flagelliform solenomere nor an evident postfemorite proper.

NAME. Derived from the Inca, the famous people of the region, whose one of the former main cities, Machu Picchu, is incidentally the type locality of the type species.

REMARKS. A process or outgrowth, or both, on the gonopodal femorite is known to only occasionally occur in species of Catharosomatini with strongly curved telopodites. Such is *Catharosoma glabratum* Schubart, 1945, from the Rio de Janeiro area, Brazil, which shows a very large, rounded, ventral lobe on the femorite [Schubart, 1945]. However, the genus *Catharosoma* Silvestri, 1897 is easily distinguished by a hypertrophied gonoprefemoral (= densely setose) region, sometimes also by

a clearly shortened femorite carrying one or two outgrowths, such as observed, e.g., in *C. laviudae* Kraus, 1955, *C. muticum* Kraus, 1955, *C. jaujensis* Kraus, 1955 or *C. mamillatum* Kraus, 1955, all from Peru [Kraus, 1955]. In demonstrating a similarly hypertrophied prefemorite and a shortened femorite, the latter supplied with an evident distomedial lobe, this group is clearly joined only by *C. nitidum* Kraus, 1954, also from Peru. This latter taxon was later designated the type, very small (width 1.2 mm) and sole species of the genus *Montesecaria* Kraus, 1956<sup>1</sup> [Kraus, 1954, 1956]. In contrast, *Incamorpha eskovi* sp.n. is unusually large for a Neotropical paradoxosomatid, reaching >30 mm in length and >3.0 mm in width.

<sup>1</sup> This implies the following new synonymy: *Catharosoma* Silvestri, 1897 = *Montesecaria* Kraus, 1956, **syn.n.** Hence *Catharosoma nitidum* Kraus, 1954, from Peru [Kraus, 1954, 1956], is returned back to *Catharosoma* where it was originally described. The following new combination is also advanced: *Iulidesmus golovatchi* (Jeekel, 2002), from Venezuela [Jeekel, 2002], **comb.n.** ex *Montesecaria*, because the latter species, on account of a relatively short gonopodal prefemorite, is better to be assigned to *Iulidesmus*, albeit as the sole component of the *golovatchi* group (see Suppl. Table).



Figs 13–17. *Incamorpha eskovi* sp.n., ♂ paratype, 13 — habitus, ventrolateral view; 14, 15 — anterior part of body, dorsal and ventrolateral views, respectively; 16, 17 — posterior parts of body, dorsal and ventral views, respectively. Photographs taken not to scale.

Рис. 13–17. *Incamorpha eskovi* sp.n., паратип ♂. 13 — общий вид, одновременно снизу и сбоку; 14, 15 — передняя часть тела, соответственно сверху и одновременно снизу и сбоку; 16–17 — задняя части тела, соответственно сверху и снизу. Фотографии сняты без масштаба.

Perhaps the only other species of Catharosomatini that shows a gonopodal conformation particularly similar to that of *I. eskovi* sp.n. seems to be *Iulidesmus unicus* (Kraus, 1959), a much smaller form (width of ♂, 1.65 mm, of ♀, 1.9 mm) also coming from Peru [Kraus, 1959b]. Indeed, both seem to share a subgeniculate gonopodal telopodite (cf. Figs 22–30 and 31, 32), the proportions and shapes of most of the main gonopodal elements (coxite, cannula, femorite, solenophore, and the distal course/part of the seminal groove) being basically the same.

Originally, Kraus [1959b] described *unicus* as *Paracatharosoma unicum* Kraus, 1959 and designated it the type species of the independent monobasic genus *Paracatharosoma* Kraus, 1959. However, since Jeekel [1963] correctly perceived especially strong similarities in gonopodal structure between *P. unicum* and *Mestosoma differens* (Kraus, 1956), a species that Kraus [1956] had described from Bolivia (Fig. 33), *Paracatharosoma* was formally synonymized first with *Mestosoma* Silvestri, 1897 [Jeekel, 1963, 1968], an opinion followed by Hoffman [1980] and Nguyen & Sierwald [2013], and later with *Iulidesmus* Silvestri, 1895 [Hoffman, 2012].

The prefemorite in *Incamorpha* gen.n. is as usual, considerably shorter than in *Catharosoma* spp. and the same as in *Iulidesmus*, while the seminal groove runs entirely on the mesal side of the femorite like in numerous, apparently more typical members of Catharosomatini, and only near the geniculation cingulum/sulcus does it seem to become recurved distally, via bulge **k**, to move onto the ventral side of the longer branch (lamina lateralis)

of the solenophore (Figs 22–30). Neither traces of a usual long and flagelliform solenomere nor an evident postfemoral sulcus to delimit a postfemorite proper are visible in *Incamorpha* gen.n. In *Iulidesmus unicus* (Figs 31, 32) or *I. differens* (Fig. 33), however, the seminal groove is quickly shifted laterad already at the base of the gonofemorite to run largely along its dorsolateral edge and then to move a little mesad onto an independent and at least basally exposed solenomere, ending up on the shorter branch of the solenophore. Such a situation definitely implies certain torsion of the gonofemorite which thereby seems to be totally devoid of a process distally, but a typical, long, flagelliform solenomere (**sl**) is traceable, same as something like a bulge **k** (Fig. 31). A free solenomere is evident, starting just beyond the geniculation (Figs 31, 32) or distofemoral sulcus (Fig. 33).

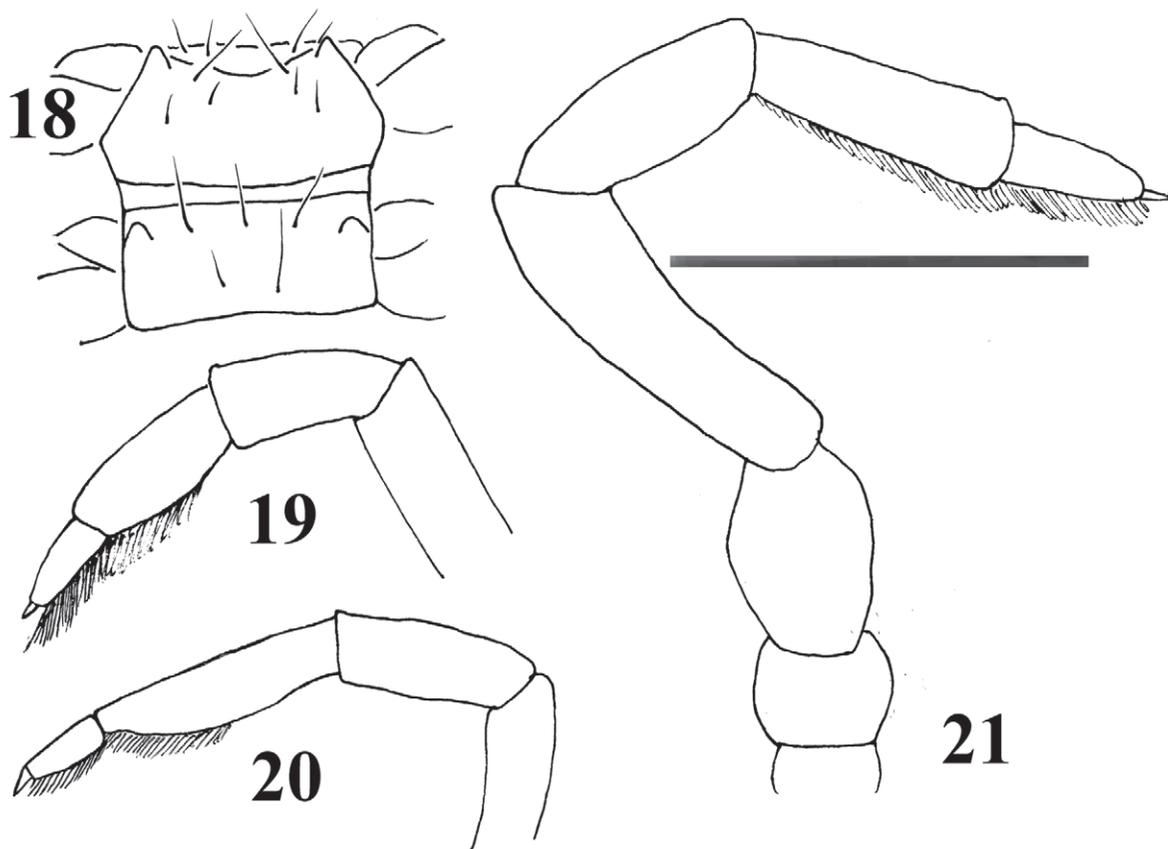
#### *Incamorpha eskovi* sp.n.

Figs 13–30.

HOLOTYPE ♂ (ZMUM), Peru, Cusco Region, Machu Picchu, 2000 m a.s.l., cloud forest (Fig. 146), under logs, 10.X.2017, K.Y. Eskov leg.

PARATYPES: 1 ♂, 1 ♀ (ZMUM), same locality, together with holotype.

NAME. To honour Kirill Y. Eskov, the collector and a renowned Russian arachnologist, palaeontologist and biogeographer.



Figs 18–21. *Incarmorpha eskovi* sp.n., ♂ paratype. 18 — midbody sterna, caudal sternum shown above, ventral view; 19 — distal half of leg 4, lateral view; 20 — distal half of leg 7, lateral view; 21 — leg 9, lateral view. Scale bar: 1.0 mm.

Рис. 18–21. *Incarmorpha eskovi* sp.n., паратип ♂. 18 — стерниты середины тела, задний стернит показан сверху, вид снизу; 19 — дистальная часть ноги 4, сбоку; 20 — дистальная часть ноги 7, сбоку; 21 — нога 9, сбоку. Масштаб: 1,0 мм.

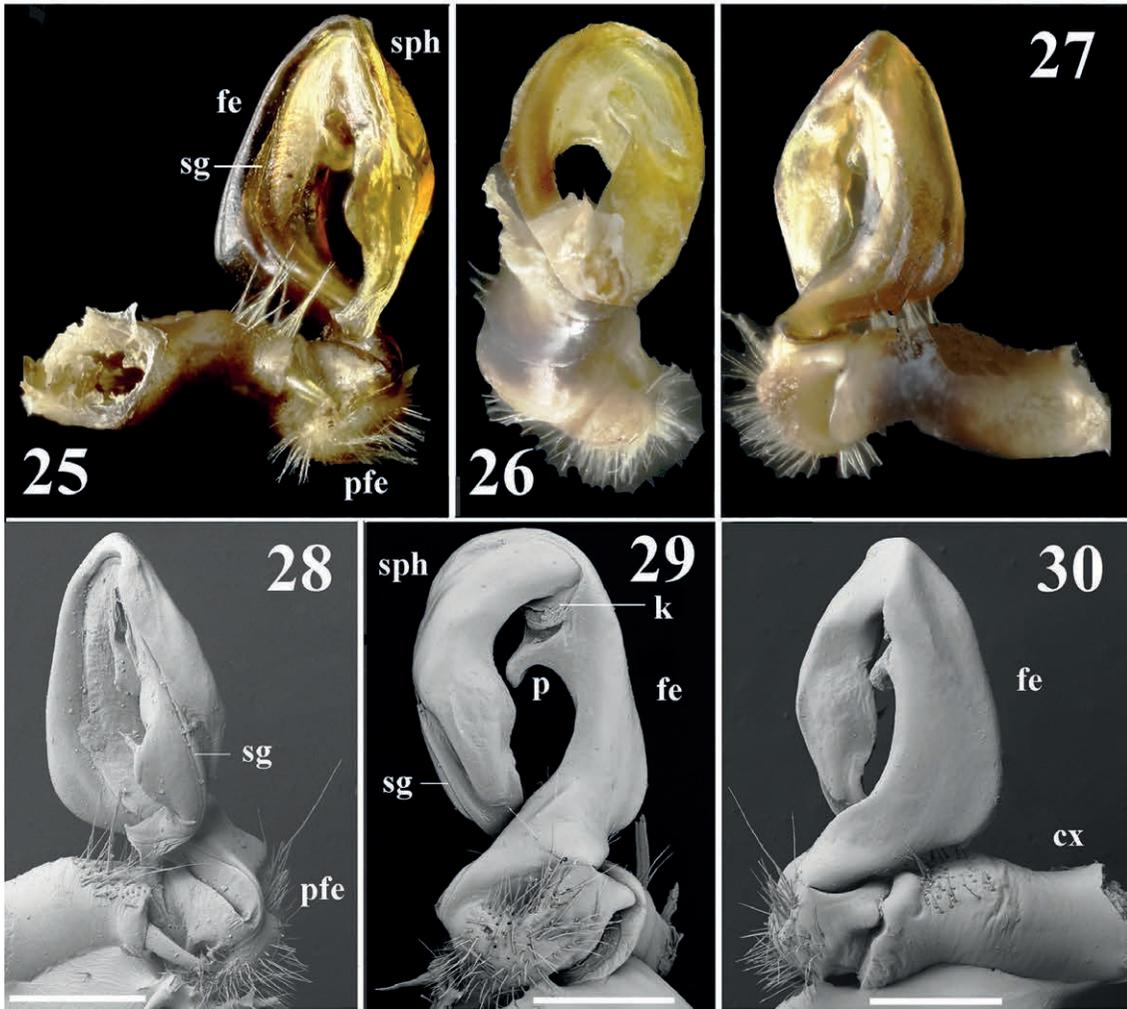
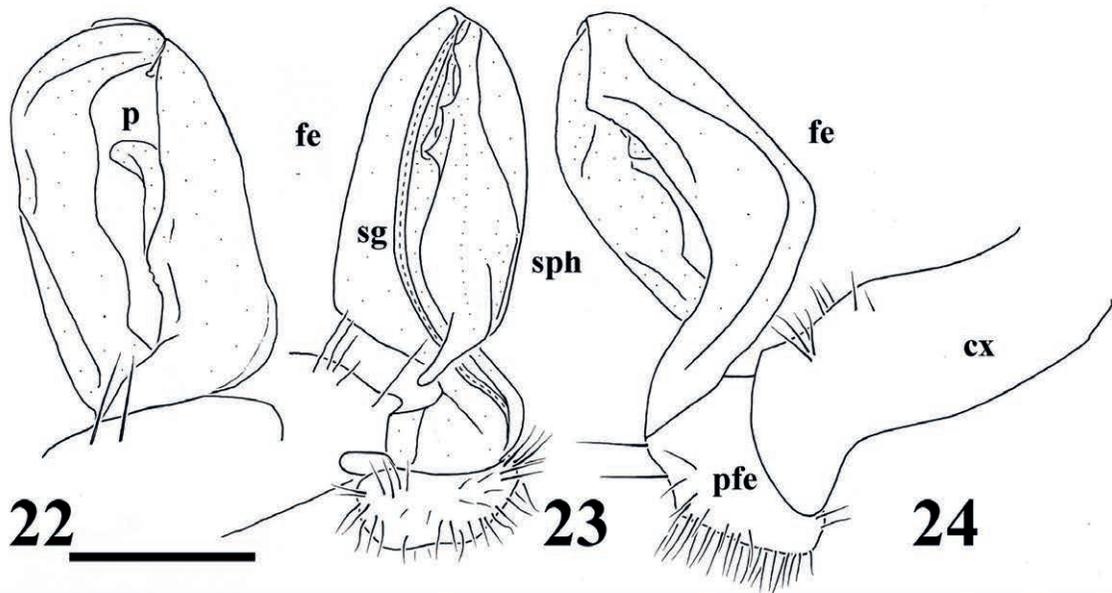
**DESCRIPTION.** Length of both ♂ holotype and ♂ paratype *ca* 31 mm, width of midbody pro- and metazona 2.8 and 3.0 mm, respectively. Length of ♀ paratype *ca* 34 mm, width of midbody pro- and metazona 4.3 and 4.7 mm, respectively. Colouration mainly dark brown to nearly blackish, somewhat contrasting to a more or less complete, rather vague, axial, yellowish stripe consisting of oblong wider spots on metaterga and of triangular smaller spots on proterga, both spots often forming a subhorologiform pattern in attenuating towards stricture; an oblong axial spot starting with caudal half of collum, present until ring 18, sometimes (♀) taking up to half the dorsal surface of metaterga. Legs mostly grey-brown, sometimes red-brown (Figs 13–17).

Body submoniliform, with 20 rings (Figs 13–17). Tegument generally smooth and shining, faintly rugulose only below paraterga and sometimes longitudinally also in rear halves of metaterga. Clypeolabral region very densely setose, vertex nearly bare to bare, epicranial suture rather faint; isthmus between antennae about as broad as diameter of antennal socket. Antennae long and slender, *in situ* extending past ring 3 (♂) or 2 (♀) dorsally; in length, antennomeres 2=6>1=7 (Fig. 13). Genae round in dorsal or ventral view, gnathochilarium without peculiarities.

In width, ring 5=15 > head > collum > ring 2 > 3=4 (♂), starting with ring 16, trunk gradually tapering towards telson (Figs 14, 16). Paraterga set high (at about upper 1/3 midbody height), faint, traceable as small, regularly and broadly rounded flaps on collum or as flat squarish bars, a little thicker/higher on pore-bearing rings than on poreless ones, slightly better devel-

oped in ♂ than in ♀, delimited by distinct sulci both dorsally and ventrally, both incomplete and missing only in anterior 1/3 (Figs 13, 14, 16); paraterga 2 clearly drawn anteriorly beneath collum, caudal corners of paraterga mostly acuminate (♂) or narrowly rounded (♀), on paraterga 2–13 lying within rear tergal margin, thereafter slightly drawn past the margin until ring 18. Transverse mid-dorsal sulci absent. Pore formula normal. Ozopores lateral, invisible from above, lying close to caudal corners of paraterga inside shallow ovoid grooves. Pleurosternal carinae low, simple, smooth, broadly arcuated, poorly developed ridges visible on rings 3–18. Tergal setae simple, arranged in three transverse rows on collum, 2+2 in one anterior row on following metaterga, mostly abraded and retained only on a few anterior rings, setation pattern largely traceable as insertion points, each seta *ca* 1/3 as long as metatergum. Axial line wanting. Stricture between pro- and metazona deep, thin and smooth. Limbus evident, entire, but mostly finely cracked into bacilliform plates (Figs 13–16). Epiproct (Figs 16, 17) long, flattened dorsoventrally, subtruncate, pre-apical lateral papillae small. Hypoproct (Fig. 17) semi-circular, paramedian setigerous papillae near caudal margin small.

Sterna densely setose, cross-impressions shallow, those between ♂ legs 3–5 with a distinct setose cone behind each coxa, between ♂ legs 6, 7 and 9 with similar cones separated by an evident flat isthmus, between following ♂ legs with increasingly distinct cones, the latter a little better developed between posterior coxae than between anterior ones on each ring (Figs 17, 18); smaller sternal cones present also in ♀. No



Figs 22–30. *Incamorpha eskovi* sp.n., ♂ paratype, left gonopod, sublateral, mesal, lateral, mesal, dorsal, lateral, mesal, ventral and lateral views, respectively. Scale bars: 1.0 mm (22–24), taken not to scale (25–27), 0.5 mm (28–30, SEM).

Рис. 22–30. *Incamorpha eskovi* sp.n., паратип ♂, левый гонопод, соответственно почти сбоку, изнутри, сбоку, сверху, сбоку, изнутри, снизу и сбоку. Масштаб: 1,0 мм (22–24), снято без масштаба (25–27), 0,5 мм (28–30, SEM).

other noteworthy sternal modifications. Legs long and slender, very densely setose, prefemora moderately bulged laterally, their bulging increasingly attenuating towards telson (♂, ♀), devoid of adenostyles, incrassate in ♂ compared to ♀, mostly *ca* 1.5–1.6 (♂) or 1.1–1.2 (♀) times as long as midbody height. Legs 1 as usual, clearly shorter than others. Each ♂ coxa 2 with a distinct, apically rounded, finger-shaped gonapophysis. In ♂, distal 1/2–1/3 tibiae 2–14 increasingly poorly inflated distally, and all tarsi except two last ones entirely clothed with conspicuous ventral brushes (Figs 19–21).

Gonopods (Figs 22–30) with a clearly subgeniculate gonopodal telopodite, bent at a usual demarcation cingulum dividing a long and slender femorite (**fe**) from a similarly long and slender postfemoral region, or solenophore (**sph**). Coxite subcylindrical, about half as long as telopodite, densely setose ventrally over distal half; cannula short, unci- and tubiform as usual. Prefemorite normal, relatively small, as usual, about half as long as **fe** or **sph**. Femorite supplied with a distinct distoventral process (**p**), finger-shaped, apically rounded and slightly curved basad. A small ventral fold/bulge (**k**) present at the very base of **sph**. Telopodite with a superficially invisible free solenomere, perhaps only the latter's basalmost part traceable on **k** immediately distal to gonofemoral process (**p**). Seminal groove first running entirely on mesal side of **fe**, recurved distally only near geniculation cingulum, near bulge **k**, to move ventrad onto the longer branch (lamina lateralis) of a distally bilobed and lamellar **sph**. Neither visible traces of a usual, long and flagelliform solenomere nor an evident postfemoral sulcus to delimit a postfemoral proper.

#### Genus *Iulidesmus* Silvestri, 1895

Type species: *Iulidesmus typicus* Silvestri, 1895, by monotypy.

DIAGNOSIS. A very large genus of Catharosomatini with 20 body rings, poorly developed to totally suppressed paraterga and often evident ♂ sternal and leg modifications, distinct from the other genera by a complex and semi- to fully circular gonopodal telopodite. Coxite long and subcylindrical, oriented along the main axis, with or without a ventral bulge and with a usual mesal cannula, either tubiform or conspicuously flattened. Telopodite clearly longer than coxite, typically complex and strongly curved mesad, thus never being coaxial with coxite. Prefemorite (**pfe**) as usual, not hypertrophied, densely setose and clearly set off from femorite by an oblique cingulum. Femorite (**fe**) usually slender, simple and flattened dorsoventrally, slightly to considerably curved mesad, mostly untwisted, but sometimes with some evidence of torsion, often more or less distinctly constricted near midway or distally due to a mesobasal bulge/lobe, and excavate on mesal face, occasionally with a mesal outgrowth or dilatation, distally usually more or less enlarged and apically clearly delimited from acropodite by a distofemoral cingulum or mesal sulcus (**su1**). Postfemoral part especially complex, curved and directed mesad, split just beyond **su1** into a flagelliform solenomere (**sl**), at least its typically sigmoid basal part, often also its tip, being exposed, and a prominent, lamellar and mostly very complex acropodite, or solenophore (**sph**). An additional postfemoral sulcus or cingulum (**su2**) often present to delimit a much shorter postfemoral proper (a short subcylindrical piece lying between **su1** and **su2**), this with or without a rounded, more or less cap-shaped, apical lobe (**lo**) and often with or without a large mesobasal dilatation or lamella (**n**), from a very long and elaborate solenophore (**sph**). The latter highly variable in shape, often with outgrowths, broadly rounded to dentate and/or acuminate at tip, but usually with a lamina lateralis (**ll**) and a

lamina medialis (**lm**), both readily discernible and both sheathing much or most of, or even entire remaining **sl**.

Vivid colour patterns often present. ♂ sternal modifications usually, ventral brushes on tibiae and/or tarsi, as well as adenostyles sometimes present.

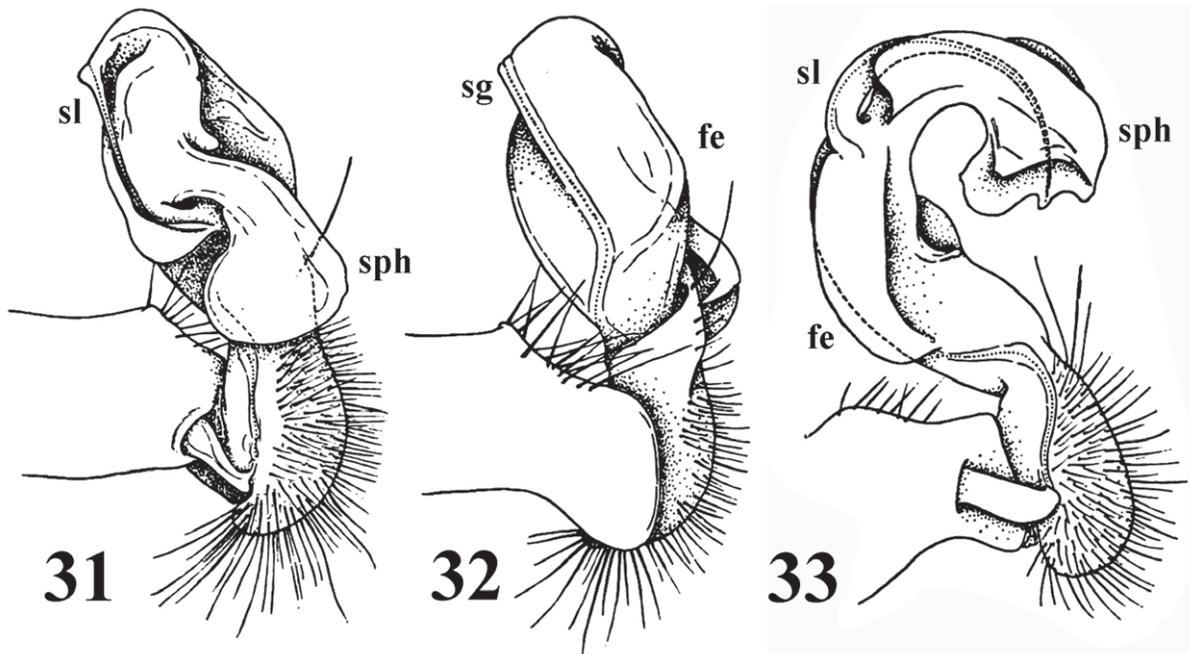
REMARKS. Generally, the gonopodal conformations in the tribe Catharosomatini appear to be unusually diverse, this actually being unprecedented within the Paradoxosomatinae and entire Paradoxosomatidae. Indeed, several genera like *Gonodrepanum* Attems, 1914, *Mogyella* Schubart, 1944 or *Pseudogonodrepanum* Schubart, 1945 and a few others show strongly to completely reduced solenophores, thus leaving the solenomere fully or largely exposed and rendering it no or little support [Jeekel, 1963]. When a solenophore is sufficiently prominent, which is the case in most Catharosomatini, the delicate solenomere is invariably long and flagelliform, presumably nearly always being sheathed by or closely attached to, and thus protected, by the lamina medialis and lamina lateralis of the solenophore, as is usual in the entire family. *Incamorpha* gen.n. seems to be unique as, in addition to a subgeniculate telopodite and a missing postfemoral proper, its solenomere is virtually entirely hidden by and remains invisible outside the solenophore, yet with both of its typical laminae being well discernible.

This is the course of the seminal groove before it moves onto a free solenomere that appears unusual in some Catharosomatini. Thus, the groove, like in most of the typical Paradoxosomatidae, always starts mesally just distal to the cannula, still within the densely setose prefemorite, but then, already on the femorite, it either remains fully on the mesal side, which is the case in most Catharosomatini and numerous other Paradoxosomatinae, or is more or less quickly shifted laterad at the base of or more distally on the usual, long femorite, either ventrolaterally (like in Graphisternini or *Onciurossoma* Silvestri, 1932, yet on a drastically reduced femorite) or dorsolaterally (like in *Iulidesmus unicus* (Figs 31–32) or *I. differens* (Fig. 33)). The latter condition definitely implies some gonofemoral torsion, an important character, usually of generic rank, in the systematics of the entire family Paradoxosomatidae.

Jeekel [1963], in his excellent review of the American Paradoxosomatidae, split *Iulidesmus* (= partly *Mestosoma*), by far the largest genus among the Neotropical paradoxosomatids, and one of the most species-rich globally, into five larger and a number of subordinate groups of species. Two of the groups have since become recognized as full-rank genera: *Catharosoma* and *Broelemannopus* Verhoeff, 1938. Now that *Montesecaria* Kraus, 1956 has been synonymized with *Catharosoma*, the number of genera accepted in the tribe Catharosomatini has presently been stabilized to eleven [Jeekel, 1963, 1968; Golovatch, 2005].

Among the Neotropical genera, *Iulidesmus* certainly remains the largest (presently 85 species, see Suppl. Table) and most widespread, ranging from the Island of Dominica, Lesser Antilles and Costa Rica in the north, via most of South America, to northern Chile, Uruguay and northern Argentina in the south. To characterize this genus, the following, more detailed description can be offered.

BRIEF DESCRIPTION. Gonopodal coxites independent, long and subcylindrical, oriented along the main axis, each with (much more frequently) or without (more rarely) a ventral bulge or tubercle and always with a usual, mesal, curved, tubiform (typically) or conspicuously flattened (more rarely) cannula. Telopodite clearly longer than coxite, typically complex and curved strongly mesad, thus never being coaxial with coxite [Jeekel, 1963], usually rather regularly semi-circular, sometimes completely circular, exceptionally subgeniculate, only rarely thick and relatively stout. Prefemorite as usual, not



Figs 31–33. Left gonopods of *Iulidesmus unicus* (Kraus, 1959) (31, 32) and *I. differens* (Kraus, 1956) (33), mesal, lateral and mesal views, respectively. Reproduced without scale after Kraus [1956, 1959b].

Рис. 31–33. Левые гоноподы *Iulidesmus unicus* (Краус, 1959) (31, 32) и *I. differens* (Краус, 1956) (33), соответственно изнутри, сбоку и изнутри. Воспроизведено без масштаба по: Краус [1956, 1959b].

hypertrophied (= shorter than to subequal to coxite or femorite), always densely setose and clearly set off from femorite by an oblique cingulum. Femorite usually slender and simple, slightly curved mesad, only occasionally somewhat shortened relative to acropodite or coxite, usually untwisted, but sometimes with slight evidence of torsion (this being traced through the laterally shifted seminal groove on the femorite), often more or less distinctly constricted at midway or distally, especially well so due to a mesobasal bulge/dilatation/lobe, only rarely with a mesal outgrowth or dilatation, often constricted at tip and usually more or less clearly delimited from acropodite by a distofemoral cingulum or mesal sulcus (**su1**). Postfemoral part especially complex, clearly curved and directed mesad, either with or without a postfemorite proper, split either just beyond **su1** into a flagelliform solenomere (**sl**), at least its often sigmoid basal part and often also its tip, both being exposed, and a prominent, lamellar and mostly very complex acropodite, or solenophore (**sph**). An additional postfemoral sulcus or cingulum (**su2**) often present to delimit a much shorter postfemorite proper, this with or without a rounded, more or less cap-shaped, apical lobe (**lo**) and with or without a large mesobasal lamella/dilatation (**n**), from a very long and elaborate **sph**. The latter highly variable in shape, typically elongate and curved, often with outgrowths, broadly rounded to dentate and/or acuminate at tip, but usually with a lamina lateralis and a lamina medialis, both readily discernible and both sheathing much or most of, or even entire remaining solenomere.

Colour patterns often vivid; ♂ sternal modifications, ventral brushes on tibiae and/or tarsi, as well as adenostyles, usually on femora, often present.

The infrageneric classification of *Iulidesmus* (partly equal to *Mestosoma*) developed by Jeekel [1963, 1968], however detailed and profound, and even accompanied by a key to most of the formal congeners, requires revision. Not only do the original descriptions of numerous species remain inadequate, even those that were based on male material [Jeekel, 1963], but

also the identity of the type species, *I. typicus*, described from a ♀ holotype from Bolivia, needs clarification using ♂ topotypic material [Hoffman, 2012].

Definitely, *Iulidesmus* is still a heterogeneous assemblage, likely to require revival of at least some of its presently quite numerous junior synonyms (cf. Jeekel [1963]). A refined grouping of the species must better consider the course of the seminal groove along a slightly twisted vs untwisted gonofemorite, the shape of the gonofemorite and its outgrowths (if any), and, above all, the postfemoral part, be it still primitively devoid of a postfemoral sulcus and structures like an apical lobe and/or a mesobasal lamella, or already showing these apomorphies, partly or in full. Somatic, sternal and leg modifications seem to only be of subordinate importance in grouping the species in natural units, but they must not be neglected either [Jeekel, 1963]. At least temporarily, such units seem best to be allotted the rank of informal species groups, i.e. without nomenclatural connotations.

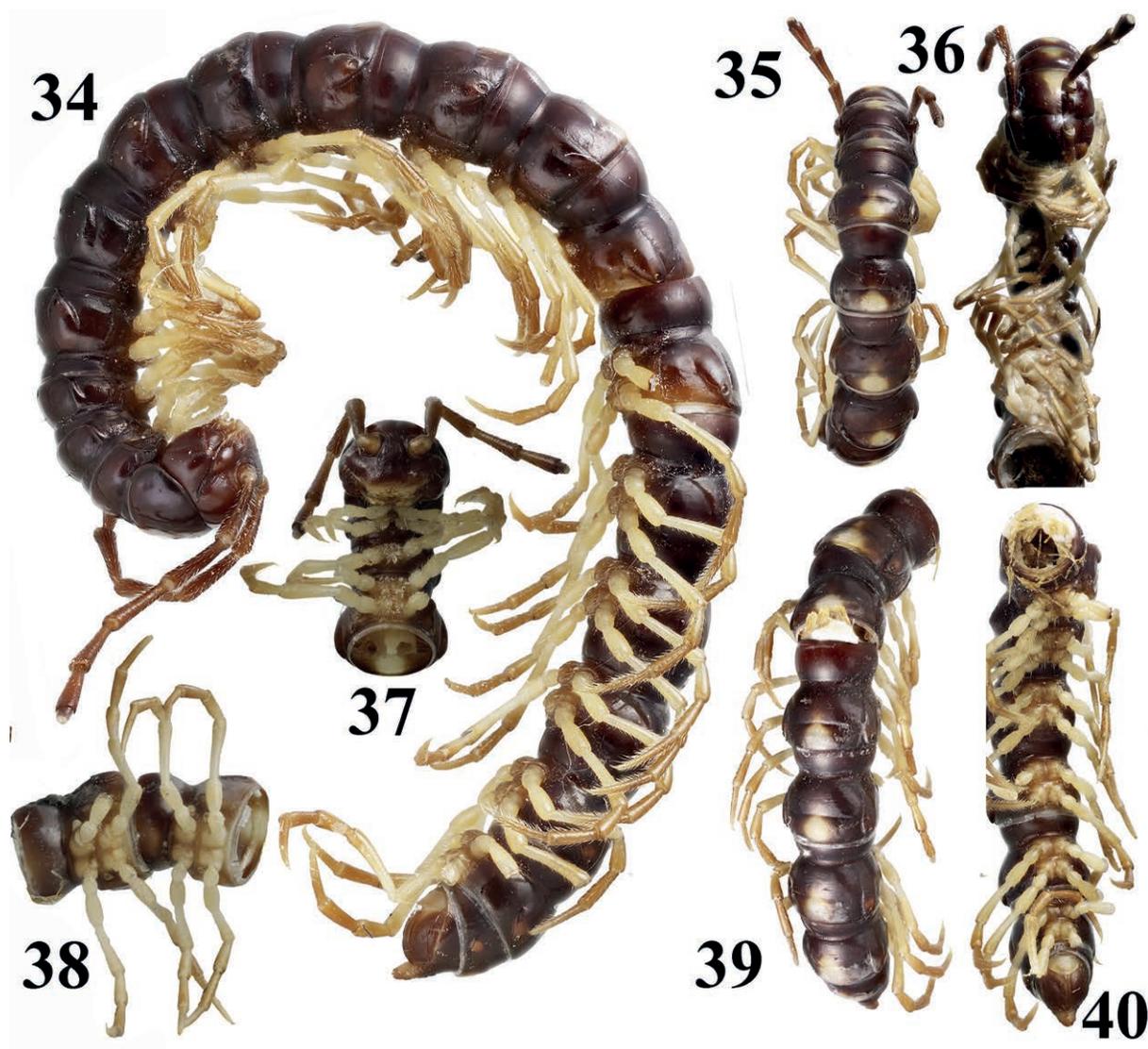
For the time being, however, we are simply bound to describe species of *Iulidesmus* in the traditional sense, also provisionally assigning them to newly circumscribed species groups.

Hoffman [1977] was the first to formalize a species group, the *salvadorii* group, and incorporated 11 species of *Iulidesmus* therein, based on gonopodal structure. Moreover, he also provided a tabular key to those species based on colouration. We shall follow that example and conclude the paper with brief accounts per recognized species (Suppl. Table), as well as diagnoses of and a key to such species groups and subgroups.

#### *Iulidesmus maculatus* sp.n.

Figs 34–50.

HOLOTYPE ♂ (ZMUM), Peru, Pasco Dept., Oxapampa Prov., ca 5 km W of Santa Rosa, 1550–1700 m a.s.l., 10°23'S, 75°27'36"W, subtropical rainforest, 22–29.XI.2016, I. Melnik leg.



Figs 34–40. *Iulidesmus maculatus* sp.n., ♂ paratype. 34 — habitus, lateral view; 35, 36 — anterior part of body, dorsal and ventral views, respectively; 37 — head and rings 1–5, ventral view; 38 — rings 10 and 11, ventral view; 39, 40 — posterior part of body, dorsal and ventral views, respectively. Photographs taken not to scale.

Рис. 34–40. *Iulidesmus maculatus* sp.n., паратип ♂. 34 — общий вид, сбоку; 35, 36 — передняя часть тела, соответственно сверху и снизу; 37 — голова и сегменты 1–5, снизу; 38 — сегменты 10 и 11, снизу; 39, 40 — задняя части тела, соответственно сверху и снизу. Фотографии сняты без масштаба.

PARATYPES: 4 ♂♂, 3 ♀♀ (one ♀ incomplete, lacking the posterior half of body) (ZMUM), same locality, together with holotype.

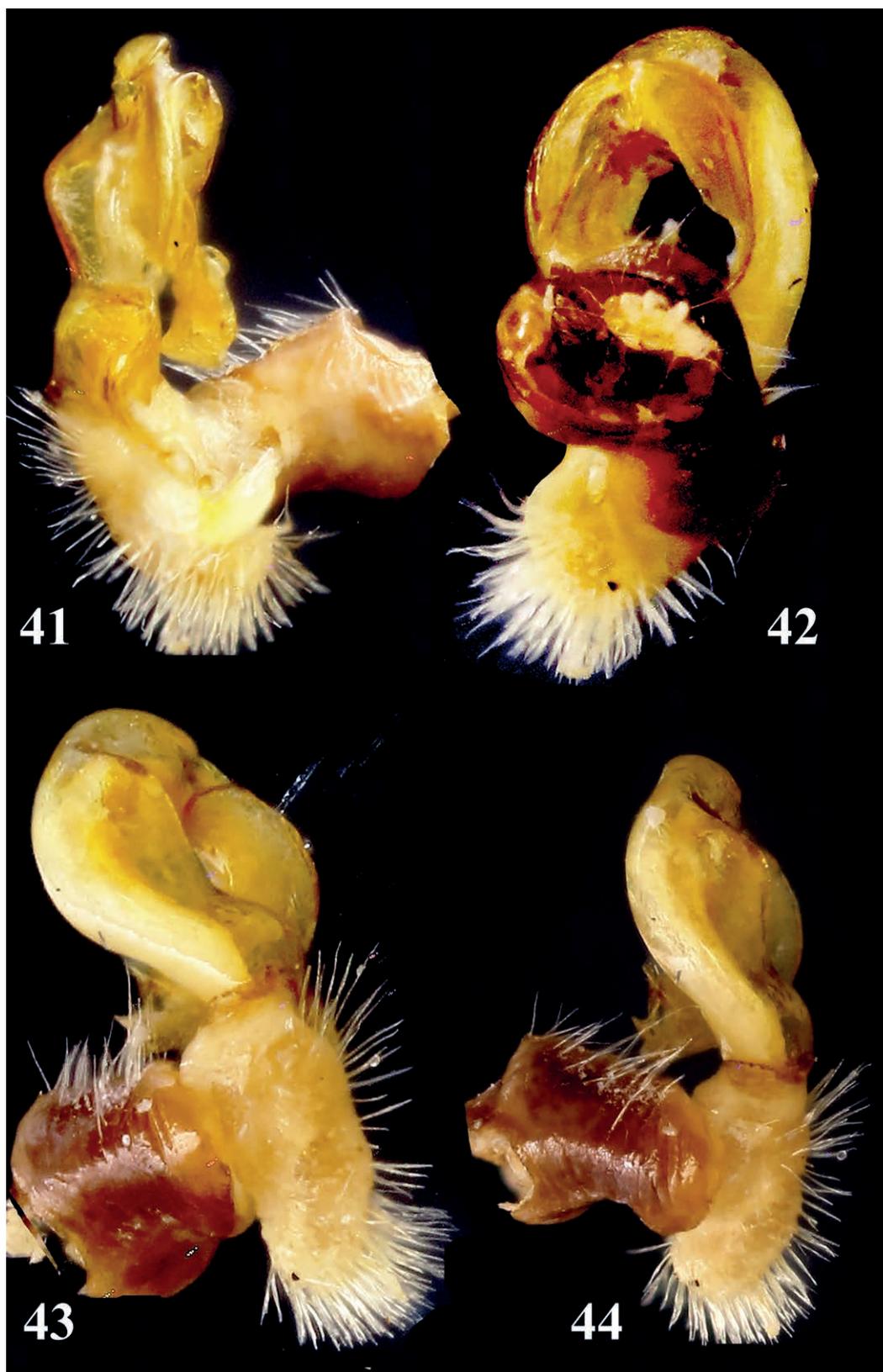
NAME. To emphasize the distinct axial spots/pattern on the dorsum.

DIAGNOSIS. A member of the *salvadorii* group (see below). Differs from congeners by the distinctive colour pattern, combined with the presence of several peculiar ♂ sternal modifications, the absence of adenostyles, and the shapes of the cannula and gonopodal telopodite (see Suppl. Table). The lamina medialis of the solenophore being larger than the lamina lateralis, not *vice versa*, is still another feature to distinguish this new species.

DESCRIPTION. Length of holotype ca 27 mm, width of its midbody pro- and metaterga 1.6 and 2.0 mm, respectively. ♂ paratypes 24–27 mm long, 1.5–1.6 and 1.9–2.0 mm wide on midbody pro- and metaterga, respectively. ♀ paratypes 32 or 36 mm long, 3.1–3.3 and 3.6–3.8 mm wide on midbody pro-

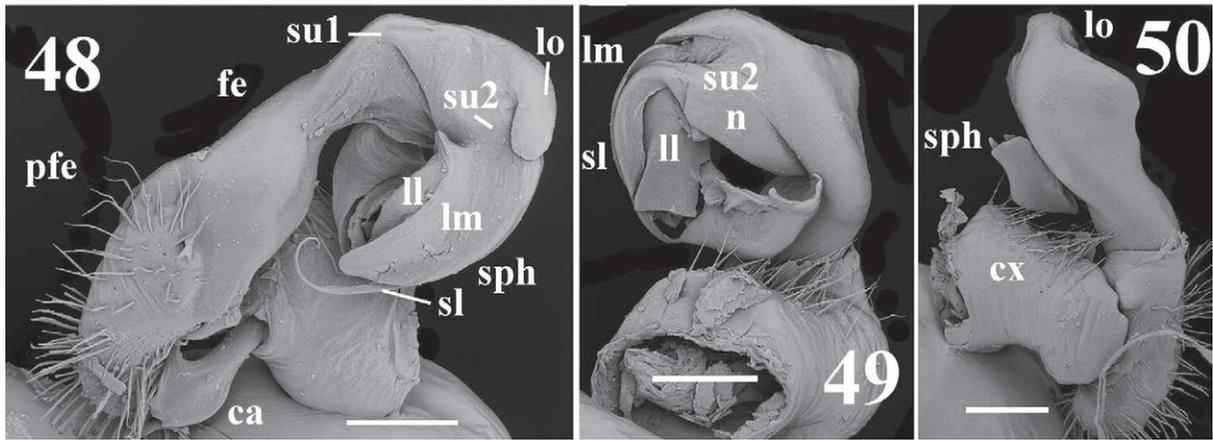
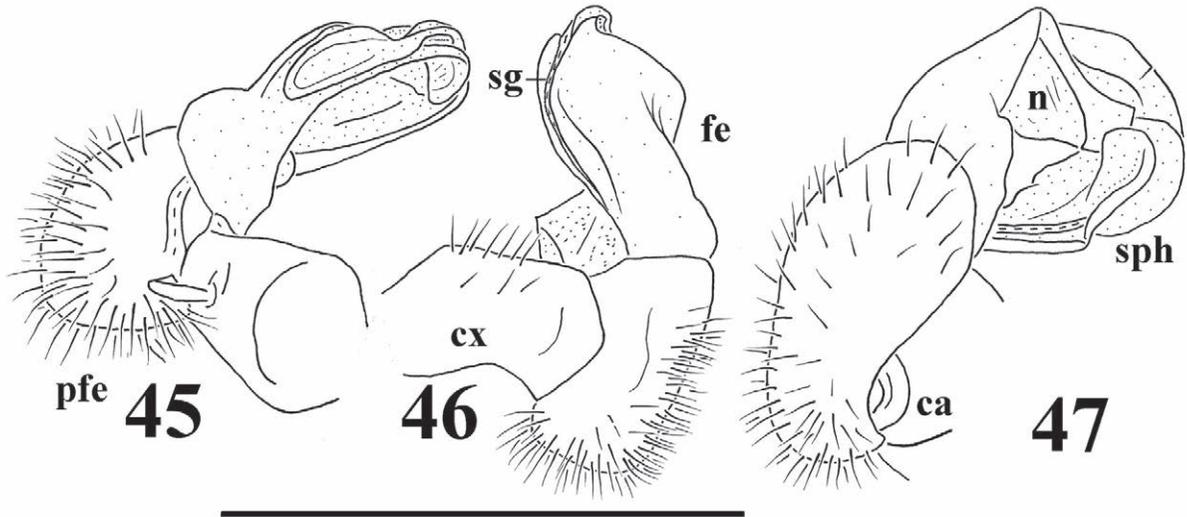
and metaterga, respectively. General colouration red-brown to brown, only antennomere 7 dark brown; legs contrasting light yellow brownish, increasingly infuscate distally. Starting with collum, a series/stripe of light yellow to pallid, axial, oblong spots covering most of collum and all following metaterga, including their posterior halves and sometimes extending onto anterior halves in front of transverse sulci (Figs 34–40); spiracles, distal half of epiproct and entire hypoproct also light.

Tegument generally smooth and shining, only surface below paraterga sometimes very faintly rugulose. Clypeolabral region densely setose, vertex bare, epicranial suture rather faint; isthmus between antennae about as broad as diameter of antennal sockets. Antennae long and slender, *in situ* almost reaching the end of ring 4 (♂) or 3 (♀) dorsally; in length, antennomeres  $2 > 3 = 5 > 6 > 1 = 7$ . Genae round in dorsal or ventral view. In width, ring 5 = 15 > head > collum > ring 2 > 3 = 4 (♂), starting with ring 16, trunk gradually tapering towards telson. Paraterga set



Figs 41–44. *Iulidesmus maculatus* sp.n., ♂ paratype, right gonopod, mesal, dorsal, ventral and lateral views, respectively. Photographs taken not to scale.

Рис. 41–44. *Iulidesmus maculatus* sp.n., паратип ♂, правый гонопод, соответственно изнутри, сверху, снизу и сбоку. Фотографии сняты без масштаба.



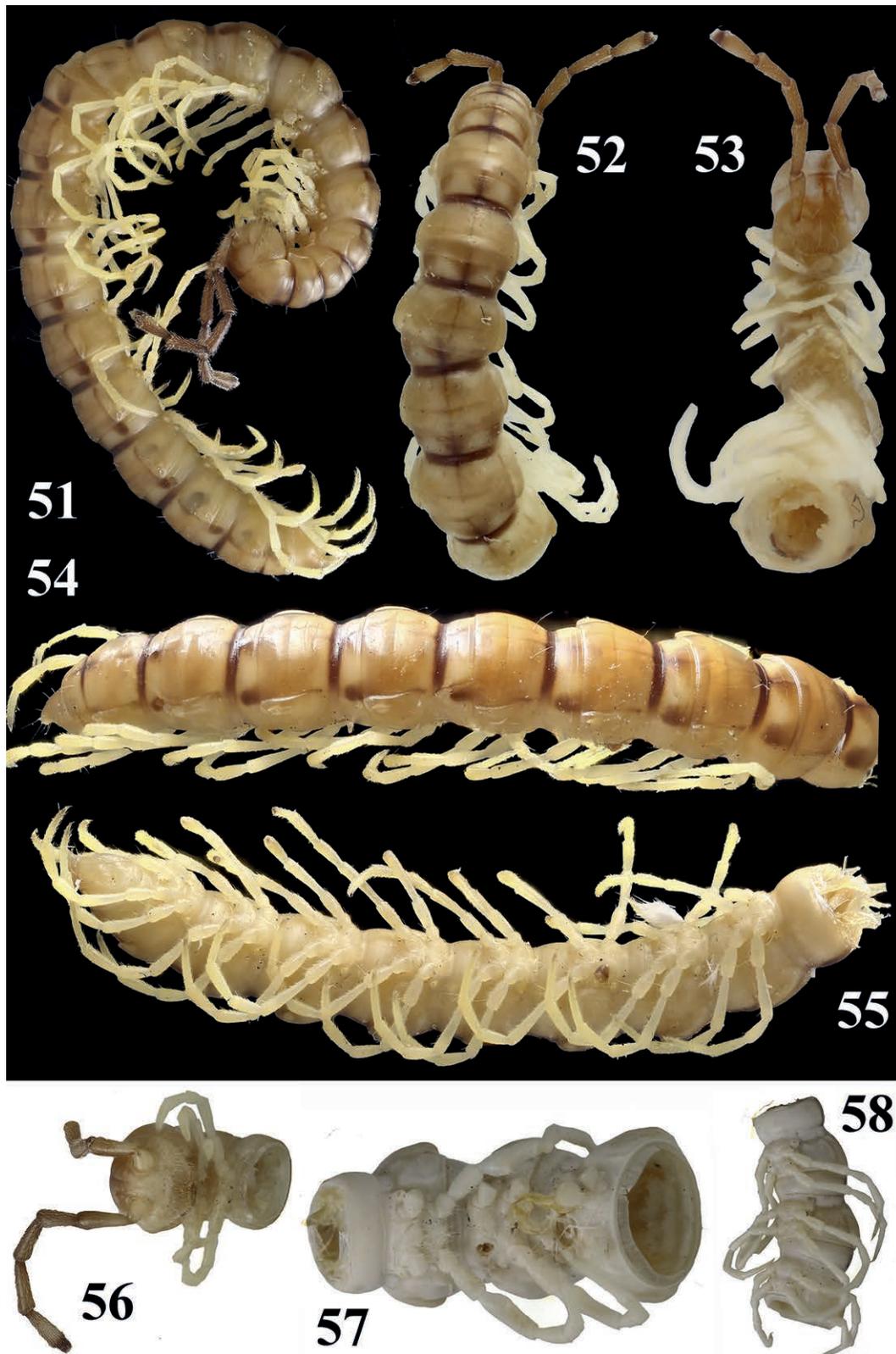
Figs 45–50. *Iulidesmus maculatus* sp.n., ♂ paratype, right gonopod, mesal, lateral, ventral, mesal, dorsocaudal and lateral views, respectively. Scale bars: 1.0 mm (45–47), 0.2 mm (48–50, SEM).

Рис. 45–50. *Iulidesmus maculatus* sp.n., паратип ♂, правый гонопод, соответственно изнутри, сбоку, снизу, изнутри, одновременно сверху и сзади, а также сбоку. Масштаб: 1,0 мм (45–47), 0,2 мм (48–50, SEM).

low (at about half midbody height), faint, a little flatter in ♀ compared to ♂, traceable as small, regularly and broadly rounded flaps on collum or as flat roundish bars thereafter, these being a little thicker/higher on pore-bearing rings than on poreless ones, delimited by distinct sulci both dorsally and ventrally, both incomplete and missing only in anterior 1/3 metaterga (Fig. 34); caudal corners of paraterga rounded (♂), lying within rear tergal margin. Transverse mid-dorsal sulci present on rings 5–18, thin lines not reaching the bases of paraterga; ozopores lateral, invisible from above, lying close to caudal ends of poriferous paraterga inside oval to increasingly ovoid grooves. Pleurosternal carinae mostly evident, granulate, arcuated to straight ridges increasingly obliterated towards telson, with small caudal teeth traceable until ring 13, these teeth extending past base of an unusually long, but simple limbus (Figs 34–40). Tergal setae almost fully abraded, a single seta retained on collum and ring 5, longer (ca 1/4 as long as collum) or shorter; setation pattern poorly traceable, perhaps 2+2 in anterior halves of metaterga. Axial line missing. Stricture between pro- and metazona deep, thin and striolate longitudinally. Epiproct long, flattened dorsoventrally, rounded at tip, subapical lateral papillae small, but evident. Hypoproct semi-circular, paramedian setigerous papillae very small and well removed from caudal margin.

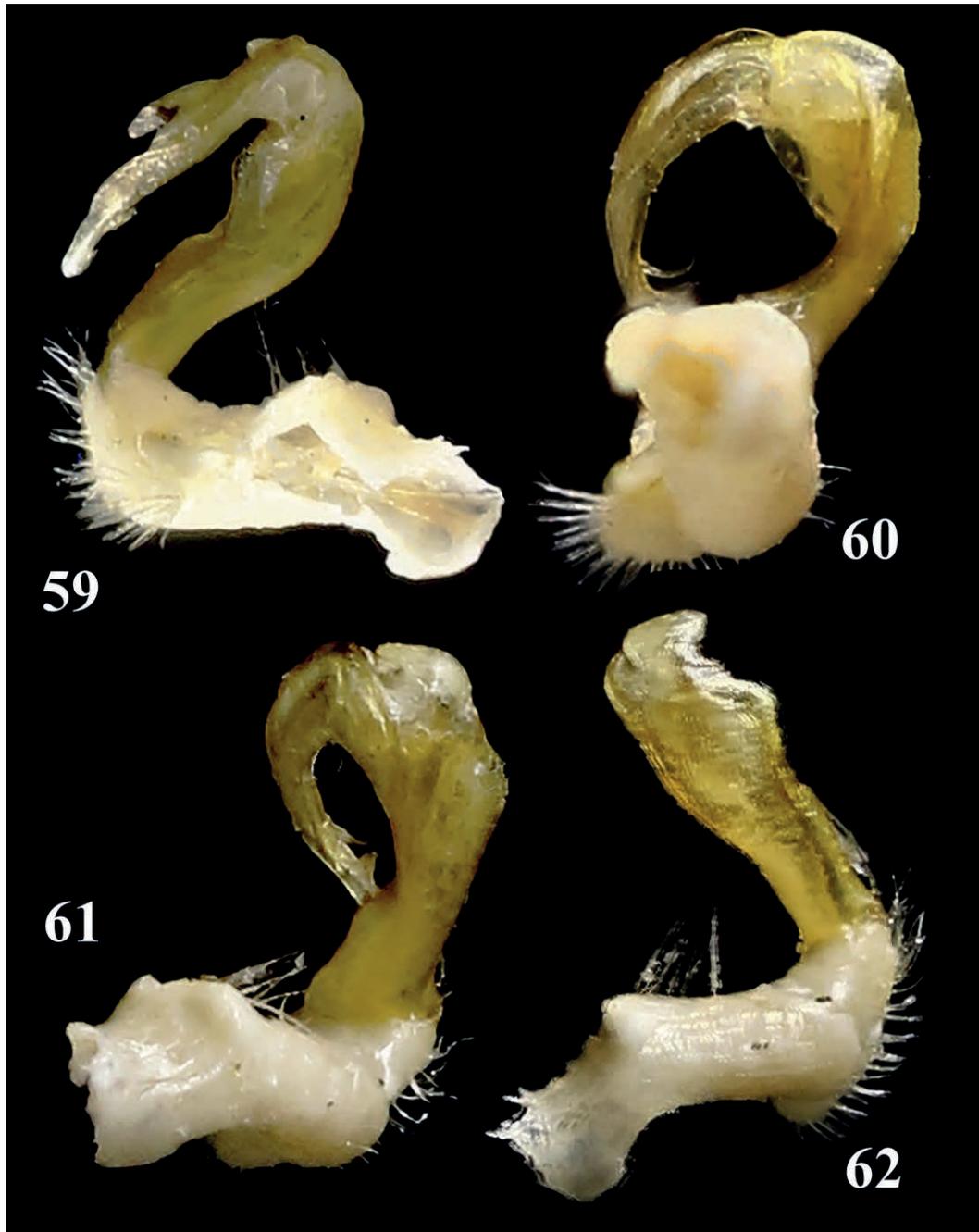
Sterna moderately setose, cross-impressions largely evident, transverse ones usually being more distinct than axial ones; sternal cones traceable until ring 18, each posterior pair of cones a little larger than each anterior pair, more evident in ♂ than in ♀. Sternum between ♂ coxae 3 a flattened platform with a central bunch of setae and rather numerous similar peripheral setae directed outwards. Sternum between ♂ coxae 4 similar, but slightly divided axially and with two small tubercles directed caudally. Sternum between ♂ coxae 5 a slightly divided platform, densely setose, each half with a distinct rounded process directed both forward and caudally (Fig. 37). Sternum between ♂ coxae 6 a similar platform, but anterior tubercles higher, while posterior tubercles smaller and directed caudally. Sternum between ♂ coxae 7 broader, flattened, slightly concave, bare and with a small tubercle anteriorly near each coxa. Midbody legs slender, clearly thicker and much longer in ♂ than in ♀, 2.0–2.1 (♂) or 1.2–1.3 (♀) times as long as body height, devoid of adenostyles; ♂ tarsal brushes present only on a few anterior legs, gradually thinning out thereafter. In length, femur = tarsus > prefemur = postfemur = tibia > coxa. ♂ prefemora slender, not bulged laterad.

Gonopods (Figs 41–50) complex, typical of *Iulidesmus*. Coxite (cx) subcylindrical, rather densely setose ventrally, subequal in length to prefemorite (pfe); cannula (ca) special in



Figs 51–58. *Iulidesmus cingulatus* sp.n., ♂ paratype. 51 — habitus, lateral view; 52, 53 — anterior part of body, dorsal and ventral views, respectively; 54, 55 — posterior half of body, dorsolateral and ventrolateral views, respectively; 56 — head and rings 1–4, ventral view; 57 — rings 5–7, ventral view; 58 — rings 8–10, subventral view. Photographs taken not to scale.

Рис. 51–58. *Iulidesmus cingulatus* sp.n., паратип ♂. 51 — общий вид, сбоку; 52, 53 — передняя часть тела, соответственно сверху и снизу; 54, 55 — задняя половина тела, одновременно сверху и сбоку и одновременно снизу и сбоку; 56 — голова и сегменты 1–4, снизу; 57 — сегменты 5–7, снизу; 58 — сегменты 8–10, почти снизу. Фотографии сняты без масштаба.



Figs 59–62. *Iulidesmus cingulatus* sp.n., ♂ paratype, right gonopod, mesal, dorsocaudal, sublateral and lateral views, respectively. Photographs taken not to scale.

Рис. 59–62. *Iulidesmus cingulatus* sp.n., паратип ♂, правый гонопод, соответственно изнутри, одновременно сверху и снизу, почти сбоку и сбоку. Фотографии сняты без масштаба.

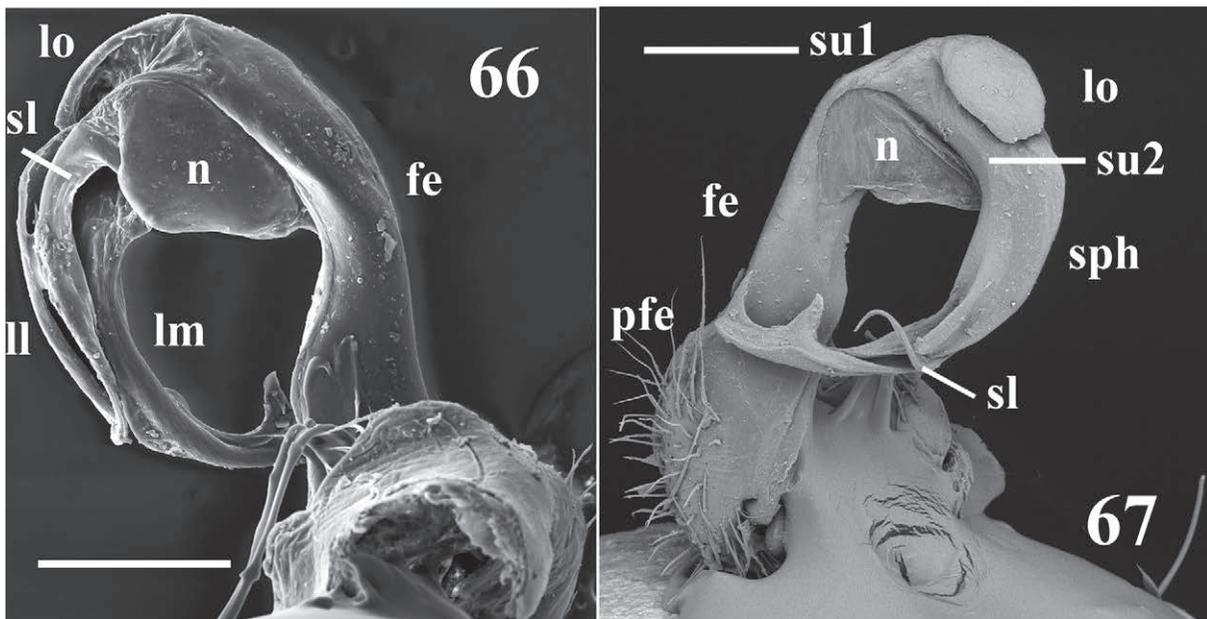
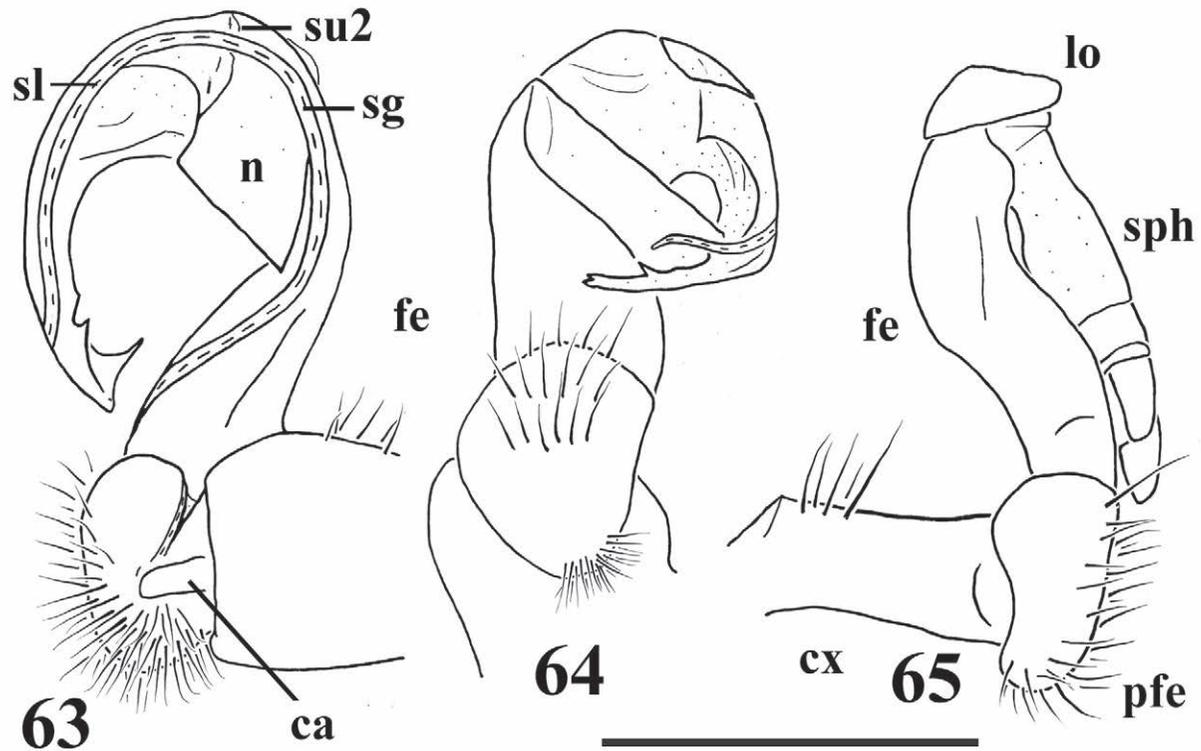
being strongly flattened in distal half, strongly curved as usual. Prefemurite (**pfe**) subequal in length to femurite (**fe**), densely setose as usual. Femurite (**fe**) clearly constricted in distal  $\frac{2}{3}$ , set off from acropodite by a distinct, mesal, ellipsoid lobe in about basal  $\frac{1}{3}$ ; solenophore (**sph**) consisting of an unusually much larger lamina medialis (**lm**) and a smaller lamina lateralis (**ll**), both subequal in length; distofemoral sulcus (**su1**) distinct, marking the beginning of a thin, long, flagelliform solenomere (**sl**), the latter considerably, but far from fully sheathed by both laminae and leaving the tip strongly exposed. Postfemurite proper set off from acropodite/solenophore (**sph**) by a rather

indistinct postfemoral sulcus (**su2**) with a rather large, elongate and subtriangular dilatation/lobe (**n**) mesally at base and a rounded, cap-shaped apical lobe (**lo**), tip of **sph** with a few small prongs.

*Iulidesmus cingulatus* sp.n.

Figs 51–67.

HOLOTYPE ♂ (ZMUM), Peru, Junin Region, Pichiquia (Fig. 147), S 11°23'07", 74°36'05", 500 m a.s.l., secondary forest in valley, under bark, 26.IX.2017, K. Eskov leg.



Figs 63–67. *Iulidesmus cingulatus* sp.n., ♂ paratype, right gonopod, mesal, ventral, lateral, dorsocaudal and subventral views, respectively. Scale bars: 1.0 mm (64–65), 0.2 mm (66, 67, SEM).

Рис. 63–67. *Iulidesmus cingulatus* sp.n., паратип ♂, правый гонопод, соответственно изнутри, снизу, сбоку, одновременно сверху и сзади, а также почти снизу. Масштаб: 1,0 мм (64–65), 0,2 мм (66, 67, SEM).

PARATYPES: 1 ♂, 5 ♀♀ (ZMUM), same place, together with holotype.

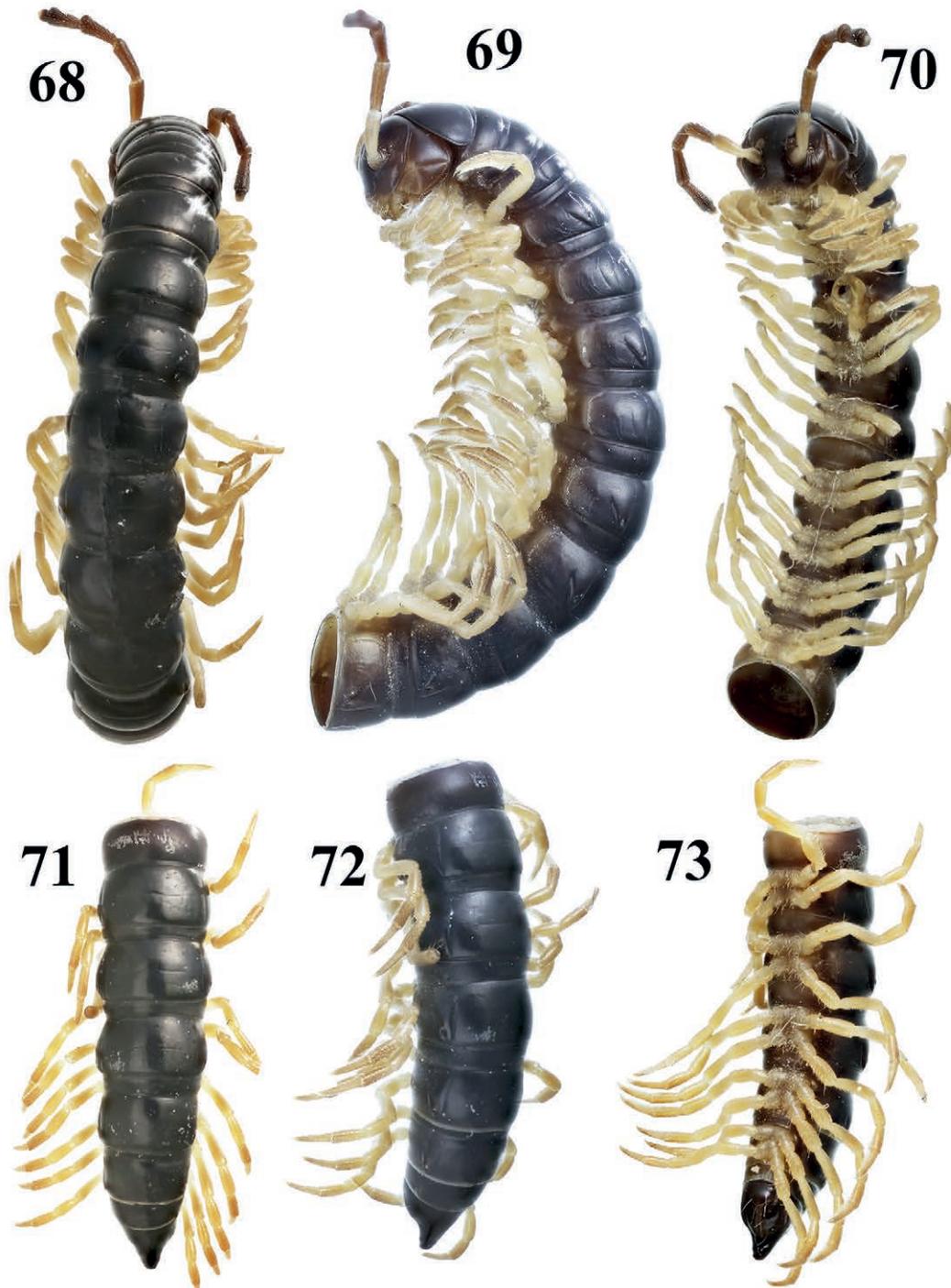
NAME. To emphasize the clearly cingulated pattern.

DIAGNOSIS. A member of the *salvadorii* group (see below). Differs from congeners by the complete cingulate colour pattern, coupled with several details of ♂ sternal, leg and gonopodal structure (see Suppl. Table).

DESCRIPTION. Holotype 24 mm long, 1.7 and 2.0 mm wide on midbody pro- and metazona, respectively. Length of ♂

paratype 21 mm, width on midbody pro- and metazona 1.4 and 1.7 mm, respectively. ♀ paratypes 22–27 mm long, 1.7–1.8 and 2.1–2.5 mm wide on midbody pro- and metazona, respectively.

General colouration light beige, dorsum beige, venter and sides with paraterga almost white, legs almost white, but tarsi faintly infuscate, light brown only apically. Antennae light yellow-brown, antennomere 7 brown, tip pallid. Pattern as infuscate, brown strictures gradually growing lighter down to paraterga. Prozona 5–18 each with an ellipsoid, light brown, lateral spot



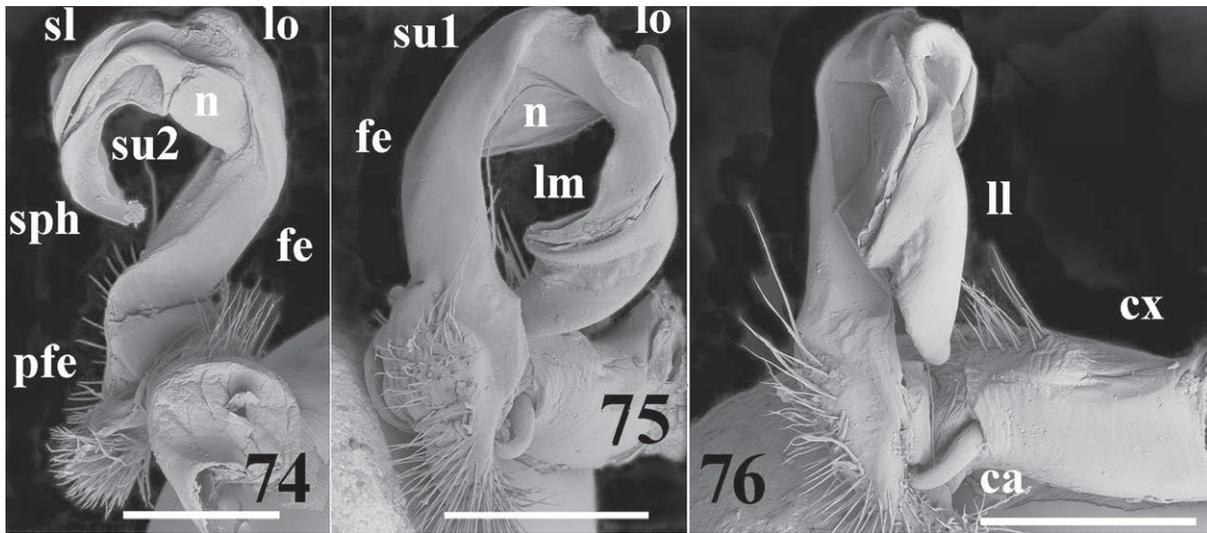
Figs 68–73. *Iulidesmus satipo* sp.n., ♂ holotype. 68–70 — anterior and middle parts of body, dorsal, lateral and ventral views, respectively; 71–73 — posterior third of body, dorsal, lateral and ventral views, respectively. Photographs taken not to scale.

Рис. 68–73. *Iulidesmus satipo* sp.n., голотип ♂. 68–70 — передняя и средняя части тела, соответственно сверху, сбоку и снизу. Фотографии сняты без масштаба.

about level to paraterga; a small, vague, triangular, axial, light brown spot in caudal third of collum and oblong on prozona 2–18; a thin, dark, axial line present on metaterga 2–19 (Figs 51–58).

Tegument smooth and shining; collum broadly and regularly rounded laterally. Paraterga 2 the lowest, small, but evident and narrow bars drawn anteriorly beneath collum, but not drawn caudally. Paraterga 3 a weak and arcuate ridge located at about ring midheight. Following paraterga faint, rounded and flattened

bars, mostly set at about upper 1/3 midbody height, thicker on pore-bearing rings than on poreless ones, completely delimited dorsally by an evident and arcuate sulcus and ventrally by an incomplete and weaker sulcus evident only in caudal third, none drawn past rear tergal margin (Figs 51, 54). Clypeolabral region densely setose, vertex bare, epicranial suture clear; interantennal isthmus 1.2 times as broad as diameter of antennal socket (Fig. 56). Antennae long and slender, *in situ* extending past ring 3 (♂)



Figs 74–76. *Iulidesmus satipo* sp.n., ♂ holotype, right gonopod, dorsal, subventral and mesal views, respectively. Scale bars: 0.5 mm (SEM).  
Рис. 74–76. *Iulidesmus satipo* sp.n., голотип ♂, правый гонопод, соответственно сверху, почти снизу и изнутри. Масштаб: 0,5 мм (SEM).

or 2 (♀) dorsally; in length, antennomeres 4=5>2>6>1=7 (Fig. 56). Genae round in dorsal or ventral view.

In width, rings 5=16 > head > collum > 2 > 3=4; starting with ring 17, trunk gradually tapering towards telson. Transverse metatergal sulcus thin, line-shaped, slightly sinuous medially, far from reaching the bases of paraterga, present in rings 5–18. Stricture thin, deep and nearly smooth, often very faintly striolate. Limbus thin, simple, long and entire (Fig. 58). Pleurosternal carinae arcuate, small, but evident ridges, on rings 2–4 each with a minute, caudal, rounded lobule, thereafter faint arcuate ridges traceable until ring 18 (♂) or 14 (♀).

Epiroct subtruncate, with a pair of small subapical incisions/papillae laterally. Hypoproct roundly subtriangular, 1+1 small setigerous tubercles near caudal margin (Fig. 55).

Legs long and slender (Figs 51, 55), 1.8–1.9 (♂) or 1.1–1.2 times (♀) as long as midbody height; tarsal brushes present only on ♂ legs 1–5, thereafter gradually thinning out; ♂ femora 4–7 each incrassate and with a swollen, parabasol, ventral, granular adenostyle (Fig. 57). In length, femur > tarsus > tibia > postfemur > coxa. Sternal cones absent, cross-impressions weak, both similarly deep, densely setose (Fig. 58).

Gonopods (Figs 59–67) complex. Coxite (cx) slender and long, about as long as femorite (fe) and either ca 2/3 as long as prefemorite (pfe), with several setae ventrally on a small, low, but evident bulge; cannula (ca) as usual, unci- and tubiform. Telopodite circular, Pfe as usual, densely setose. Femorite (fe) slender, slightly curved mesad, clearly constricted in distal 2/3, set off from acropodite by a fine distofemoral sulcus (su1). Postfemoral part with a large, roundly subquadrate, lobe-shaped dilatation (n) mesally at base and with a distinct, ovoid, flat, apical lobe (lo) set off from acropodite by an indistinct postfemoral sulcus (su2), consisting of a long, flagelliform solenomere (sl) exposed over most of its extent and largely attached on mesal side to a long, curved, subacuminate and attenuated lamina lateralis (ll), the latter ending in two strong teeth. Seminal groove (sg) running entirely on mesal side of fe before moving onto a nearly straight, short and non-sigmoid base of sl.

*Iulidesmus satipo* sp.n.  
Figs 68–76.

HOLOTYPE ♂ (ZMUM), Peru, Junin Region, Satipo, fruit orchard, under wooden planks and stones, 21.09.2017, K. Eskov leg.

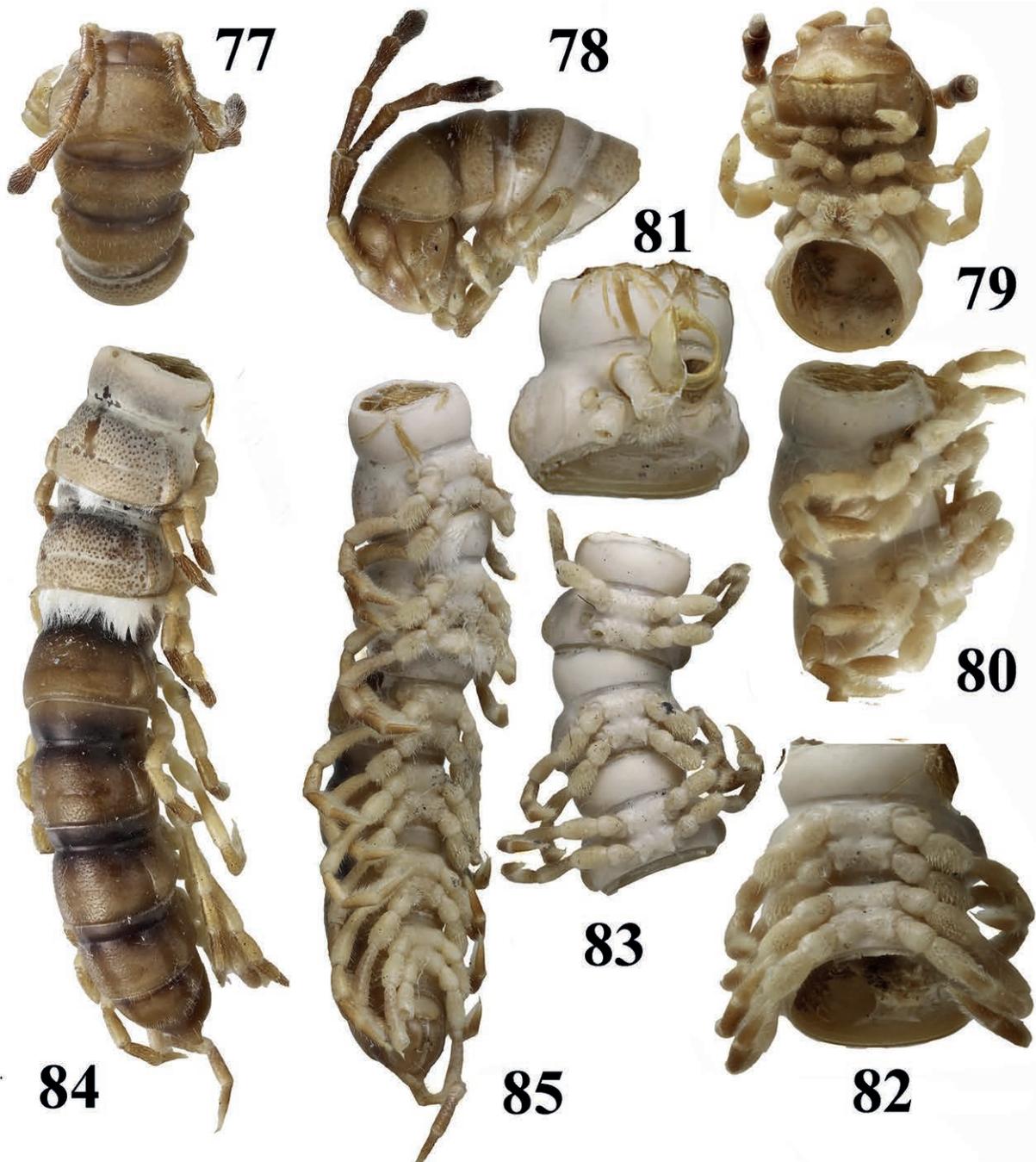
PARATYPES: 3 ♀♀ (ZMUM), same place, together with holotype. NAME. To emphasize the type locality; a noun in apposition.

DIAGNOSIS. A member of the *salvadorii* group (see below). Differs from congeners by the dark, black to dark brown general colouration with contrasting light, yellow-brown venter and legs, coupled with a low transverse ridge between ♂ coxae 6 being the only meaningful sternal modification, the absence of adenostyles (except for the usual gonapophyses) and the peculiar shape of the solenomere (see Suppl. Table).

DESCRIPTION. Length of holotype 25 mm, width of midbody rings 2.0 and 2.4 mm, respectively. ♀ paratypes 18–20 mm long, 3.4–3.5 and 3.8–4.0 mm wide on midbody rings, respectively. General colouration black (♂, ♀) to dark brown (♀), venter and legs mostly contrasting yellow-brown, tibiae and tarsi brown, head and antennae dark brown, but antennomeres 1 and 2 yellow-brown (Figs 68–72).

Tegument smooth and shining. Collum broadly and regularly rounded laterally. Clypeolabral region sparsely setose, vertex bare; epicranial suture faint; interantennal isthmus 1.8 times as broad as diameter of antennal socket. Antennae long and slender, *in situ* extending past ring 3 (♂) or 2 (♀) dorsally; in length, antennomeres 2=5>6>1=7. Genae round in dorsal or ventral view.

In width, head < collum < 2 < ring 3=4 < 5=14; starting with ring 15, trunk gradually tapering towards telson. Paraterga set low (at about half midbody height), faint, slightly better developed in ♂ than in ♀. Paraterga 2 small, but evident, bar-shaped. Paraterga 3 and 4 weakly arcuate. Following paraterga faint, rounded, flat; set a little higher on pore-bearing rings than on poreless ones; completely delimited by almost straight sulci dorsally and by incomplete sulci in caudal half ventrally; none drawn past rear tergal margin (Figs 69, 72). Transverse mid-dorsal sulci very faint, traceable on rings 6–18, far from reaching the bases of paraterga. Ozopores as usual, located inside ovoid grooves near caudal end of poriferous paraterga. Pleurosternal carinae small, but evident, slightly better developed in ♂ than in ♀, rounded, arcuate, smooth ridges present on rings 2–18, with small, rounded, caudal lappets on rings 2–7, gradually decreasing in size towards telson (Figs 69, 71). Tergal setae fully abraded, setation pattern as usual, 2+2 in anterior row, traceable through insertion points. Axial line missing. Stricture between pro- and metazona deep, narrow and usually only very



Figs 77–85. *Iulidesmus pubescens* sp.n., ♂ holotype. 77–79 — head and rings 1–4, dorsal, lateral and ventral views, respectively; 80 — rings 5 and 6, subventral view; 81 — ring 7, ventral view; 82 — rings 8 and 9, ventral view; 83 — rings 10–12, ventral view; 84, 85 — rings 13–20, dorsal and ventral views, respectively. Photographs taken not to scale.

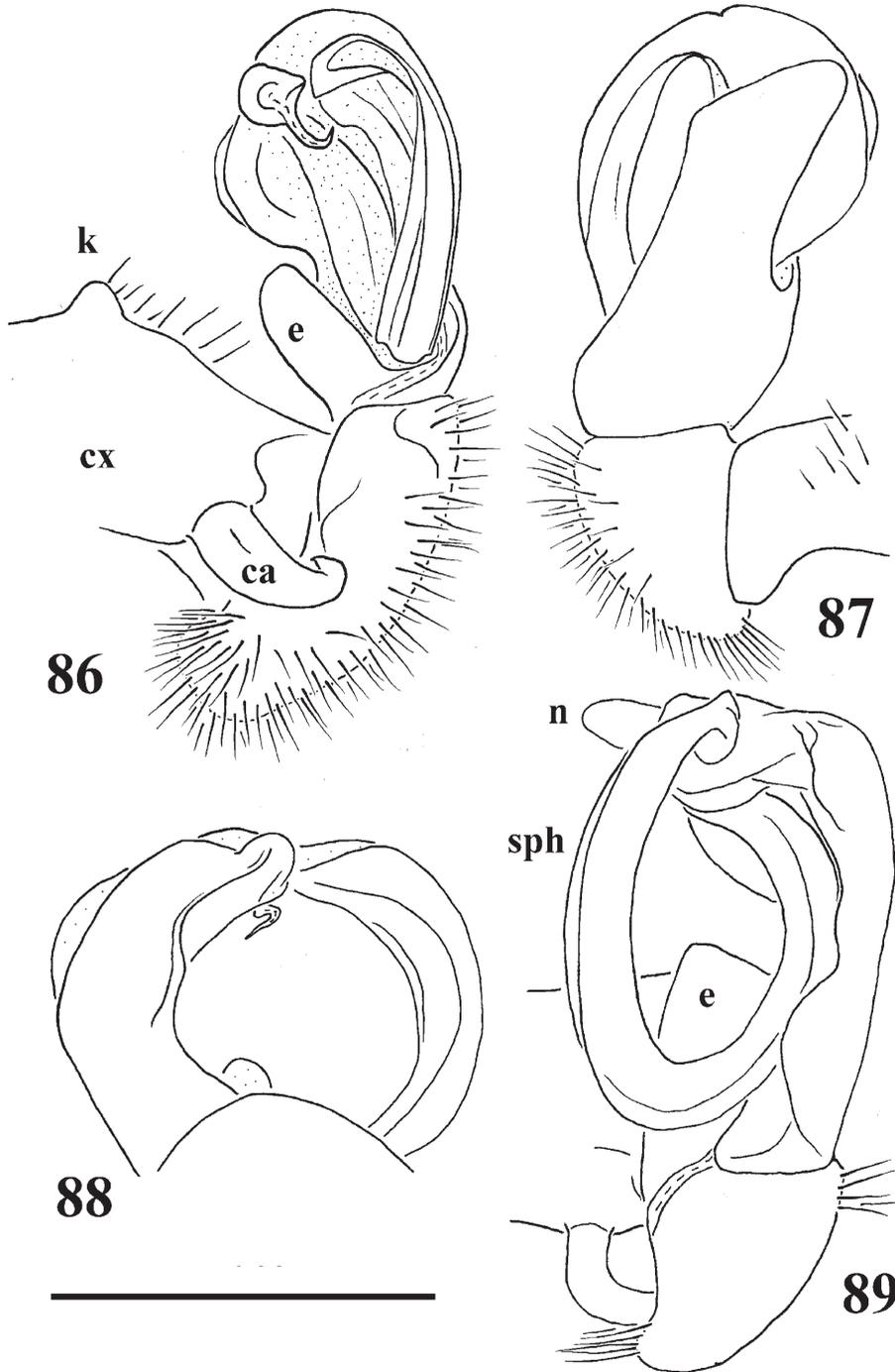
Рис. 77–85. *Iulidesmus pubescens* sp.n., голотип ♂. 77–79 — голова и сегменты 1–4, соответственно сверху, сбоку и снизу; 80 — сегменты 5 и 6, почти снизу; 81 — сегмент 7, снизу; 82 — сегменты 8 и 9, снизу; 83 — сегменты 10–12, снизу; 84, 85 — сегменты 13–20, соответственно сверху и снизу. Фотографии сняты без масштаба.

faintly striolate. Limbus as usual, thin and entire (Figs 69, 70). Epiproct as usual, narrow and flattened dorsoventrally, roundly subtruncate, lateral subapical papillae faint (Figs 71–73). Hypoproct subtriangular, tip rounded, 1+1 setigerous papillae small, located near caudal margin.

Sternal cones missing (Fig 70, 73). Sterna between ♂ legs 1–7 densely setose, excavate, only between coxae 6 with a subquadrate, very low, setose, transverse ridge. Legs slender

and long, 1.7–1.8 (♂) or 1.1–1.2 times (♀) as long as midbody height, densely setose; adenostyles missing except for a short round tubercle with gonopore on each ♂ coxa 2. Tarsal and tibial brushes present on all ♂ legs except for two last pairs (Figs 69, 70, 73).

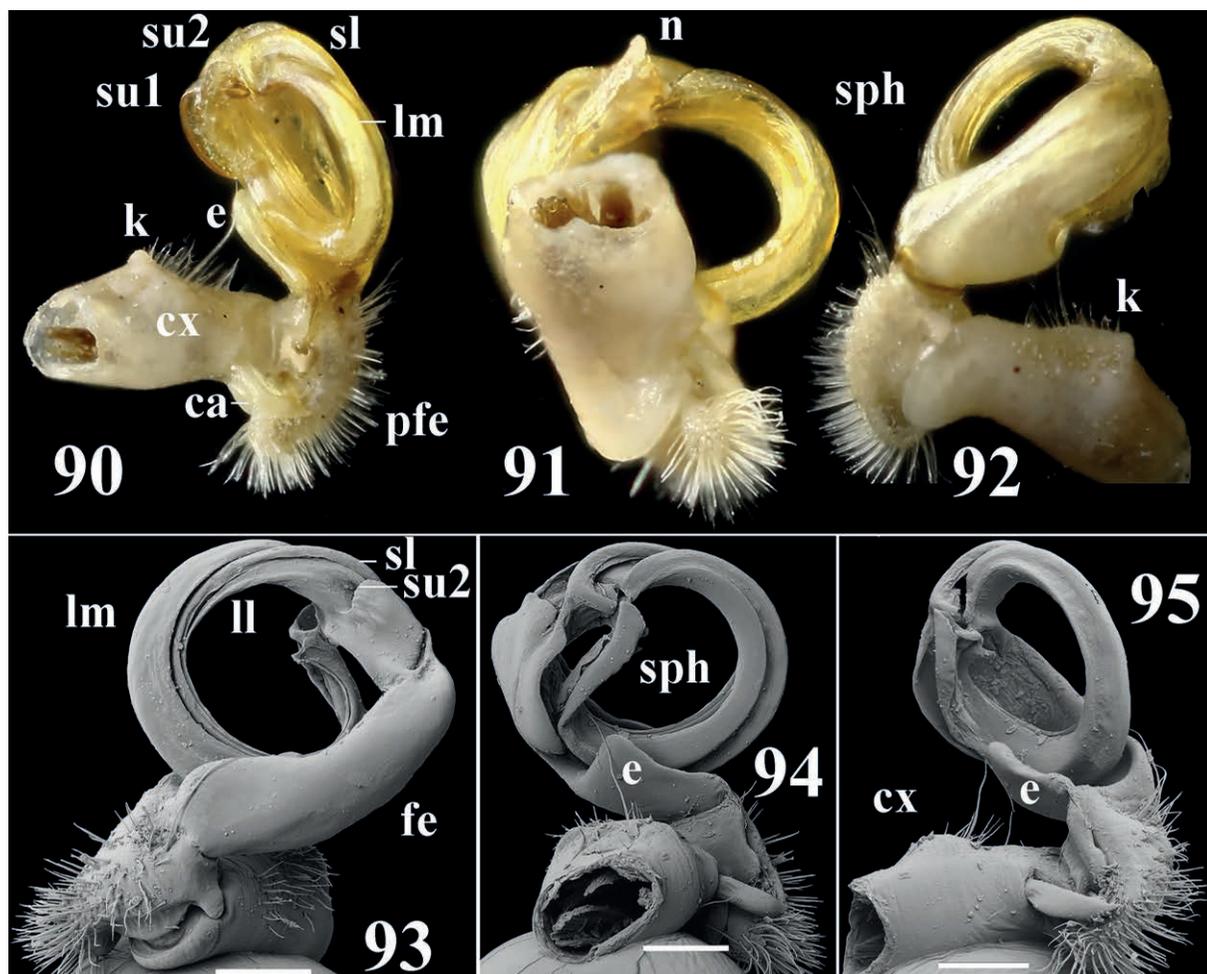
Gonopods (Figs 74–76) complex. Coxite (cx) subcylindrical, about as long as either prefemorite (pfe) or femorite (fe), with a rather small field of dense setae distoventrally; canulla



Figs 86–89. Left gonopod of *Iulidesmus pubescens* sp.n., ♂ holotype, mesal, lateral, dorsal and ventral views, respectively. Scale bar: 0.5 mm.  
 Рис. 86–89. Левый гонопод *Iulidesmus pubescens* sp.n., голотип ♂, соответственно изнутри, сбоку, сверху и снизу. Масштаб: 0,5 мм.

(**ca**) as usual, tubiform. Telopodite as usual, circular, strongly curved mesad. Prefemorite (**pfe**) as usual, densely setose, not hypertrophied. Femorite (**fe**) long and slender, only slightly curved mesad, hollow on mesal face, devoid of a midway constriction, distofemoral sulcus (**su1**) delimiting a distinct, large, squarish, medial lobe (**n**) at base of postfemoral part, the latter with a characteristic, roundish, apical lobe (**lo**) and a fine

postfemoral sulcus (**su2**) at base of a usual, basally only slightly curved, long, flagelliform solenomere (**sl**). Both lamina medialis (**lm**) and lamina lateralis (**ll**) of solenophore (**sph**) strongly developed, **ll** regularly rounded apically and considerably longer than **lm**, both clearly curved mesad and sheathing entire distal half of **sl**. Seminal groove running mesally along **fe** to move onto **sl** at end of lobe **n**.



Figs 90–95. Left gonopod of *Iulidesmus pubescens* sp.n., ♂ holotype, mesal, subdorsal, lateral, subventral, dorsal and mesal views, respectively. Scale bars: taken not to scale (90–92), 0.2 mm (93–95, SEM).

Рис. 90–95. Левый гонопод *Iulidesmus pubescens* sp.n., голотип ♂, соответственно изнутри, почти сверху, сбоку, почти снизу, сверху и изнутри. Масштаб: снято без масштаба (90–92), 0,2 мм (93–95, SEM).

*Iulidesmus pubescens* sp.n.  
Figs 77–95.

HOLOTYPE ♂ (ZMUM), Peru, Junin Region, Calabaza, 2200 m a.s.l., S 11°30'38", W 74°49'15", cloud forest (Fig. 148), 16–20.09.2017, K. Eskov leg.

NAME. To emphasize the densely pubescent collum and following metaterga.

DIAGNOSIS. A member of the *salvadorii* group (see below). Differs readily from congeners by the collum and following metaterga being very densely and irregularly pubescent, the pubescence being very short and light, coupled with the gonopodal telopodite being unusually long and slender, distally attached to a clearly excavate femorite (see Suppl. Table).

DESCRIPTION. Length 24 mm, width of midbody pro- and metazona 1.6 and 2.0 mm, respectively.

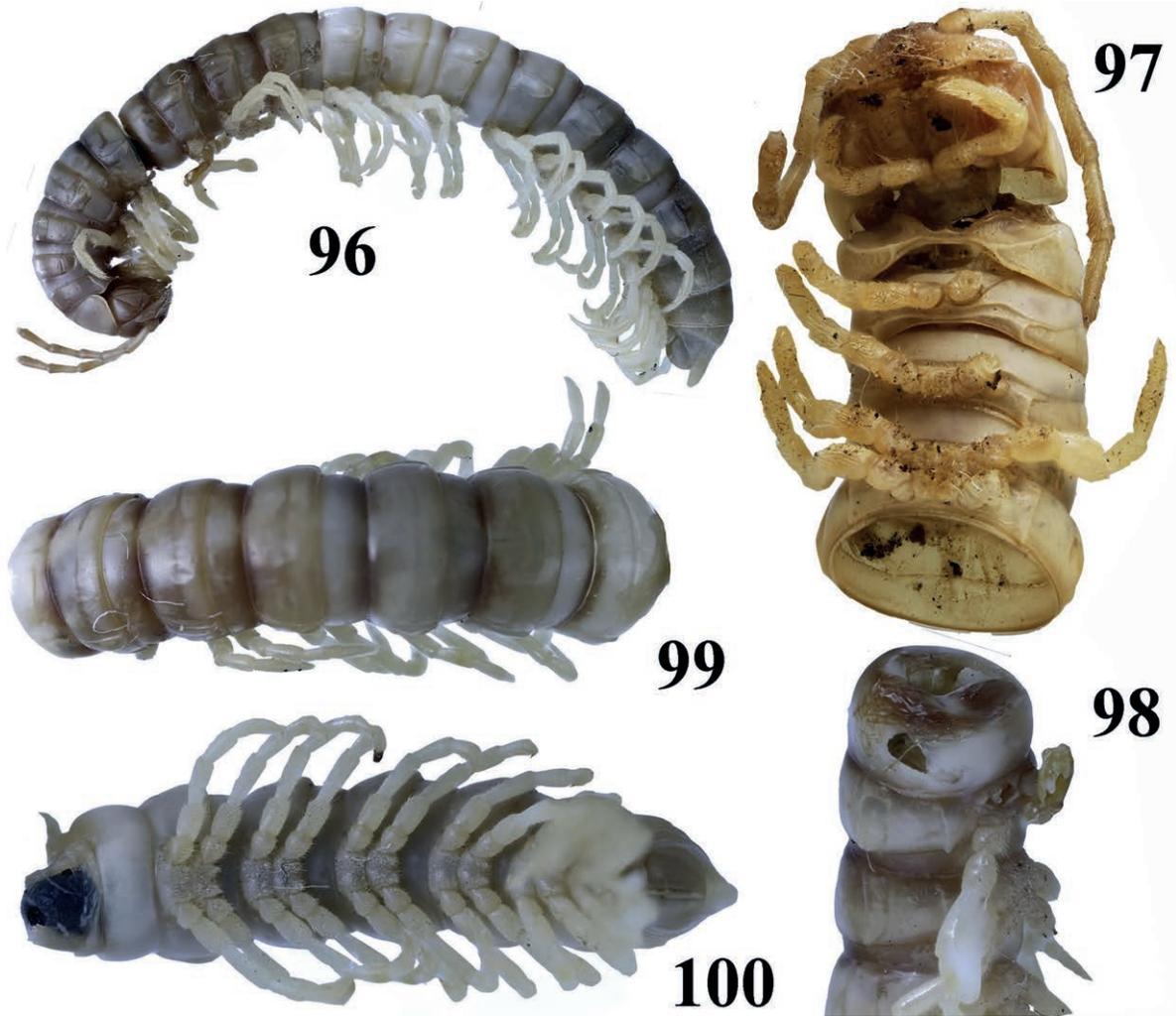
General colouration light yellow-brown with a pattern of light brown rings covering strictures and immediately adjacent parts of pro- and metazona. Legs yellow-brown, but tibiae and tarsi light brown. Antennae light brown (Figs 77–85).

Tegument poorly shining, smooth even below paraterga; metaterga very densely and irregularly pubescent, pubescence being very short and light (Figs 77, 78, 84). Clypeolabral region densely setose, vertex sparsely setose; epicranial suture

clear. Interantennal isthmus 1.2 times as broad as diameter of antennal socket. Antennae relatively short, extending past ring 2 dorsally (♂). In length, antennomeres 3=5>2>6>1=7 (Fig. 78). Genae rounded.

In width, head < ring 3=4 < collum < ring 2=4 < 5–14; starting with ring 15, trunk gradually tapering towards telson (♂). Paraterga set low (at about upper 1/3 midbody height), relatively strongly developed. Paraterga 2 clearly drawn anteriorly beneath collum (Fig. 78). Paraterga 3–19 regularly and broadly rounded, delimited by a complete sulcus dorsally and an incomplete sulcus ventrally in caudal 3/4; transverse sulci on metaterga 4–18 almost reaching the bases of paraterga (Fig. 84). Ozopores as usual, lying inside ovoid grooves in front of caudal corner of poriferous paraterga. Pleurosternal carinae low, broadly arcuated, poorly developed ridges visible on rings 3–18. Tergal pilosity very short, simple and abundant, on collum and following metaterga arranged irregularly; each seta ca 0.1 times as long as metatergum. Axial line absent. Stricture between pro- and metazona faint, thin and smooth. Epiproct oblong, subtriangular, with small subapical lateral papillae. Hypoproct semi-circular, with 1+1 small paramedian papillae near caudal margin.

Sternal cones faint, poorly visible, tips rounded. A rounded subtrapeziform lobe between coxae 3, clearly excavate, cup-



Figs 96–100. *Iulidesmus semicingulatus* sp.n., ♂ holotype. 96 — habitus, lateral view; 97 — head and rings 1–6, ventral view; 98 — rings 7–9, sublateral view; 99, 100 — posterior part of body, dorsal and ventral views, respectively. Photographs taken not to scale.

Рис. 96–100. *Iulidesmus semicingulatus* sp.n., голотип ♂. 96 — общий вид; 97 — голова и сегменты 1–6, снизу; 98 — сегменты 7–9, почти сбоку; 99, 100 — задняя часть тела, соответственно сверху и снизу. Фотографии сняты без масштаба.

shaped and densely setose on caudal face, setae being mostly directed conspicuously outside (♂). A small, but high, tongue-shaped, densely setose prong between coxae 4 (♂). Legs relatively short, 1.2–1.3 times as long as midbody height. Tarsal and tibial brushes present on all legs except for two last pairs (Figs 79, 80, 82–85). Adenostyles present on coxae 2 as gonopores on high and sharp tubercles, and on enlarged femora 3 and 4 as basally swollen glandular apophyses (♂) (Figs 79, 80).

Gonopods (Figs 86–95) complex and fully circular. Coxite (cx) long, subcylindrical, with a considerable distoventral group of setae in front of a small parbasal tubercle (k), about as long as femorite (fe) and about  $\frac{2}{3}$  as long as prefemorite (pfe); canulla (ca) flattened. Telopodite unusually long, slender and regularly curved. Femorite slightly curved mesally, clearly excavate because of a distinct, basal, mesal lobe (e) followed first by a clear-cut constriction and then by a gradual expansion in distal  $\frac{1}{3}$ ; acropodite hinged inside the hollow fe. Distofemoral sulcus (su1) distinct, clearly demarcating a short postfemorite proper. Postfemoral sulcus (su2) devoid of an apical lobe and demarcating both an elongate and roundish postfemorite (n) and a long, basally only slightly sigmoid, flagelliform solenomere (sl), this latter completely sheathed by subequally

prominent lamina medialis (lm) and lamina lateralis (ll) of solenophore (sph), both laminae ending up in three indistinct, rounded and small teeth.

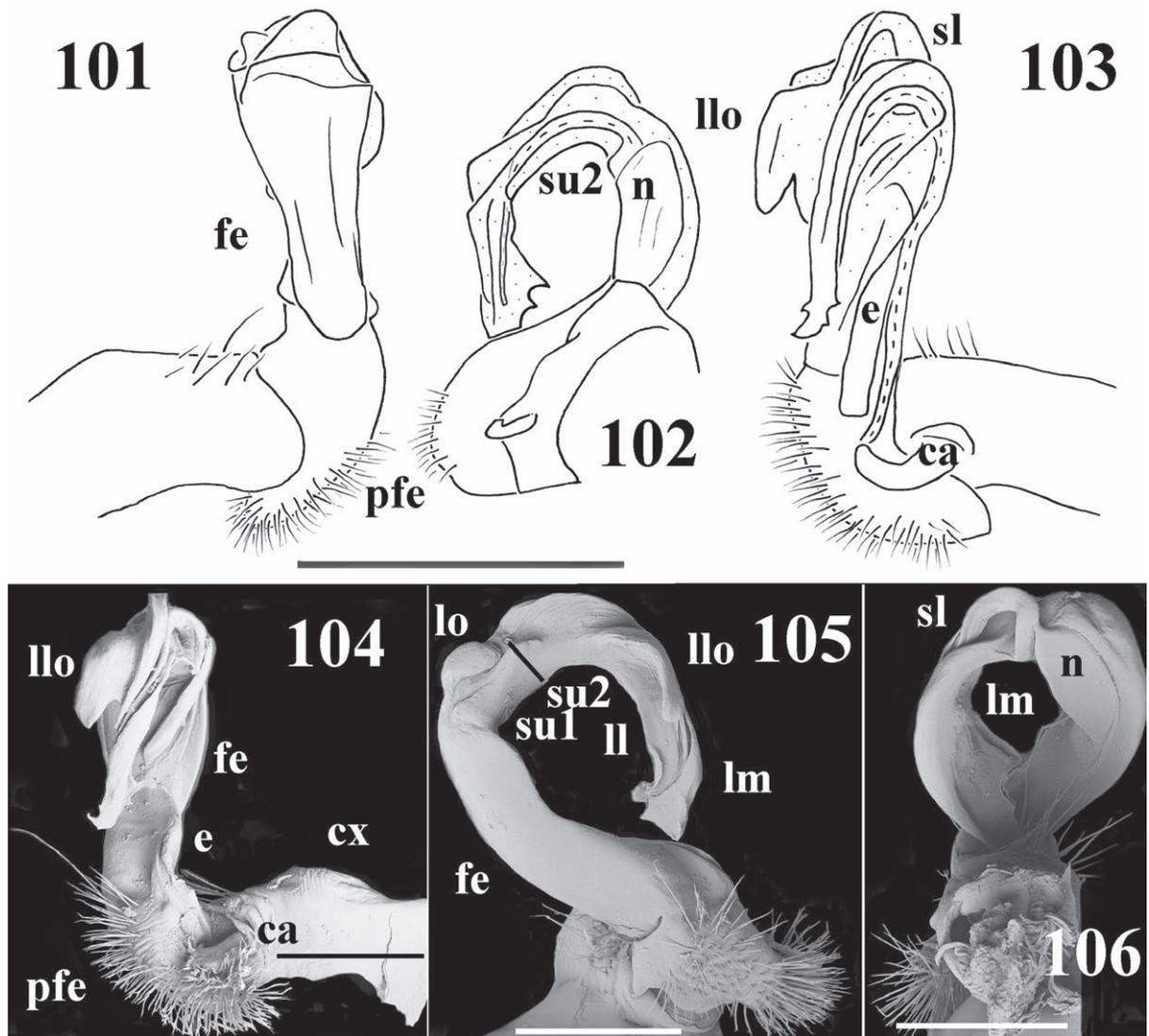
*Iulidesmus semicingulatus* sp.n.  
Figs 96–106.

HOLOTYPE ♂ (ZMUM), Peru, Junin Region, 16 km NW of Satipo, Rio Venado, 1120 m a.s.l., secondary forest on slope (Fig. 149), 13–14. IX.2017, K. Eskov leg.

NAME. Derived from an incomplete cingulate colour pattern which covers only the dorsal part of the strictural region.

DIAGNOSIS. A member of the *salvadorii* group (see below). Differs from congeners by the peculiar, semicingulate colour pattern, coupled with the complete absence of transverse metatergal sulci and the peculiar shape of the solenophore (see Suppl. Table).

DESCRIPTION. Length ca 41 mm, width 3.5 and 3.9 mm on midbody pro- and metazona, respectively (♂). General colouration pallid to light beige, with a faint, light grey-brown, vague and incomplete cingulation pattern covering only strictures and immediately adjacent parts of pro- and metaterga above level of



Figs 101–106. Right gonopod of *Iulidesmus semicingulatus* sp.n., ♂ holotype, lateral, dorsal, mesal, mesal, lateral and dorsal views, respectively. Scale bars: 1.0 mm (101–103), 0.5 mm (104–106, SEM).

Рис. 101–106. Правый гонопод *Iulidesmus semicingulatus* sp.n., голотип ♂, соответственно сбоку, сверху, изнутри, изнутри, сбоку и сверху. Масштаб: 1,0 мм (101–103), 0,5 мм (104–106, SEM).

paraterga. Head light brown, antennae beige, legs pale to light yellow (Figs 96–100).

Tegument smooth and shining. Clypeolabral region densely setose, vertex bare, epicranial suture rather faint. Interrantennal isthmus ca 1.1 times as broad as diameter of antennal socket. Antennae relatively short and slender (Fig. 96), extending past ring 2 dorsally (♂); in length, antennomeres 2–6 > 1 = 7. Genae rounded.

In width, ring 5 = 14 > collum > head > ring 3 = 4 > 2. Starting with ring 15, trunk gradually tapering towards telson. Paraterga faint bars, mostly set at about half midbody height, dorsal sulcus slightly not reaching the stricture region, ventral sulcus taking up about caudal 1/2 paraterga (Fig. 99). Paraterga 2 small, slightly drawn anteriorly beneath collum. Following paraterga rounded and slightly flattened. Ozopores as usual. Transverse mid-dorsal sulci absent (Figs 96, 99). Pleurosternal carinae small, low, arcuate to almost straight ridges with small caudal teeth gradually reduced towards telson, visible on rings 3–17. Tergal setae simple, short, usually 1/4 as long as metatergum, often abraded, retained only on few rings, arranged in three transverse rows on collum, 2+2 on

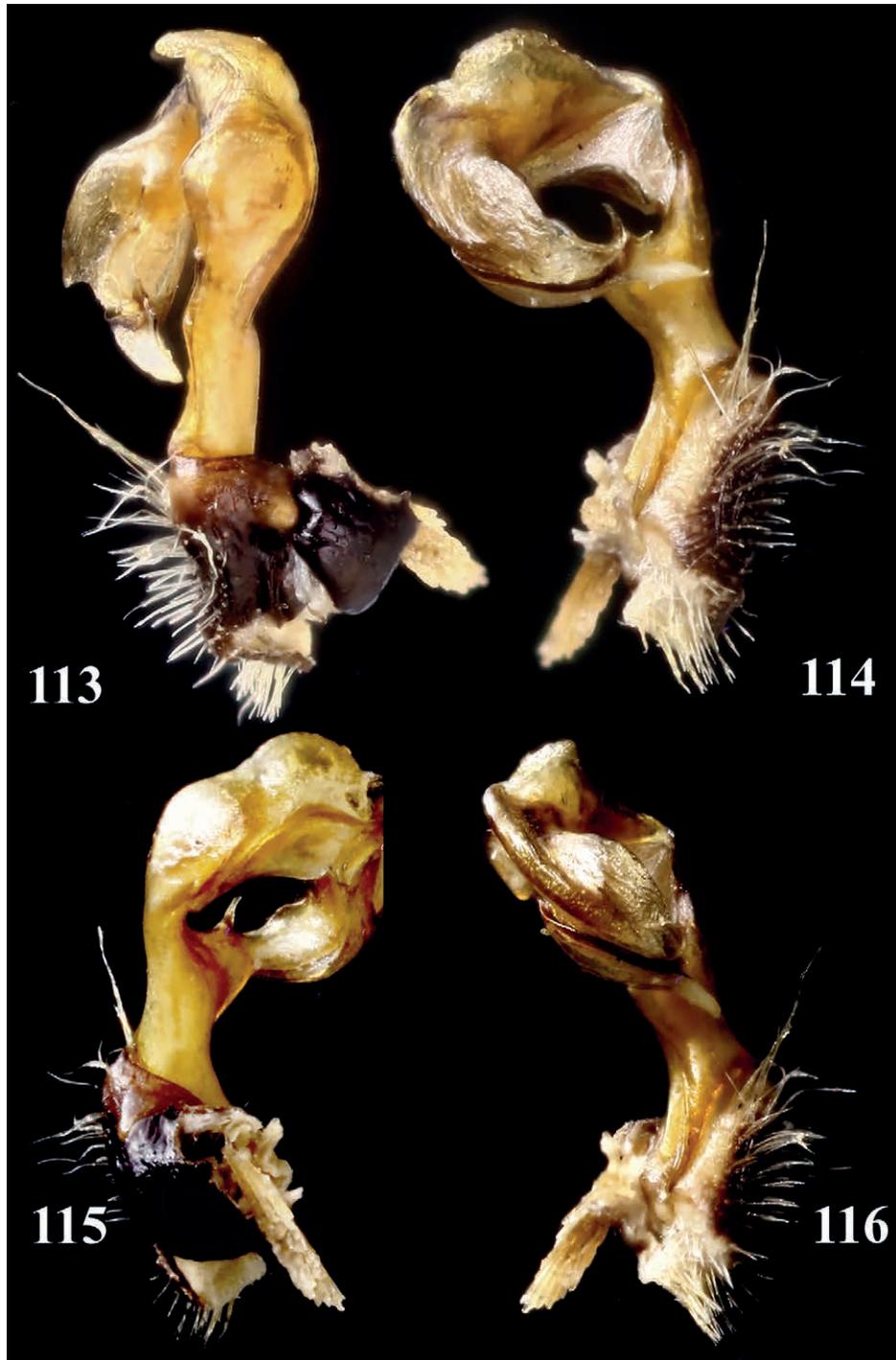
most following rings, but pattern 3+4 on rings 2–5. Axial line faint (Fig. 99). Stricture between pro- and metazona relatively deep, striolate. Epiproct long, thick, slightly curved ventrad distally, finger-shaped, subtruncate, with small, pre-apical, setigerous, lateral papillae (Figs 96, 100). Hypoproct semi-circular, with 1+1 small paramedian papillae near caudal margin.

Sterna densely setose (Figs 97, 100), sternal cones present, smaller between each anterior leg-pair, larger and almost pointed between each posterior leg-pair. Cross-impressions evident. Sternum between ♂ coxae 2 very narrow and deep, coxae subcontiguous. Sterna between ♂ coxae 3–6 each densely setose, small, rounded, paramedian, contiguous bulges devoid of any evident outgrowths. Sternum between ♂ legs 7 much broader, clearly excavate and nearly bare (Fig. 97). Adenostyles as a small and rounded gonapophysis on each ♂ coxa 2 and a short, rounded, setose, glandular, ventral tubercle in distal 2/3 of a clearly swollen ♂ femur 4 (Fig. 97). Legs relatively short (1.2–1.3 times as long as midbody height) (Fig. 96). Tarsal and tibial brushes present clearly in anterior half of body, gradually thinning out thereafter (♂).



Figs 107–112. *Iulidesmus asulcatus* sp.n., ♂ holotype. 107 — habitus, lateral view; 108, 109 — anterior half of body, dorsal and ventral views, respectively; 110 — posterior half of body, ventral view; 111 — head and rings 1–4, ventral view; 112 — rings 5–9, ventral view. Photographs taken not to scale.

Рис. 107–112. *Iulidesmus asulcatus* sp.n., голотип ♂. 107 — общий вид, сбоку; 108, 109 — передняя половина тела, соответственно сверху и снизу; 110 — задняя половина тела, снизу; 111 — голова и сегменты 1–4, снизу; 112 — сегменты 5–9, снизу. Фотографии сняты без масштаба.

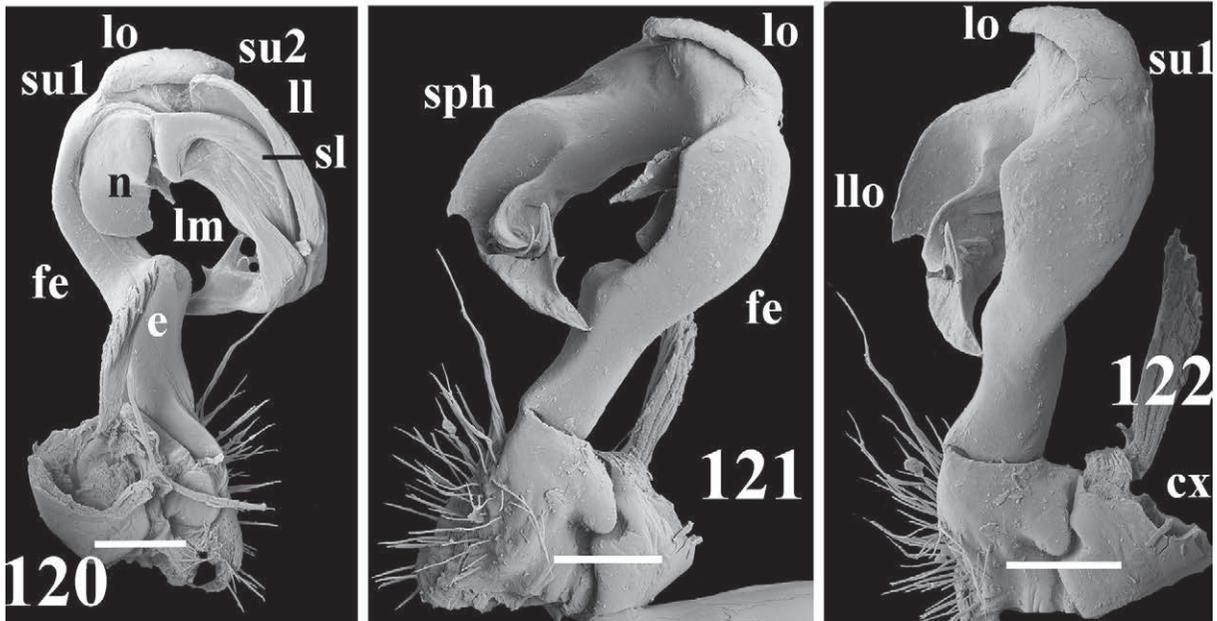
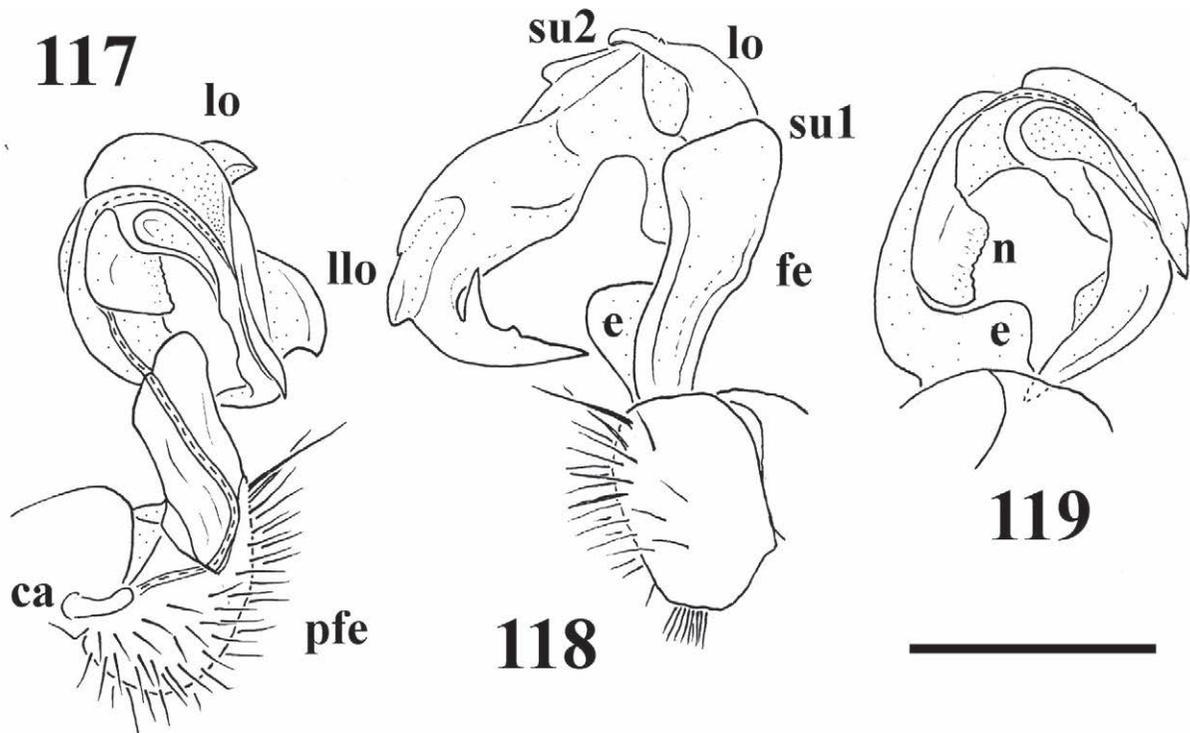


Figs 113–116. Left gonopod of *Iulidesmus asulcatus* sp.n., ♂ holotype, lateral, subventral, subdorsal and submesal views, respectively. Photographs taken not to scale.

Рис. 113–116. Левый гонопод *Iulidesmus asulcatus* sp.n., голотип ♂, соответственно сбоку, почти снизу, почти сверху и почти изнутри. Фотографии сняты без масштаба.

Gonopods (Figs 98, 101–106) complex, strongly curved mesad. Coxite (**cx**) subcylindrical, about as long as femorite (**fe**) and only slightly longer than prefemorite (**pfe**), only faintly bulged near base and with only a few setae distoventrally; canula (**ca**) as usual, tubiform. Femorite (**fe**) only slightly curved, with only a rather small mesal lobe (**e**) basally and only faintly constricted medially, but not enlarged distally, hollow/excavate on mesal face. Distofemoral sulcus (**su1**) clearly set off from

postfemoral part, with a small, but evident, roundish, apical lobe (**lo**). Postfemoral sulcus (**su2**) evident, with a distinct, elongate, mesal lobe (**n**) at base. Solenomere (**sl**) distinctly sigmoid basally and mostly sheathed by a longer lamina medialis (**lm**) and a slightly shorter lamina lateralis (**ll**) with its distinct lateral lobe (**llo**) near midway. Tip of solenophore (**sph**) subtruncate, with several small teeth. Seminal groove before **sl** running only along **fe**.



Figs 117–122. Left gonopod of *Iulidesmus asulcatus* sp.n., ♂ holotype, mesal, ventral, dorsal, dorsal, ventral and ventrolateral views, respectively. Scale bars: 0.5 mm (117–119), 0.2 mm (120–122, SEM).

Рис. 117–122. Левый гонопод *Iulidesmus asulcatus* sp.n., голотип ♂, соответственно изнутри, снизу, сверху, сверху, снизу и одновременно снизу и сбоку. Масштаб: 0,5 мм (117–119), 0,2 мм (120–122, SEM).

***Iulidesmus asulcatus* sp.n.**  
Figs 107–135.

HOLOTYPE ♂ (ZMUM), Peru, Junin Region, Calabaza, 2200 m a.s.l., S 11°30'38", W 74°49'15", cloud forest (Fig. 148), 16–20. IX.2017, K. Eskov leg.

PARATYPE ♂ (ZMUM), same place, together with holotype.

NAME. Derived from the absence of transverse metatergal sulci; adjective.

DIAGNOSIS. A member of the *salvadorii* group, the *junki* subgroup (see below). Differs from congeners by the absence of transverse metatergal sulci, coupled with the unusually thick epiproct and the peculiar shape of the solenophore (see Suppl. Table).

DESCRIPTION. Length of holotype ca 22 mm, width of midbody pro- and metazona 1.5 and 2.0 mm, respectively. Length of paratype ca 25 mm, width on midbody pro- and metazona 1.4 and 1.9 mm, respectively. General colouration



Figs 123–127. *Iulidesmus asulcatus* sp.n., ♂ paratype. 123 — habitus, lateral view; 124, 125 — anterior half of body, dorsal and ventral views, respectively; 126, 127 — posterior half of body, dorsal and ventral views, respectively. Photographs taken not to scale.

Рис. 123–127. *Iulidesmus asulcatus* sp.n., паратип ♂. 123 — общий вид, сбоку; 124, 125 — передняя половина тела, соответственно сверху и снизу; 126, 127 — задняя половина тела, соответственно сверху и снизу. Фотографии сняты без масштаба.

black to dark red-brown. Venter, paraprocts, vertex and ends of tarsi red-brownish. Spiracles contrasting light yellow to nearly whitish (Figs 107–111, 123–127).

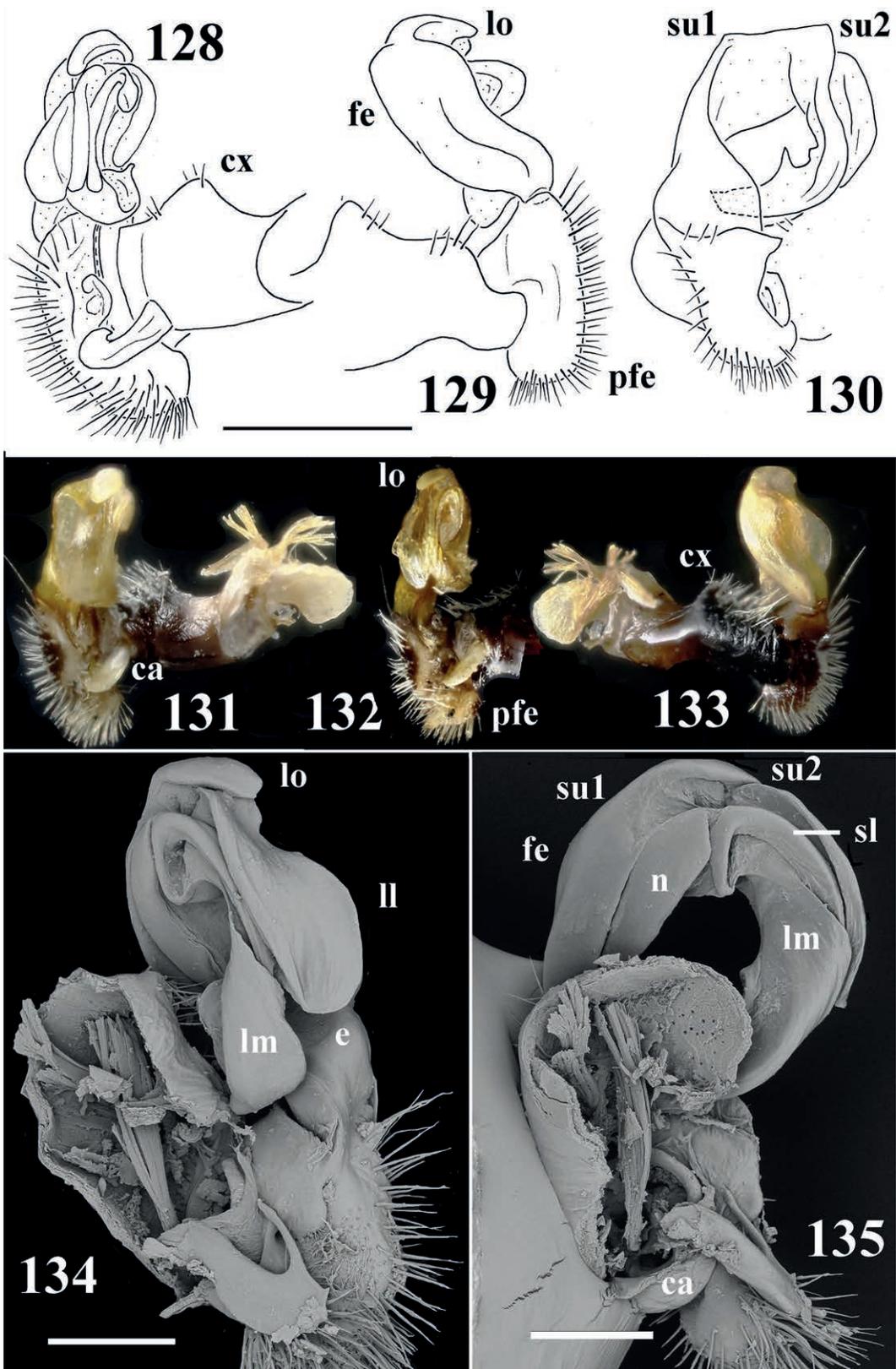
Tegument smooth and shining, very poorly, transversely and densely striolate behind strictures. Clypeolabral region densely setose, vertex nearly bare, epicranial suture relatively deep. Interantennal isthmus 0.8–0.9 times as broad as diameter of antennal socket. Antennae long and slender, almost reaching ring 4 dorsally. In length, antennomeres 2=3>4-6>1>7. Genae squarish.

Body submoniliform (Figs 107–111, 123–127). In width, rings 5=15 > collum > ring 2 > 4 > 3; starting with ring 16, body gradually and only slightly tapering towards telson, on rings 19 and 20 distinctly so. Paraterga flat and rounded bars, mostly set at about half midbody height, relatively strongly developed, nearly reaching caudal margin of metaterga, delimited by almost complete sulci dorsally, to caudal 2/3 by sulci ventrally; always lying within rear tergal margin (Figs 107–109, 123). Collum broadly and regularly rounded laterally. Paraterga 2 clearly drawn into a rounded lappet anteriorly beneath collum and a much smaller and also rounded lappet caudally, on following rings increasingly faint towards telson, larger on pore-bearing rings than on poreless ones. Transverse metatergal sulci absent, sometimes traceable at most as very faint impressions. Ozopores as usual, located inside round to ovoid pits near caudal margin. Pleurosternal carinae low, rounded, slightly granulated

and broadly arcuated ridges with small teeth directed caudally, present on rings 3–18. Anterior spiracles considerably larger than posterior ones. Tergal setae simple, almost fully abraded, ca 1/4 length of metatergum; setation pattern 2+2 in anterior row. Axial line missing. Stricture between pro- and metazona shallow, broad and smooth, sometimes very faintly striolate. Limbus as usual, but often striolate longitudinally. Epiproct unusually thick, subcylindrical, in distal part slightly curved ventrally (Figs 107, 110, 123). Hypoproct semi-circular, paramedian setigerous papillae small and located near caudal margin.

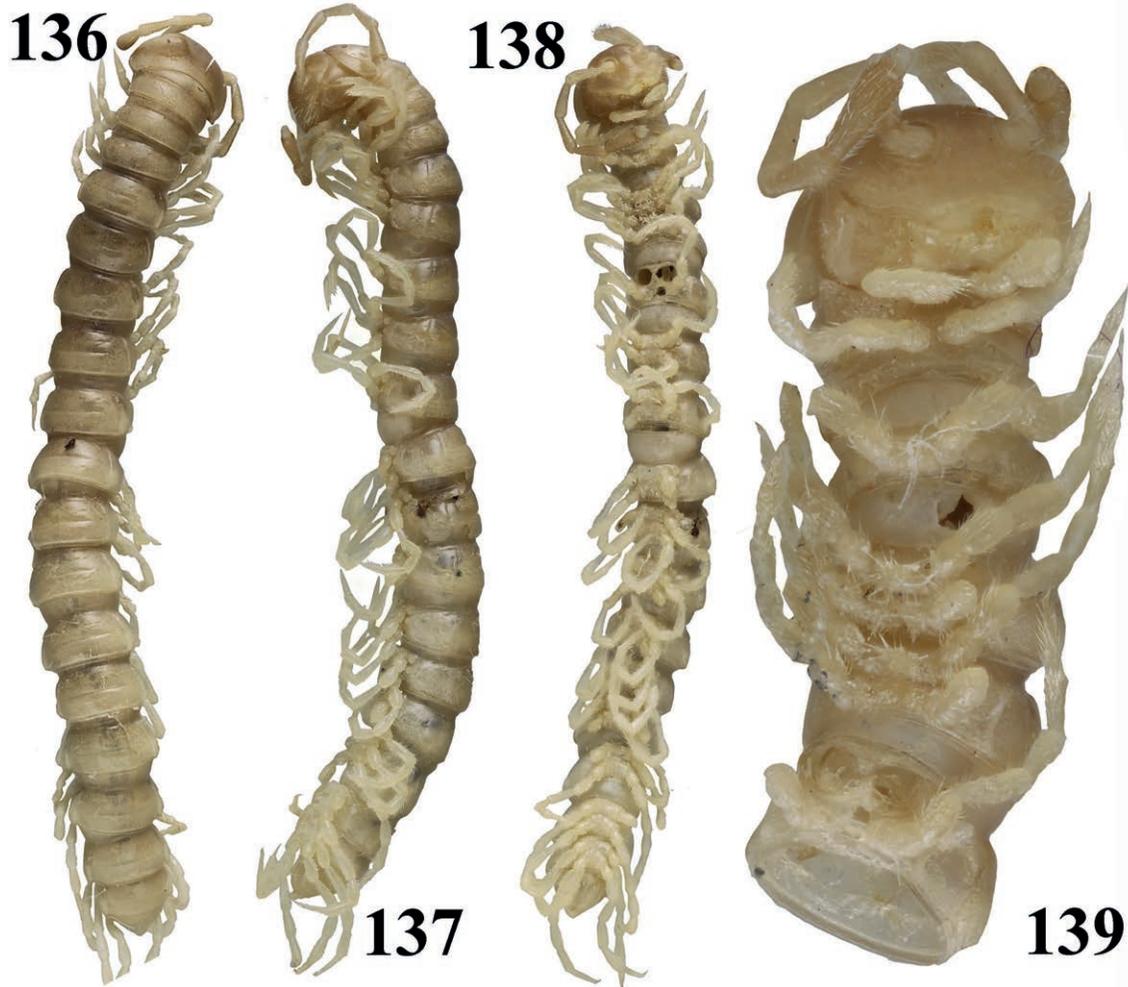
A small, central, densely setose ridge between ♂ coxae 3. Sternum between ♂ coxae 4 slightly excavate, with a high, densely setose, tongue-shaped, subtruncate process particularly densely setose on caudal face near base (Fig. 111). A broad, high, roundly subtrapeziform process between ♂ coxae 6 (Fig. 112). Sternum between ♂ coxae 7 broadly and clearly excavate. Adenostyle in distal 2/3 of a clearly enlarged femur 7 very small, glandular, crowned with a bunch of setae (♂). Gonopores on ♂ coxae 2 borne on small rounded tubercles. Legs very long and slender, 2.5–2.6 times as long as midbody height, prefemora not bulged laterally (Figs 107–111, 123–127). ♂ femora 3 and 4, unlike 7<sup>th</sup>, not enlarged, each also with a densely setose, glandular, light, ventral adenostyle in distal 2/3. Tarsal brushes present only on ♂ leg-pairs 1–5(6), tibial brushes only on legs 1–3.

Gonopods (Figs 113–122, 128–135) complex, circular. Coxite (cx) and femorite (fe) subequal in length, either slightly



Figs 128–135. Right gonopod of *Iulidesmus asulcatus* sp.n., ♂ paratype, mesal, lateral, ventral, submesal, lateral, mesal and dorsal views, respectively. Scale bars: 0.5 mm (128–130), taken not to scale (131–133), 0.2 mm (134, 135, SEM).

Рис. 128–135. Правый гонопод *Iulidesmus asulcatus* sp.n., паратип ♂, изнутри, соответственно изнутри, сбоку, снизу, почти изнутри, сбоку, изнутри и сверху. Масштаб: bars: 0,5 мм (128–130), снято без масштаба (131–133), 0,2 мм (134, 135, SEM).



Figs 136–139. *Iulidesmus carpish* sp.n., ♂ paratype. 136–138 — habitus, dorsal, lateral and ventral views, respectively; 139 — head and rings 1–7, ventral view. Photographs taken not to scale.

Рис. 136–139. *Iulidesmus carpish* sp.n., паратип ♂. 136–138 — общий вид, соответственно сверху, сбоку и снизу; 139 — голова и сегменты 1–7, снизу. Фотографии сняты без масштаба.

longer than prefemurite (**pfe**). Coxite with a distinct, midway, ventral tubercle with a field of dense setae in front; cannula (**ca**) simple, tubiform. Femorite (**fe**) only slightly curved mesad, subcylindrical, with an evident mesal lobe/bulge (**e**) at base, without midway constriction, hollow on mesal side, delimited by a distinct distofemoral sulcus (**su1**) from postfemoral part; postfemorite proper with a prominent, squarish, leaf-shaped, mesal lobe (**n**) at base, a relatively large, flattened, elongate, cap-shaped, apical lobe (**lo**) and a distinct postfemoral sulcus (**su2**) marking the beginning of a long and flagelliform solenomere (**sl**), the latter sheathed by a somewhat smaller lamina medialis (**lm**) and a stronger lamina lateralis (**ll**) with its sharp lateral tooth (**llo**) or rounded lobe in distal third. Tip of solenophore (**sph**) knife-shaped, subunciform, sharp and dentate.

*Iulidesmus carpish* sp.n.

Figs 136–145.

HOLOTYPE ♂ (ZMUM), Peru, Huanoco Region, Carpish Pass, 2400 m a.s.l., S 09°41'34", W 76°05'06", cloud forest, in epiphytes, 9.09.2017, K. Eskov leg.

PARATYPE ♂ (ZMUM), same place, together with holotype.

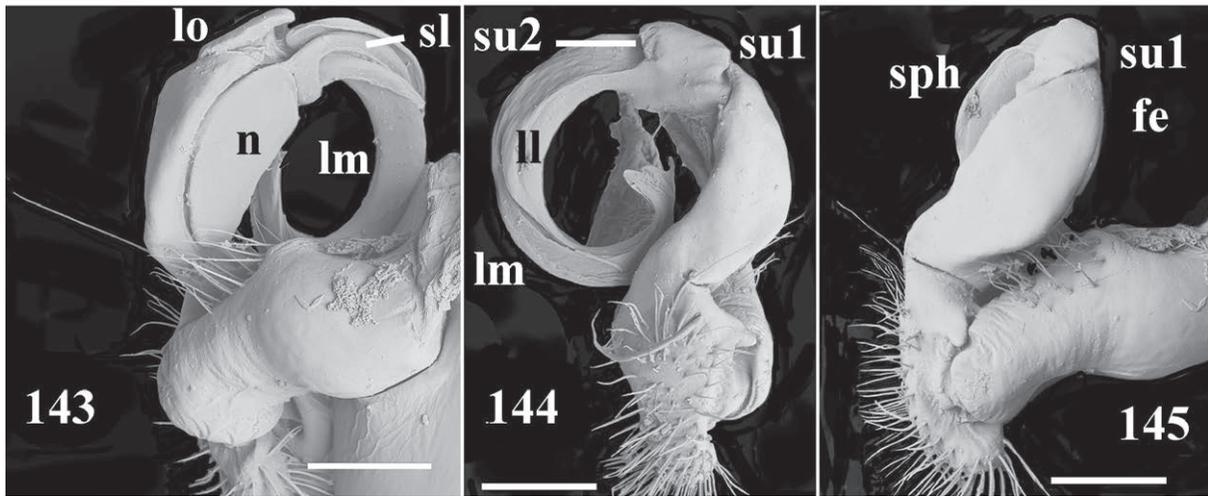
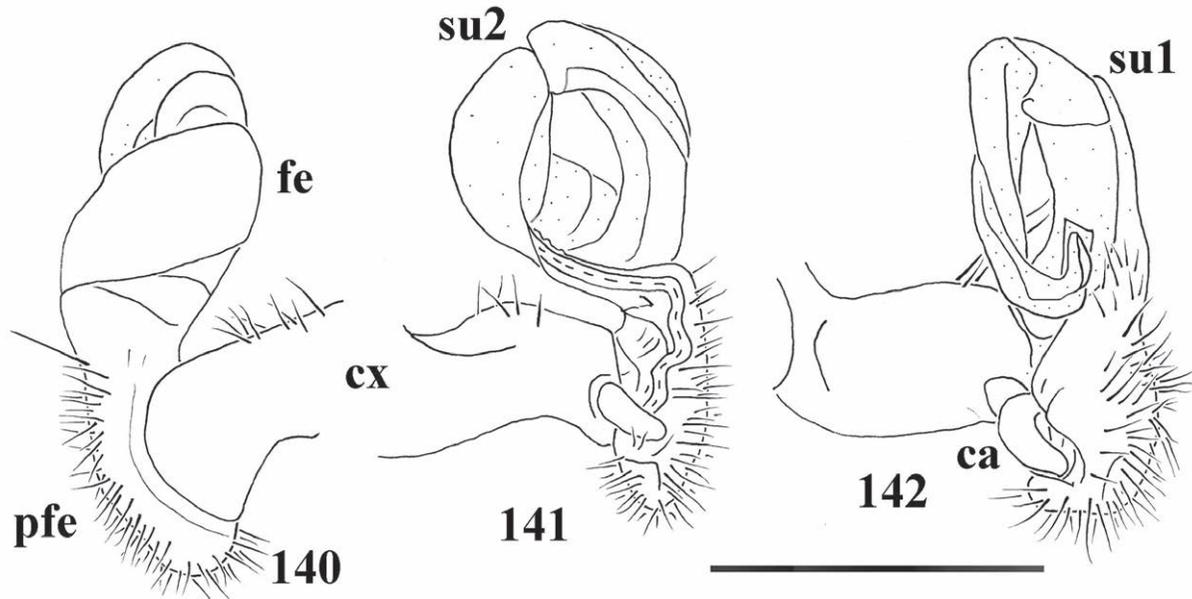
NAME. Derived from the type locality; noun in apposition.

DIAGNOSIS. A member of the *salvadorii* group (see below). Differs from congeners primarily by the peculiar solenophore structure (see Suppl. Table).

DESCRIPTION. Holotype ca 14 mm long, 1.1 and 1.5 mm wide on midbody pro- and metazona, respectively. Paratype ca 16 mm long, 1.1 and 1.4 mm wide on midbody pro- and metazona, respectively. General colouration from pale to light beige (paratype) or light beige (holotype) (Figs 136–139).

Tegument smooth and shining. Clypeolabral region sparsely setose, vertex nearly bare, epicranial suture faint. Interantennal isthmus 0.9 times as broad as diameter of antennal socket. Antennae long and slender, *in situ* reaching until half ring 4 dorsally. In length, antennomeres 2>3>4>6>5>7=1. Collum broadly and regularly rounded laterally. Genae squarish.

Body submoniliform (Figs 136–138). In width, rings 6=18 > collum > ring 5 > 2 > 3=4; starting with ring 19, body rapidly tapering towards telson. Paraterga mostly set at about half midbody height, never produced caudally past rear tergal margin, oblong and flattened, delimited by distinct sulci, almost complete dorsally and to about half ventrally (Figs 136–138). Paraterga 2 clearly drawn anteriorly into a small tooth and reaching beneath collum. Transverse metatergal sulci relatively strong, present on rings 5–19 (Fig. 136). Ozopores as usual,



Figs 140–145. Left gonopod of *Iulidesmus carpish* sp.n., ♂ paratype, lateral, mesal, ventral, dorsolateral, ventral and lateral views, respectively. Scale bars: 0.5 mm (140–142), 0.2 mm (143–145, SEM).

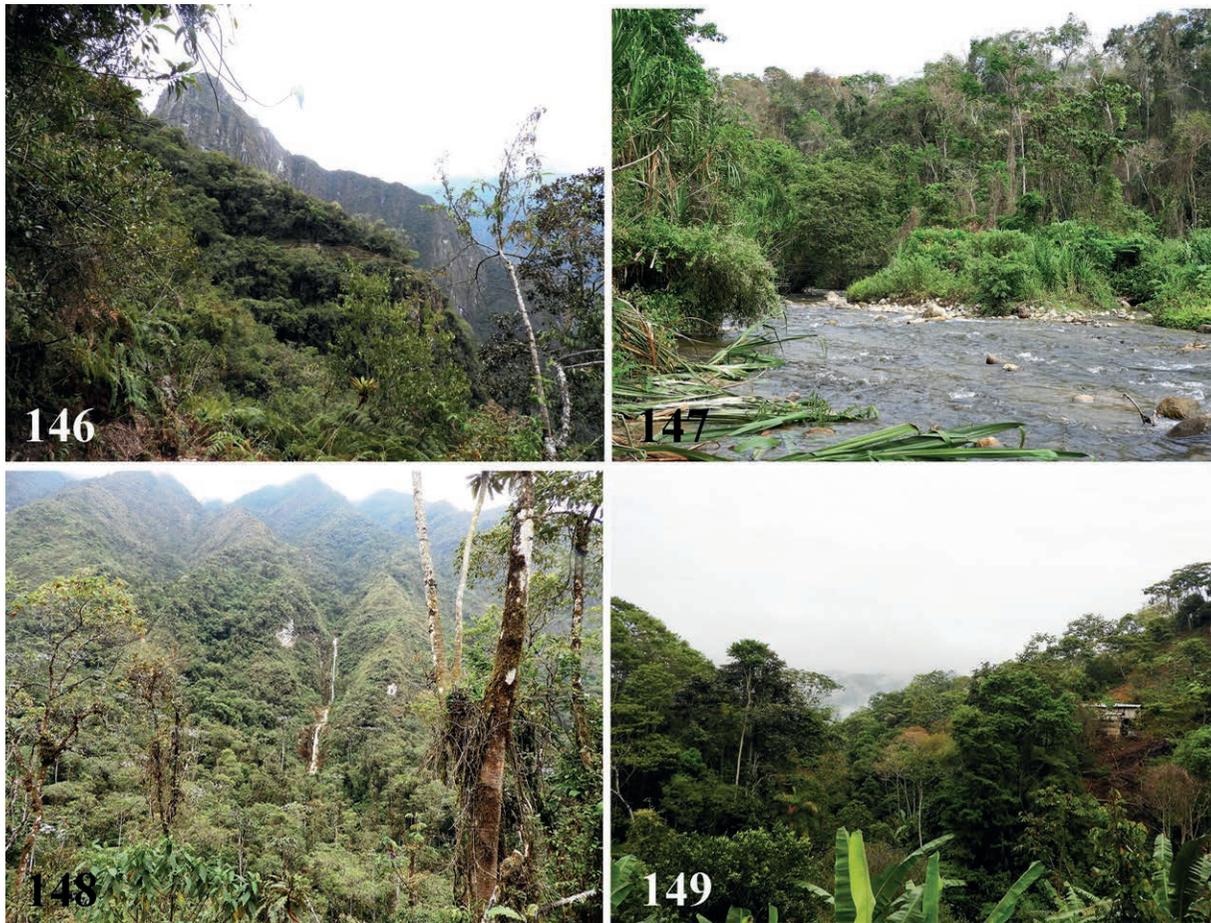
Рис. 140–145. Левый гонопод *Iulidesmus carpish* sp.n., паратип ♂, соответственно сбоку, изнутри, одновременно сверху и сбоку, снизу и снизу. Масштаб: 0,5 мм (140–142), 0,2 мм (143–145, SEM).

located inside ovoid grooves near caudal ends of paraterga on poriferous rings. Pleurosternal carinae on rings 3 and 4 almost squarish, without teeth, on following rings broadly arcuated and slightly granulated, visible on rings 2–18, increasingly faint starting with ring 14. Tergal setae simple, mostly abraded, arranged in three transverse rows on collum, setation pattern 4+4 in an anterior row on following metaterga, each seta ca  $\frac{1}{4}$  as long as metatergum. Axial line faint, but visible (Fig. 136). Stricture between pro- and metazona broad, shallow and smooth. Limbus evident, thin and entire. Epiproct roundly subtruncate, short, with small paramedian papillae near end (Fig. 136). Hypoproct subtrapeziform, 1+1 setae without papillae.

A small, bifid, densely setose bulge between coxae 3 (♂) (Fig. 139). A rather high, densely setose and roundly subtrapeziform lobe between coxae 4, with a field of long setae on posterior face (♂) (Fig. 139). A small and densely setose bulge between coxae 5 (♂). A high, narrow, tongue-shaped, densely setose and roundish lobe between coxae 6 (♂). Sternum between coxae 7 broadly rounded and deeply excavate, almost bare (♂) (Fig.

139). Legs long and slender, ca 2.0 times as long as midbody height (♂) (Figs 136–138). Tarsal and tibial brushes present on ♂ pairs 1–15. Adenostyles as small tubercles of gonopores on coxae 2, as distinct, glandular, distoventral tubercles, each crowned with a bunch of setae on both somewhat inflated ♂ femora 3 and 4 (Fig. 139).

Gonopods (Figs 140–145) complex. Coxite (cx) slightly longer than both subequally long prefemorite (pfe) and femorite (fe), with an extensive midway field of setae, but devoid of a ventral tubercle; cannula (ca) as usual, tubiform. Femorite (fe) slightly curved mesad, subcylindrical, without midway constriction, hollow on mesal side, delimited by a distinct distofemoral sulcus (su1) from posfemoral part; postfemorite proper with a prominent, leaf-shaped, mesal lobe (n), a rather small, flattened, roundish, apical lobe (lo) and a distinct postfemoral sulcus (su2) marking the beginning of a long flagelliform solenomere (sl), the latter sheathed by subequally strong lamina lateralis (ll) and lamina medialis (lm). Tip of solenophore (sph) complex, dentate, but not acuminate.



Figs 146–149. Some of the relevant habitats in Peru: 146 — Machu Picchu, cloud forest (*Incamorpha eskovi* sp.n.); 147 — Pichiquia, secondary forest in valley (*Iulidesmus cingulatus* sp.n.); 148 — Calabaza, cloud forest (*Iulidesmus pubescens* sp.n. and *I. asulcatus* sp.n.); 149 — Rio Venado, secondary forest on slope (*Iulidesmus semicingulatus* sp.n.). All pictures courtesy K. Eskov.

Рис. 146–149. Некоторые из значимых биотопов в Перу: 146 — Machu Picchu, туманный лес (*Incamorpha eskovi* sp.n.); 147 — Pichiquia, вторичный лес в долине (*Iulidesmus cingulatus* sp.n.); 148 — Calabaza, туманный лес (*Iulidesmus pubescens* sp.n. и *I. asulcatus* sp.n.); 149 — Rio Venado, вторичный лес на склоне (*Iulidesmus semicingulatus* sp.n.). Все фотографии любезно предоставлены К. Еськовым.

REMARKS. Interestingly, two new congeners have been found at Calabaza (Fig. 148), Junin Province: *I. asulcatus* sp.n. and *I. pubescens* sp.n., both belonging to different species subgroups of the *salvadorii* group.

### Infrageneric reclassification of *Iulidesmus*

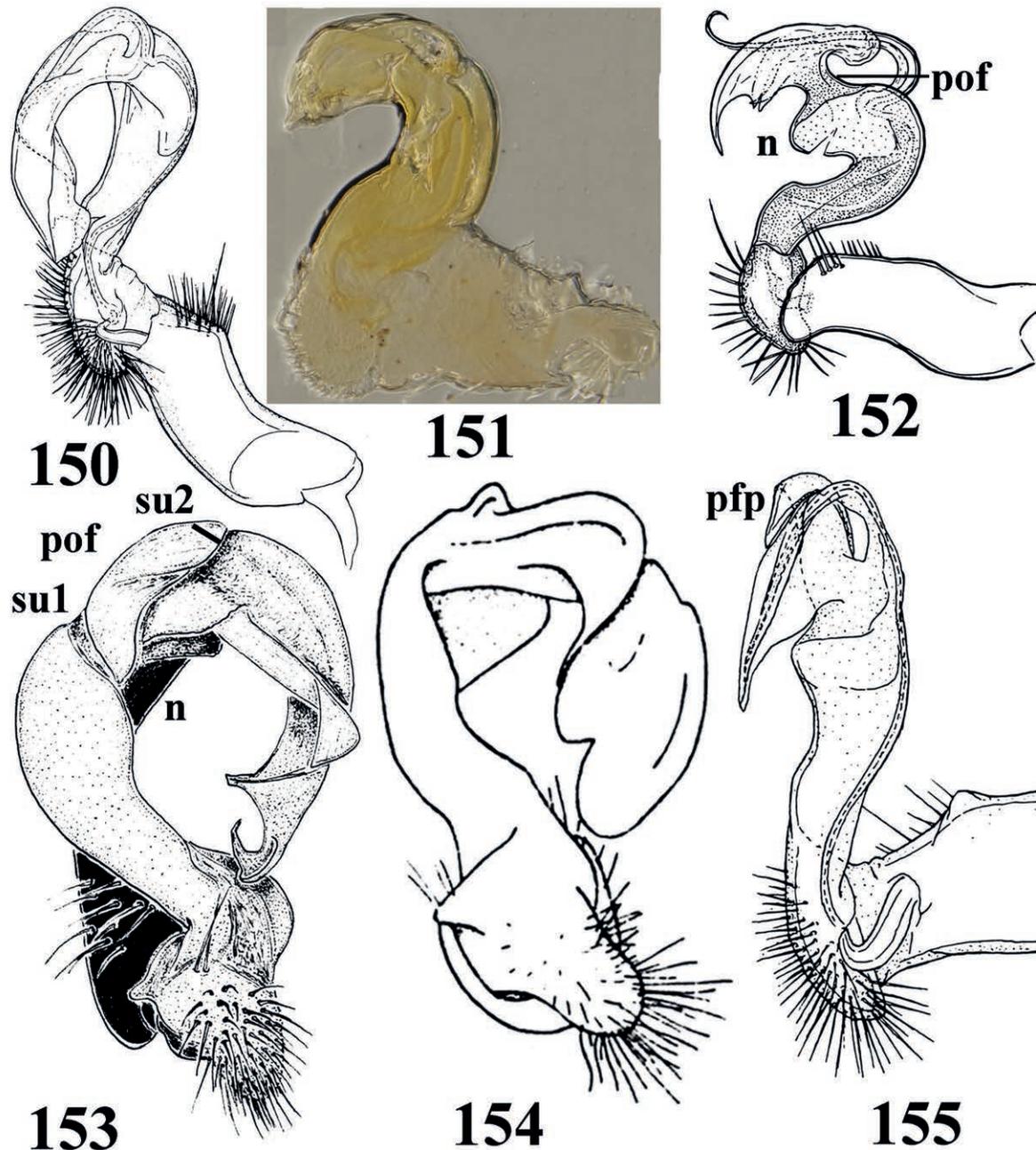
As noted above, the only relevant classification of *Iulidesmus* (partly equal to *Mestosoma*) is the one developed by Jeekel [1963, 1968]. He split the genus into a number of informal groups (I to V) and subgroups of species, considering not only certain details of gonopodal conformation, but also some somatic characters and sternal modifications. He also provided detailed catalogues of and keys to all genera and species of Paradoxosomatidae known in the Americas to that date, also considering their distributions. Hoffman [1977] proposed the first formal species group, the *salvadorii* group, and incorporated 11 species of *Iulidesmus* therein, based both on gonopodal structure and colouration.

Our approach differs in relying solely on a possible scenario of progressive gonopodal evolution in *Iulides-*

*mus*, from presumably more primitive/simple conditions to the most advanced ones. Only little coincidence is thus observed between Jeekel's [1963] classification and ours, not only because the former is strongly outdated, but also in that our approach is much more stringent and logical.

The following 85 accepted species are presently considered as belonging in *Iulidesmus*, all listed below in alphabetic order and each supplied with brief accounts of the main structural peculiarities, distribution, and underlying record history (Suppl. Table).

Of all 85 presently known species of *Iulidesmus*, four cannot be properly considered because their male characters remain totally enigmatic: *I. glabrus*, *I. laetus*, *I. lateralis*, and *I. typicus*. Yet *I. typicus*, the type species of *Iulidesmus*, is quite easy to recognize once male topotypic material becomes available for study, as its body shows no traces of paraterga even on ring 2 [Silvestri, 1895a]. The same condition is only observed in *I. unicus*, but superficially both species differ clearly enough at least in colouration: light brown with red posterior margins of rings, vs deep castaneous brown with contrasting lighter, horn brown legs (Suppl. Table). In addition, they



Figs 150–155. Gonopods of some old *Iulidesmus* species: 150 — *I. hylaeicus* (Jeekel, 1963) (after Jeekel [1963]); 151 — *I. alacer* (Attems, 1944) (♂ syntype, courtesy Nesrine Akkari, NHMW); 152 — *I. marthae* (Schubart, 1939) (after Schubart [1939]); 153 — *I. junki* (Golovatch et Hoffman, in Golovatch *et al.*, 2003) (after Golovatch *et al.* [2003]); 154 — *I. isthmianus* (Loomis, 1961) (after Loomis [1961]); 155 — *I. golovatchi* (Jeekel, 2002) (after Jeekel [2002]). Reproduced not to scale.

Рис. 151–155. Гonoпoды некоторых старых видов рода *Iulidesmus*: 150 — *I. hylaeicus* (Jeekel, 1963) (по: Jeekel [1963]); 151 — *I. alacer* (Attems, 1944) (синтип ♂, любезно предоставлено Nesrine Akkari, NHMW); 152 — *I. marthae* (Schubart, 1939) (по: Schubart [1939]); 153 — *I. junki* (Golovatch et Hoffman, in Golovatch *et al.*, 2003) (по: Golovatch *et al.* [2003]); 154 — *I. isthmianus* (Loomis, 1961) (по: Loomis [1961]); 155 — *I. golovatchi* (Jeekel, 2002) (по: Jeekel [2002]). Воспроизведено без масштаба.

come from two very different parts of the Andes: eastern versant, Bolivia, Departamento de La Paz, 1600 m a.s.l. [Silvestri 1895a; Hoffman, 2012], vs northern versant, northern Peru, Departamento de Cajamarca, 30 km NE of Cutervo, 2650 m a.s.l. [Kraus, 1959b].

A condition deemed perhaps the basalmost in the gonopodal evolution of *Iulidesmus* seems to be represented by the species which still lack any trace of a postfemoral sulcus and thus have no postfemorite proper yet. This group includes *I. acariguensis*, *I. bicolor*, *I. ca-*

*merani*, *I. carioca*, *I. hylaeicus*, *I. pulvillatus*, *I. silvestrii*, *I. simplex*, *I. venezuelanus* and probably some others. Because *I. hylaeicus* seems best to illustrate this condition (Fig. 150), the group is named the *hylaeicus* group. Six further species that seem to show the same pattern, *I. alacer*, *I. luctuosus*, *I. lugubris*, *I. pseudomorphus*, *I. tricuspis* and *I. vittatus*, all apparently to form the *alacer* group (Fig. 151), are clearly distinct in having unusually thick, stout and unciform telopodites, *vs* long, slender and more regularly curved in the *hylaeicus* group.

The next group to distinguish is the *differens* group (Figs 31–33) which members, such as *I. differens*, *I. ethophor* and *I. unicus*, in contrast to the closely related *hylaeicus* group, show the seminal groove largely running strictly along the lateral margin of the femorite, the latter thus being slightly torsate laterad, *vs* the femorite is non-torsate and the seminal groove runs fully on the mesal side, albeit usually quite close to its lateral edge. As a similar situation also concerns at least *I. florezi*, *I. minerus* and *I. sabaneta*, all species that clearly belong in the *salvadorii* group (Suppl. Table), slight femoral torsion seems to have appeared in the gonopodal evolution of *Iulidesmus* more than once.

The next, also relatively primitive step/stage in a presumed evolution of *Iulidesmus* gonopods is seen in *I. marthae* (Fig. 152) and *I. perfidus*, both to form the *marthae* group, in which the postfemoral part starts with a very conspicuous constriction just beyond the distofemoral cingulum (**su1**), the postfemorite proper (**pof**) being a simple stalk with a hypertrophied lobe **n**, but without **lo**; the solenophore is shortened and acuminate, supporting only some of the distal part of a basally unusually strongly sigmoid solenomere; both **ll** and **lm** from small and short to slender and long. Schubart [1939] established the genus *Pernambucosoma* Schubart, 1939 to solely incorporate *P. marthae*, the type species. Later, he [Schubart, 1943, 1945] added *P. perfidus* and *P. carioca* therein, but Jeekel [1963] synonymized *Pernambucosoma* with *Mestosoma*, hence present-day *Iulidesmus*, while the *I. carioca* gonopodal structure actually shows all characters of the *hylaeicus* group (see Suppl. Table). The *marthae* group roughly corresponds to group III of Jeekel [1963].

The species *I. golovatchi* (Jeekel, 2002), from Venezuela [Jeekel, 2002], seems particular in showing the postfemorite proper prolonged into a prominent, lateral and acuminate process (**pfp**) which is about half as long as a similarly acuminate solenophore (Fig. 155), thus obviously meriting a species group of its own: the *golovatchi* group.

The most species-rich group of *Iulidesmus*, the *salvadorii* group, appears to comprise the bulk of *Iulidesmus* diversity (Suppl. Table). A postfemorite proper (**pof**) is typically already well discernible, lying between the distofemoral (**su1**) and postfemoral (**su2**) sulci, often with such adjacent structures as a mesobasal lobe **n** and/or an apical, largely cap-shaped lobe **lo**. The progressive development of a more or less distinct postfemoral sulcus (**su2**), largely coupled with its adjacent **n** and/or **lo** lobes, is deemed to add to the gonopod's flexibility and an increasingly better protection of the always flagelliform

solenomere.

Within the *salvadorii* group, which incidentally appears to harbour all new *Iulidesmus* spp. described above, at least the following two subgroups can be distinguished. One is the *junki* subgroup, in which the solenophore is terminated in a strong sharp uncus or knife always accompanied by a distolateral tooth and often also with a subapical denticle (Figs 113–122, 128–135, 153). This subgroup comprises *I. asulcatus* sp.n., *I. balzanii*, *I. garciae*, *I. junki*, *I. mediatatus* and *I. sphinx*, and it grossly corresponds to Jeekel's [1963] group V, subgroup 1b.

The other subgroup, the *isthmianus* subgroup, encompasses the species in which the tip of the solenophore is basically flattened, broadened and roundly bilobed. Such are *I. casimiranus*, *I. derelictus*, *I. florezi*, *I. isthmianus* (Fig. 154), *I. minerus*, *I. monaguensis*, *I. moorei*, *I. sabaneta*, *I. satipo* sp.n. (Figs 74–76), *I. zeaensis* and possibly a few other congeners.

The following key can be proposed to separate the species groups and subgroups of *Iulidesmus* based on gonopodal conformation:

- 1(2) Seminal groove on femorite quickly shifted laterad to largely run strictly all along its lateral margin (Figs 31–33). ...  
..... the *differens* group
- 2(1) Seminal groove running fully on mesal side of femorite, albeit usually along and rather close to its lateral margin .  
..... 3
- 3(4) No trace of a postfemoral sulcus, i.e. a postfemorite proper absent. .... 5
- 4(3) A more or less evident postfemoral sulcus present, i.e. a postfemorite proper discernible between distofemoral and postfemoral sulci..... 7
- 5(6) Telopodite long and slender, solenophore about as long as femorite (Fig. 150). .... the *hylaeicus* group
- 6(5) Telopodite short and stout, unciform, solenophore considerably shorter than femorite (Fig. 151). .... the *alacer* group
- 7(8) Postfemorite proper a long, lateral and acuminate process (**pfp**) about half as long as a similarly acuminate solenophore (Fig. 155). .... the *golovatchi* group
- 8(7) Postfemorite proper without lateral process..... 9
- 9(10) Postfemoral part starting with a very conspicuous constriction, postfemorite proper (**pof**) being a free simple stalk with a hypertrophied lobe **n**, but without apical lobe; solenophore shortened, supporting only some of the distal part of a basally unusually strongly sigmoid solenomere (Fig. 152). ....the *marthae* group
- 10(9) Postfemorite proper neither free nor stalk-like, more elaborate. ....the *salvadorii* group
- 11(12) Solenophore terminating in a strong sharp uncus or knife always accompanied by a distolateral tooth and often also with a subapical denticle (Fig. 153). ....  
..... the *junki* subgroup
- 12(11) Solenophore tip otherwise. .... 13
- 13(14) Solenophore tip flattened, broadened and roundly bilobed (Fig. 154). .... the *isthmianus* subgroup
- 14(13) Solenophore otherwise (e.g., Figs 45–50, 63–67, 74–76, 90–95, 101–106, 155). ....  
.....other members of the *salvadorii* group

## Conclusions

Compiling an updated key following Jeekel's [1963] and Hoffman's [1977] strongly outdated ones would not

require too much effort, especially considering the comparative information already contained in Supplementary Table. This information could easily be extended by adding some more, presumably mostly species-specific characters such as tegument texture, lateral outline and border sulcus of collum, pleurosternal carinae, metatergal setation pattern, length of tergal setae, relative lengths of antennae and legs, further details of gonopodal structure etc. But even a more complete character matrix could hardly help too much given the so many lacunae in the numerous old original descriptions. Too many species cannot be assigned to a certain species group or subgroup yet.

Congruence between our new classification and Jeekel's [1963, 1968] old one appears to be quite little. This is hardly surprising because we try to present ours in an evolutionary context, delimiting the species groups and subgroups as a succession of stages from simple and primitive to increasingly complex and advanced. Repeating and expanding Jeekel's [1963] key to update and correct it would be rather easy, but at present this hardly makes sense. The comparative information presented in Supplementary Table seems best to presently be used as a sound basis and tool for building up a complete character matrix and conducting computerized phylogenetic analyses. Finally, molecular data, once available, would come in most handy as well.

Given the still ongoing revision of several old type collections and the undoubtedly still very high number of further new and old congeners to be revealed, recorded and described [Romero-Rincon, Golovatch, 2024], it seems enough to stop now where we are. Peru appears to presently harbour as many as 33 *Iulidesmus* species, the highest number per country. As the main body of congeners not only in Peru, but everywhere else has been recorded from a single place, this alone suggests a real wealth of novelties ahead.

#### Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

**Ethical approval:** No ethical issues were raised during our research.

#### Supplementary Issues

Supplementary Table. *Iulidesmus* species and their main morphological characteristics.

**Acknowledgements.** We are most grateful to the collectors involved, Kirill Y. Eskov and Ilya Melnik, both Moscow, Russia, who entrusted us with their material for study. Kirill Eskov generously supplied us with several pictures of the relevant habitats in Peru. Kirill V. Makarov, Moscow, helped immensely in taking many colour pictures, while Roman A. Rakitov assisted much in taking SEM images at the Paleontological Institute, Russian Academy of Sciences, Moscow. Juan Romero-Rincon, Bogotá, Colombia most helpfully commented on an advanced draft.

## References

Adis J. 1992. On the survival strategy of *Mestosoma hylaicum* Jeekel, a millipede from Central Amazonian floodplains (Paradoxosomatidae, Polydesmida, Diplopoda) // *Berichte des Natur-*

- wissenschaftlich-Medizinischen Vereins Innsbruck. Supplement 10. P.183–187.
- Attems C. 1898. System der Polydesmiden. 1. Theil // *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*. Bd.67. H.1. S.221–482.
- Attems C. 1937. Myriapoda 3, Polydesmoidea 1. Fam. Strongylosomidae // *Das Tierreich*. Lfg.68. S.1–300.
- Attems C. 1944. Neue Polydesmoidea // *Zoologischer Anzeiger*. Bd.144. H.11/12. S.223–251.
- Bueno-Villegas J., Sierwald P., De Ascensão A.A. 2019. Check list of the Venezuelan millipede species // *Zootaxa*. Vol.4686. No.2. P.151–201.
- Carl J. 1902. Exotische Polydesmiden // *Revue suisse de Zoologie*. T.10. P.563–679.
- Carl J. 1914. Die Diplopoden von Columbien nebst Beiträgen zur Morphologie der Stemmatoiluliden // *Mémoires de la Société neuchâteloise des Sciences naturelles*. T.5. P.821–993.
- Chamberlin R.V. 1952. Some American polydesmid millipeds in the collection of the Chicago Museum of Natural History // *Annals of the Entomological Society of America*. Vol.45. P.553–584.
- Chamberlin R.V. 1955. New millipeds from Peru and adjacent parts // *University of Utah Biological Series*. Vol.11. No.5. P.1–47.
- Chamberlin R.V. 1957. The Diplopoda of the Lund University and California Academy of Sciences expeditions // *Lunds Universitets Årsskrift*, N.F. Avd.2. Vol.53. No.8. P.3–44.
- Enghoff H., Golovatch S.I., Short M., Stoev P.E., Wesener T. 2015. Diplopoda – taxonomic overview // Minelli A. (ed.). *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda*. Vol.2. Leiden – Boston: Brill. P.363–453.
- Golovatch S.I. 2005. The millipede family Paradoxosomatidae in Paraguay, with descriptions of five new species (Diplopoda, Polydesmida) // *Revue suisse de Zoologie*. T.112. Fasc.4. P.807–830.
- Golovatch S.I., Gallo J.S., Bichuette M.E. 2022. Two new species of the millipede family Paradoxosomatidae from Bahia state, northeastern Brazil, including a remarkable presumed troglodyte (Diplopoda: Polydesmida) // *Arthropoda Selecta*. Vol.31. No.2. P.143–156.
- Golovatch S.I., Hoffman R.L., Mármol A., Adis J. 2003. A new, apparently arboricolous species of the millipede genus *Mestosoma* Silvestri, 1897 from near Iquitos, Peruvian Amazonia (Diplopoda: Polydesmida: Paradoxosomatidae) // *Amazoniana*. Vol.17. Nos 3/4. P.343–348.
- Golovatch S.I., Korotaeva A.M. 2023a. A new, montane record of the millipede, *Thrinnoxethus verhoeffi* (Kraus, 1956) from the Andes of Peru (Diplopoda: Polydesmida: Aphelidesmidae) // *Russian Entomological Journal*. Vol.32. No.2. P.243–251.
- Golovatch S.I., Korotaeva A.M. 2023b. On a collection of the millipede family Platyrrhacidae from Peru (Diplopoda: Polydesmida) // *Arthropoda Selecta*. Vol.32. No.3. P.239–249.
- Golovatch S.I., Liu W.x. 2020. Diversity, distribution patterns, and fauno-genesis of the millipedes (Diplopoda) of mainland China // *ZooKeys*. Vol.930. P.153–198.
- González-Sponga M.A. 2004. Miriápodos de Venezuela. Descripción de nueve especies nuevas del género *Neactoma* Chamberlin, 1952 (Polydesmida: Strongylosomidae) // *Boletín de la Academia de Ciencias Físicas, Matemáticas y Naturales, Caracas*. Vol.64. Nos 3–4. P.9–16.
- Hoffman R.L. 1966. Polydesmoid Diplopoda from the Pacaraima Mountains // *Journal of Zoology*. Vol.148. P.540–553.
- Hoffman R.L. 1977. The millipede genus *Mestosoma* in Costa Rica (Polydesmida: Paradoxosomatidae) // *Studies on Neotropical Fauna and Environment*. Vol.12. P.207–215.
- Hoffman R.L. 1980. Classification of the Diplopoda. Genève: Muséum d'histoire naturelle. 237 pp.
- Hoffman R.L. 1999. Checklist of the millipeds of North and Middle America // *Virginia Museum of Natural History Special Publication* 8. 581 pp.
- Hoffman R.L. 2012. On the identity of the generic name *Iulidesmus* Silvestri, 1895 (Polydesmida: Paradoxosomatidae) // *Zootaxa*. Vol.3204. P.65–68.
- Jeekel C.A.W. 1963. Diplopoda of Guiana (1–5) // Geijskes D.C., Wagenaar Hummelinck P. (eds.). *Studies on the Fauna of Suriname and Other Guyanas*. Vol.4. No.11. P.1–157.
- Jeekel C.A.W. 1965. Revision of the South American Paradoxosomatidae in the Museo Civico di Storia Naturale di Genova (Diplopoda,

- Polydesmida) // *Annali del Museo Civico di Storia Naturale di Genova*. Vol.75. P.99–125.
- Jeekel C.A.W. 1968. On the classification and geographical distribution of the family Paradoxosomatidae (Diplopoda, Polydesmida). Rotterdam: Academisch Proefschrift. 162 pp. (privately published)
- Jeekel C.A.W. 2002. Paradoxosomatidae from Venezuela, with the description of a new species (Diplopoda, Polydesmida) // *Myriapod Memoranda*. Vol.5. P.40–51.
- Kraus O. 1954. Myriapoden aus Peru, II // *Senckenbergiana biologica*. Bd.35. Nr.1/2. S.17–55.
- Kraus O. 1955. Myriapoden aus Peru, III // *Senckenbergiana biologica*. Bd.36. Nr.3/4. S.173–200.
- Kraus O. 1956. Über neotropische Strongylosomatidae (Diplopoda) // *Senckenbergiana biologica*. Bd.37. Nr.5/6. S.403–419.
- Kraus O. 1957. Myriapoden aus Peru, V // *Senckenbergiana biologica*. Bd.38. Nr.1/2. S.95–114.
- Kraus O. 1959a. Myriapoden aus Peru, VII // *Senckenbergiana biologica*. Bd.40. Nr.3/4. S.191–208.
- Kraus O. 1959b. Myriapoden aus Peru, VIII // *Senckenbergiana biologica*. Bd.40. Nr.5/6. S.263–281.
- Kraus O. 1960. Myriapoden aus Peru, IX // *Senckenbergiana biologica*. Bd.41. Nr.3/4. S.241–264.
- Loomis H.F. 1961. New and previously known millipeds of Panama // *Proceedings of the United States National Museum*. Vol.113. No.3454. P.77–123.
- Nguyen D.A., Sierwald P. 2013. A worldwide catalog of the family Paradoxosomatidae Daday, 1889 (Diplopoda: Polydesmida) // *Check List*. Vol.9. No.6. P.1132–1353.
- Parra-Gómez A. 2022. Catálogo de los milpiés (Myriapoda: Diplopoda) de Chile // *Revista Chilena de Entomología*. T.48. No.3. P.451–504.
- Peters W. 1865. Übersicht der in Königl. zoologischen Museum befindlichen Myriopoden aus der Familie der Polydesmi, so wie Beschreibungen einer neuen Gattung, *Trachyjulus*, der *Juli* und neuer Arten der Gattung *Siphonophora* // *Monatsberichte der Königlichen Preussische Akademie der Wissenschaften zu Berlin*. Aus dem Jahre 1864. S.529–627.
- Pocock R.I. 1888. Contributions to our knowledge of the Myriopoda of Dominica // *Annals and Magazine of Natural History*, Ser. 6. Vol.2. P.472–483.
- Recuero E., García-París M. 2016. A new North American region colonized by the Australian millipede *Akamptogonus novarae* (Humbert & DeSaussure, 1869) (Polydesmida, Paradoxosomatidae), with a key for the known Paradoxosomatidae species from North and Central America and the Caribbean Islands // *North-Western Journal of Zoology*. Vol.12. No.2. P.385–389.
- Rodrigues P.E.S., Golovatch S.I., Ott R., Rodrigues E.N.L. 2020. Three new species of the millipede genus *Catharosoma* Silvestri, 1897 from southern Brazil, with new records and a clarified identity of *Catharosoma intermedium* (Carl, 1902) (Diplopoda: Polydesmida: Paradoxosomatidae) // *Zootaxa*. Vol.4751. No.1. P.119–130.
- Romero-Rincon J., Golovatch S.I. 2024. The millipede genus *Iulidesmus* Silvestri, 1895 in Colombia (Polydesmida, Paradoxosomatidae, Catharosomatini) // *Zootaxa*. Vol.5415. No.1. P.56–76.
- Schubart O. 1939. Die Myriapoden des Staates Pernambuco. 1. Die Familie Strongylosomidae (Diplopoda, Polydesmoidea) (Über Diplopoden Nr. 35) // *Zoologischer Anzeiger*. Bd.128. Nr.3/4. S.77–84.
- Schubart O. 1943. Espécies novas das famílias Strongylosomidae e Lep-todesmidae da ordem Proterospermophora do interior dos estados de São Paulo et Mato-Grosso // *Papéis Avulsos do Departamento de Zoologia*. Vol.3. No.8. P.127–164.
- Schubart O. 1944. Os Diplopodos de Parassununga // *Acta Zoologica Lilloana del Instituto "Miguel Lillo"*. T.2. P.321–440.
- Schubart O. 1945. Os Proterospermophora do Distrito Federal (Myriapoda, Diplopoda) // *Arquivos do Museu Nacional*. Vol.38. P.1–156.
- Shear W.A. 1971. The identity of *Ergethus perditus* Chamberlin (Diplopoda, Polydesmida, Paradoxosomatidae) // *Proceedings of the Biological Society of Washington*. Vol.83. No.39. P.455–458.
- Silvestri F. 1895a. Chilopodi e diplopodi raccolti dal Capitano G. Bove e dal Prof. L. Balzan nell'America meridionale // *Annali del Museo Civico di Storia Naturale di Genova*. Ser.2. Vol.14(34). P.764–783.
- Silvestri F. 1895b. Chilopodi e diplopodi. Viaggio del dottor Alfredo Borelli nella Repubblica Argentina e nel Paraguay XIV // *Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Università di Torino*. Vol.10. No.203. P.1–12.
- Silvestri F. 1897a. Chilopodi e diplopodi. Viaggio del Dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina. IV // *Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Università di Torino*. Vol.12. No.283. P.1–11.
- Silvestri F. 1897b. Chilopodi e diplopodi. Viaggio del Dr. Enrico Festa nell'Ecuador e regione vicine. V // *Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Università di Torino*. Vol.12. No.303. P.1–19.
- Silvestri F. 1898. Descrizione di alcuni nuovi diplopodi raccolti nell'alto Paraguay dal cav. Guido Boggiani // *Annali del Museo Civico di Storia Naturale di Genova*. Ser.2. Vol.18(38). P.670–675.
- Silvestri F. 1903. Note Diplopodologiche // *Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Università di Torino*. Vol.18. No.433. P.1–21.
- Tabacaru I. 1981. Une nouvelle espèce du genre *Graphisternum* (Diplopoda, Polydesmida, Paradoxosomatidae) du Perou // *Travaux de l'Institut Spéologie "Emile Racovitza"*. T.20. P.97–101.
- Verhoeff K.W. 1938. Über Diplopoden des Zoologischen Museums in München // *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*. Bd.71. S.1–54.
- Verhoeff K.W. 1941. Chilopoden und Diplopoden // *Titschack E. (Hrsg.). Beiträge zur Fauna Perus*. Hamburg. Bd.1. H.2. S.5–80.
- Wesener T., Moritz L. 2018. Checklist of the Myriapoda in Cretaceous Burmese amber and a correction of the Myriapoda identified by Zhang (2017) // *Check List*. Vol.14. No.6. P.1131–1140.

Responsible editor K.G. Mikhailov