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## Research article

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# The millipede genus *Tylopus* Jeekel, 1968 (Diplopoda, Polydesmida, Paradoxosomatidae), with a key and descriptions of eight new species from Indochina

Natdanai LIKHITRAKARN<sup>1</sup>, Sergei I. GOLOVATCH<sup>2,\*</sup> & Somsak PANHA<sup>3,\*</sup>

<sup>1</sup>Division of Plant Protection, Faculty of Agricultural Production,  
Maejo University, Chiang Mai 50290, Thailand.

<sup>2</sup>Institute for Problems of Ecology and Evolution, Russian Academy of Sciences,  
Leninsky pr. 33, Moscow 119071, Russia.

<sup>3</sup>Animal Systematics Research Unit, Department of Biology, Faculty of Science,  
Chulalongkorn University, Bangkok 10330, Thailand.

<sup>1</sup>Email: [kongerrrr@hotmail.com](mailto:kongerrrr@hotmail.com)

<sup>2,\*</sup>Corresponding author: [sgolovatch@yandex.ru](mailto:sgolovatch@yandex.ru)

<sup>3,\*</sup>Corresponding author: [somsak.pan@chula.ac.th](mailto:somsak.pan@chula.ac.th)

<sup>1</sup>[urn.lsid:zoobank.org:author:442E2E6E-1CB3-47B2-9896-1A922CE509E1](http://urn.lsid:zoobank.org:author:442E2E6E-1CB3-47B2-9896-1A922CE509E1)

<sup>2</sup>[urn.lsid:zoobank.org:author:71532F45-BDD5-415D-BC54-86256E5D5D4A](http://urn.lsid:zoobank.org:author:71532F45-BDD5-415D-BC54-86256E5D5D4A)

<sup>3</sup>[urn.lsid:zoobank.org:author:AC935098-D901-4F35-A414-4B0D4FE44E79](http://urn.lsid:zoobank.org:author:AC935098-D901-4F35-A414-4B0D4FE44E79)

**Abstract.** The Indochinese to southern Chinese millipede genus *Tylopus* currently comprises 62 species, including eight new ones: *T. flavolineatus* sp. nov., *T. hongkhraiensis* sp. nov. from central and northern Thailand, respectively, *T. moniliformis* sp. nov., *T. retusus* sp. nov., *T. acuminatus* sp. nov., *T. dorsalis* sp. nov., *T. thunghaihin* sp. nov., all from Laos, and *T. punctus* sp. nov. from northern Myanmar. A new record of *T. baenzigeri* Golovatch & Enghoff, 1993, from northern Thailand is given. All these species are richly illustrated, and a modified key to all known species of the genus is also provided.

**Keywords.** Myriapoda, Taxonomy, Thailand, Laos, Myanmar.

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## Introduction

*Tylopus* Jeekel, 1968, has long been recognized as one of the largest and widespread millipede Oriental genera in the entire family Paradoxosomatidae (Likhitrakarn *et al.* 2010). This genus has been reviewed and rediagnosed several times, chiefly in the context of adding new species (Jeekel 1965, 1968; Golovatch & Enghoff 1993; Likhitrakarn *et al.* 2010). One of the most recent updates considers and keys 41 species (Likhitrakarn *et al.* 2010), followed by Nguyen (2012) who added five new congeners from Vietnam and provided a key and a distribution map to all 13 *Tylopus* known to occur in that country. Liu & Luo

(2013), and Golovatch (2013, 2014) described a few other new *Tylopus* species from southern China. The latest review of *Tylopus* in Thailand (Likhitrakarn *et al.* 2014a) provides a new distribution map and an updated key to all 32 species known to occur in Thailand. As a result, *Tylopus* is currently recognized as the largest genus of Diplopoda in the Oriental realm, comprising 54 described species ranging from southern China (6) to Myanmar (2), Laos (1), Thailand (32) and Vietnam (18).

Almost all *Tylopus* species appear to be confined to high montane forest habitats (Likhitrakarn *et al.* 2014a), usually representing highly local endemics. This genus is readily distinguished from all Sulciferini (Paradoxosomatidae) except *Oxidus* Cook, 1911, by gonopodal postfemoral lamina I being separated from the femorite by a more or less distinct transverse sulcus, from the oligotypic *Oxidus* by the number and location of postfemoral outgrowths or processes (Golovatch & Enghoff 1993). In addition, most of *Tylopus* species show adenostyles (= ventral outgrowths) at least on some of the male legs. Only very few species, e.g., *T. peramatus* Hoffman, 1973, which is quite widespread in northern Thailand (Hoffman 1973; Likhitrakarn *et al.* 2010), demonstrate evident variations in gonopod structure, whereas it is gonopod conformation that provides many of the key characters for species identification.

Numerous *Tylopus* species are found to occur sympatrically in such larger montane areas as Doi Inthanon (10 species) and Doi Suthep national parks (again 10 species, mostly different) (Likhitrakarn *et al.* 2010, 2014a) in Thailand, but the adult, identifiable stages of at least some of them seem to represent distinct phenofaunas restricted to rather short time periods which fail to overlap with others.

The present paper puts on record another eight new species of *Tylopus*, this time from Myanmar, Thailand and Laos, and their distributions are mapped. A new, modified key to all 62 species of the genus is also given.

## **Material and methods**

New material was collected from northern Thailand and southern Laos from 2008 to 2014 by SP and members of the Animal Systematics Research Unit, Chulalongkorn University. Live animals were photographed in the laboratory. Specimens were preserved in 75% ethanol, and morphological investigations were carried out in the laboratory using an Olympus stereo microscope. Scanning electron micrographs (SEM) of gonopods coated with gold were taken using a JEOL, JSM–5410 LV microscope, and returned to alcohol after examination to ultimately be stored in the alcohol collection. Digital images of the specimens were taken in the laboratory and assembled using the “Cell<sup>D</sup>” automontage software of the Olympus Soft Imaging Solution GmbH package. In addition, line drawings of gonopods were also prepared. All holotypes, as well as most of the paratypes, are kept in the Museum of Zoology, Chulalongkorn University (CUMZ), Bangkok, Thailand; some duplicates were also donated to the collections of the Natural History Museum of Denmark, University of Copenhagen, Denmark (ZMUC), the Zoological Museum, State University of Moscow, Russia (ZMUM), and the Naturhistorisches Museum Wien, Austria (NHMW), as indicated in the text. The types of one species from Myanmar were revised using the NHMW collection.

Collecting sites were located by GPS using the WGS84 datum.

The terminology concerning gonopod structure and body characters mostly follows Golovatch & Enghoff (1993) and Likhitrakarn *et al.* (2010).

## Results

### *Taxonomic descriptions*

Class Diplopoda Blainville-Gervais, 1844  
Order Polydesmida Leach, 1814  
Family Paradoxosomatidae Daday, 1889  
Subfamily Paradoxosomatidae Daday, 1889  
Tribe Sulciferini Attems, 1898  
Genus *Tylopus* Jeekel, 1968

*Tylopus flavolineatus* sp. nov.

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Figs 1–3, 26

### Diagnosis

Differs in the presence of middle and lateral yellow stripes on the body, by the sterna bearing evident cones caudally near each coxa, and in ♂ femur 5 showing a large distoventral adenostyle, coupled with the gonopods being rather slender, with a quite large, slightly curved and pointed process **h**.

### Etymology

To emphasize the middle and lateral yellow stripes on the body; adjective.

### Material examined

#### Holotype

THAILAND: ♂, Wat Tham Santisuk, Nong Muang, Lopburi, 15°12'10" N, 100°39'50" E, 145 m a.s.l., 7 Jun. 2008, leg. C. Sutcharit & N. Likhitrakarn (CUMZ).

#### Paratypes

THAILAND: 2 ♂♂, 2 ♀♀ (CUMZ), same data as for holotype.

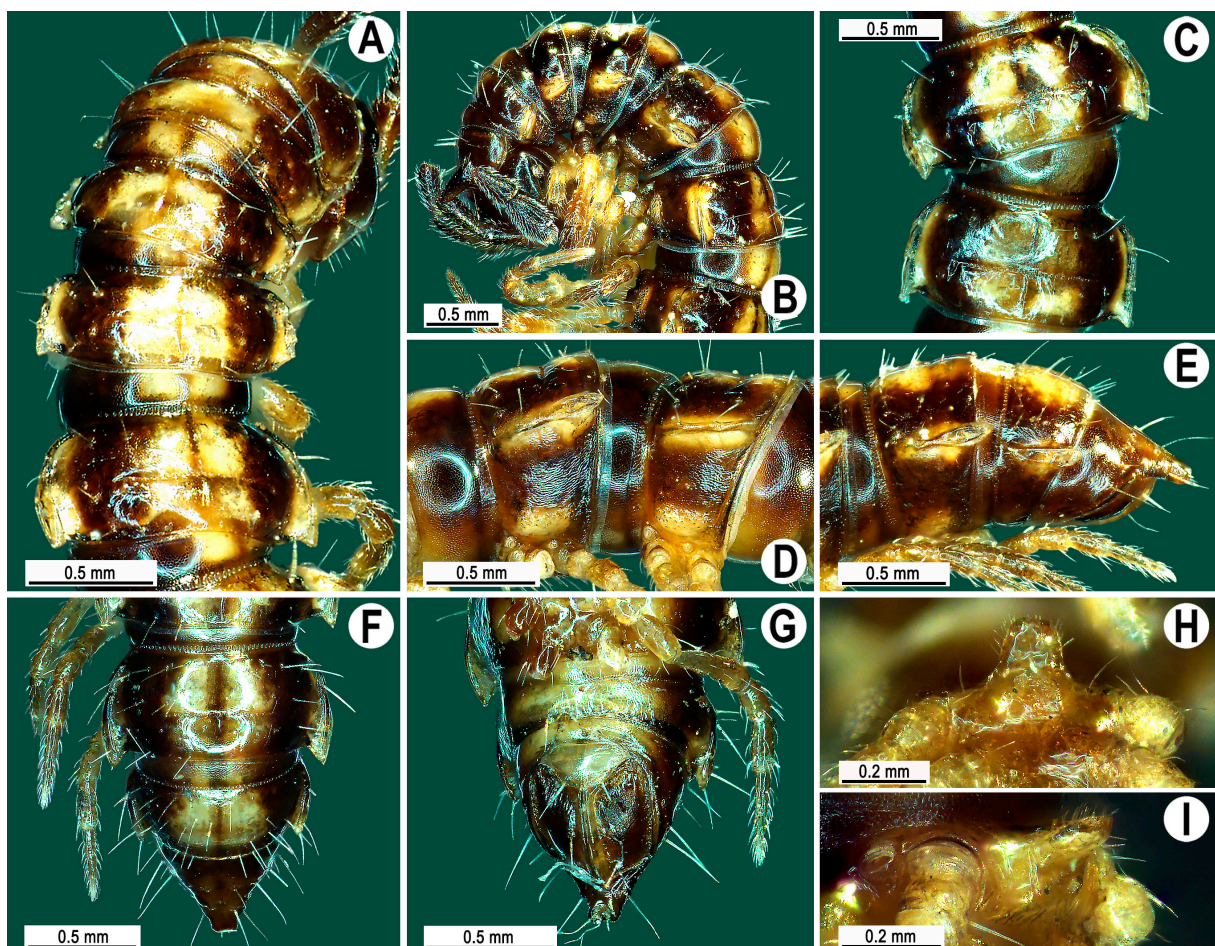
### Description

MEASUREMENTS AND COLOUR. Length 13.8–16.4 (♂) or 14.2–16.5 mm (♀), width of midbody pro- and metazonae 0.83–0.92 and 1.21–1.33 mm (♂) or 1.19–1.28 and 1.68–1.73 mm (♀), respectively. Coloration of alcohol material after six years of preservation dark brown; a pair of paramedian longitudinal stripes flanking a narrow, sometimes vague, brown, axial line; paraterga and area of pleurosternal carinae contrasting light yellow to yellowish; legs and venter dark brown to dark yellow (Fig. 1).

HEAD. Clypeolabral region densely, vertex sparsely, setose; epicranial suture distinct. Antennae rather short (Fig. 1B), clavate (antennomere 6 highest), extending behind body segment 3 (♂) or 2 (♀) when stretched dorsally. In width, segment 2 = 3 < head < collum < segment 4 < 5–15; thereafter body gently and gradually tapering. Collum with three transverse rows of very small setigerous tubercles: 6+6 anterior, 4+4 intermediate and 5+5 posterior; with a small lateral denticle at about 1/3 collum length in front of caudal corner; the latter very broadly rounded anteriorly, declined ventrad, caudal corner not surpassing rear tergal margin.

BODY. Tegument smooth and shining, prozonae and surface below paraterga largely finely shagreened, metaterga rather smooth and leathery, posterior halves faintly rugulose, surface below paraterga finely microgranulate (Fig. 1A–G). Postcollum metaterga with four transverse rows of very small setigerous tubercles or setae: an anterior transverse row of 4–6+4–6, intermediate transverse rows (one pre-sulcus,

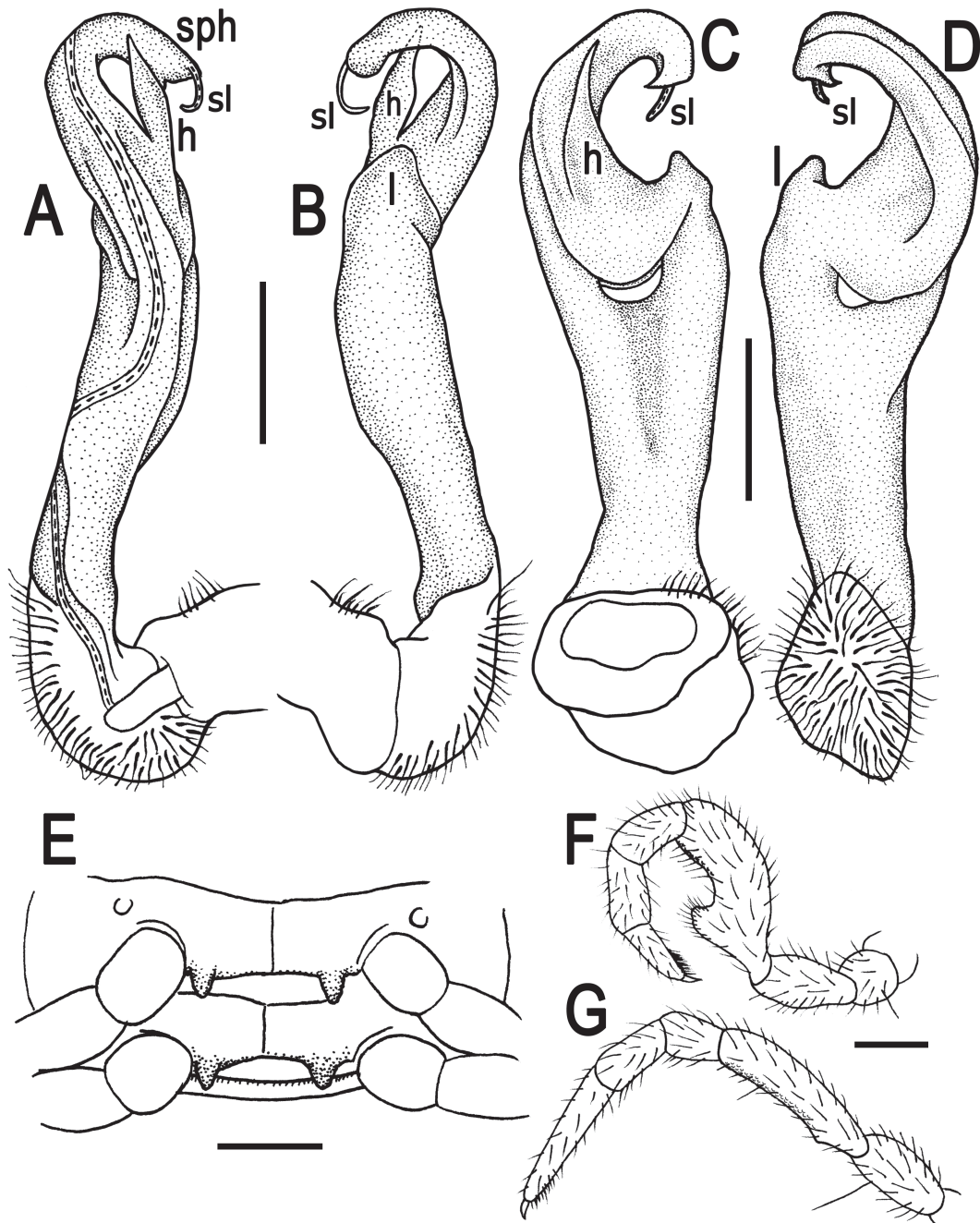
the other post-sulcus) of 3–4+3–4, and a posterior transverse row of 5–7+5–7; tergal setae long, strong, slender, about  $\frac{2}{3}$  of metatergal length (Fig. 1A, D, F). Axial line visible both on pro- and metazonae. Paraterga well-developed (Fig. 1A, D, F), especially so in ♂, lying rather high (at upper  $\frac{1}{3}$  of body height), anterior edge rounded and narrowly bordered, fused to callus; caudal corner very narrowly rounded to pointed. Paraterga 2 and 3 each with two evident setigerous incisions at lateral edge (Fig. 1A). Following poreless segments with two evident setigerous incisions; following pore-bearing segments often with one incision in front of pore (Fig. 1C–D). Calluses on paraterga delimited by a sulcus both dorsally and ventrally. Ozopores evident, lateral, lying in an ovoid groove at about  $\frac{1}{4}$  metatergal length in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 1A, D, F), slightly incomplete on segments 4 and 19, complete on segments 5–18, rather wide, line-shaped, rather deep, not reaching bases of paraterga, beaded at bottom. Stricture between pro- and metazonae evident, wide and rather deep, ribbed at bottom down to base of paraterga (Fig. 1A, C–F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2 and 3, thereafter increasingly reduced and broken, remaining as a front bulge and a caudal tooth until segment 10 (♂) or 6 (♀), on following segments retained as a small caudal tooth until segment 18 (♂) or absent starting with segment 7 (♀). Epiproct (Fig. 1E–G) conical, flattened dorsoventrally, with two evident, small, rounded apical papillae; tip subtruncate; pre-apical



**Fig. 1.** *Tylopus flavolineatus* sp. nov., holotype, ♂ (A, C–I), paratype, ♂ (B). A–B. Anterior part of body, dorsal and lateral views, respectively. C–D. Segments 10 and 11, dorsal and lateral views, respectively. E–G. Posterior part of body, lateral, dorsal and subventral views, respectively. H–I. Sternal cones between coxae 4, caudal and sublateral views, respectively.

lateral papillae evident, lying close to tip. Hypoproct roundly subtriangular, setigerous knobs at caudal edge small and well-separated (Fig. 1G).

STERNA. Densely setose, with a small, but evident cone caudally near each coxa, rear cones being a little larger than fore ones (Fig. 2E); an entire, large, tongue-shaped sternal lobe between ♂ coxae 4 (Fig. 1H, I). Legs rather long and slender, midbody ones ca 1.2–1.3 (♂) or 0.9–1.0 (♀) as long as body



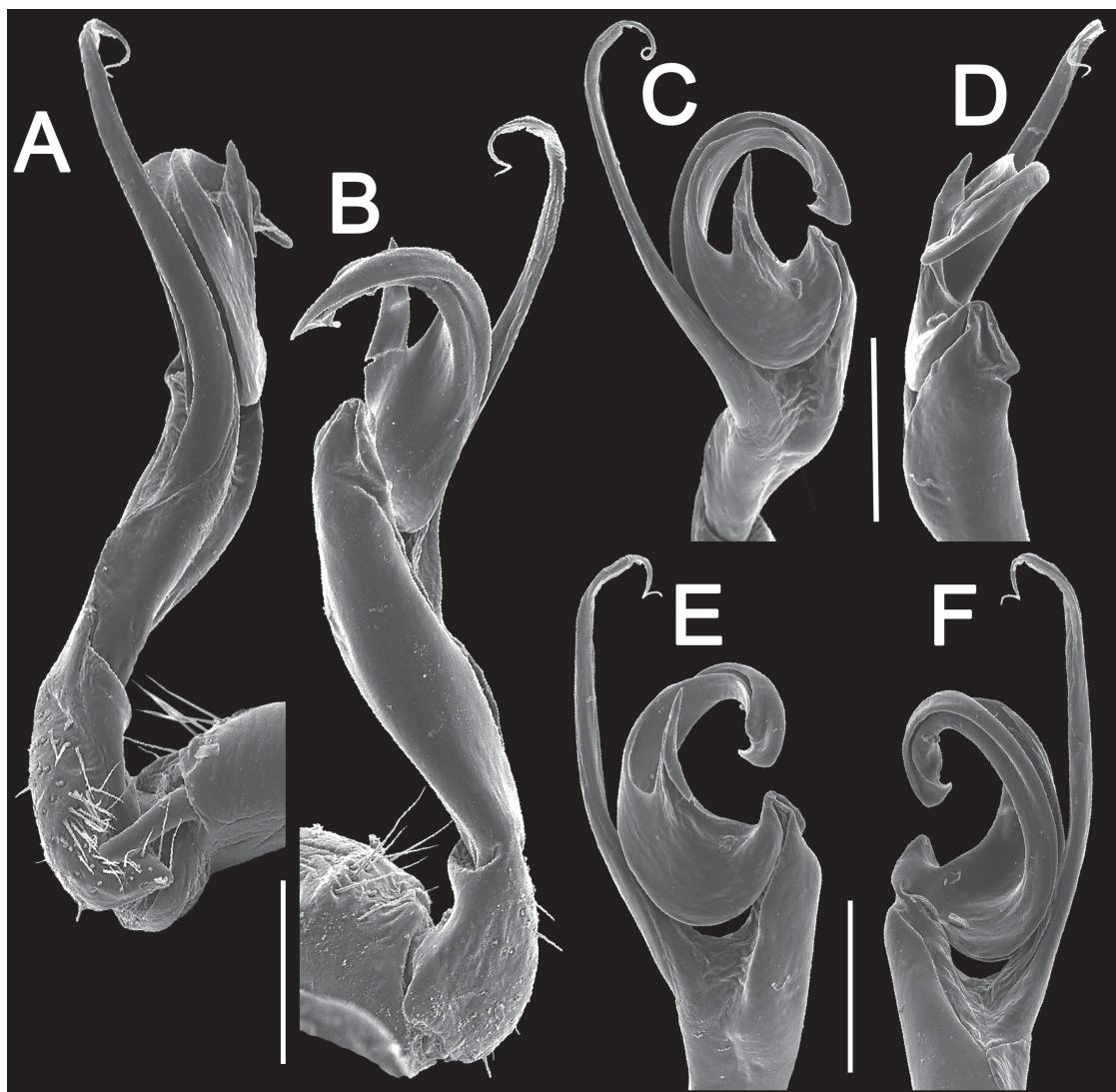
**Fig. 2.** *Tylopus flavolineatus* sp. nov., holotype, ♂, left gonopod. **A–D.** Mesal, lateral, caudal and suboral views, respectively. **E.** Sterna of segment 10. **F.** Leg 6. **G.** Leg 10. Scale bars = 0.5 mm. Abbreviations are explained in the text.

height (Fig. 2G); ♂ femora 5 (Fig. 2F) each with a very strong, distoventral, densely pilose adenostyle in distal 1/3, ♂ prefemora 10–12 each with a small parbasal adenostyle (Fig. 2G); ♂ prefemora 2 until segment 12 each with microgranulations; tarsal brushes present until ♂ leg 6.

GONOPOD. Rather simple (Figs 2A–D, 3); coxa slightly curved caudad, sparsely setose distoventrally. Prefemur as usual, densely setose, about 1/3 as long as femorite + postfemoral part. Femorite slightly curved and rather slender, with an evident mesal groove and a strong distolateral sulcus demarcating a postfemoral part; lobe **I** rather small, rounded apically, process **h** large, slightly curved and pointed; solenophore (**sph**) clearly curved mesad, long, vaguely bifid, lamina medialis supporting a long flagelliform solenomere (**sl**).

#### Remark

In the normal condition, the solenomere is sheathed by the solenophore (Fig. 2A–D), broken off in Fig. 3.



**Fig. 3.** *Tylopus flavolineatus* sp. nov., holotype, ♂, right gonopod. **A–B.** Mesal and lateral views, respectively. **C–F.** Distal part, subcaudal, subcaudal, suboral and sublateral views, respectively. Scale bars = 0.2 mm.

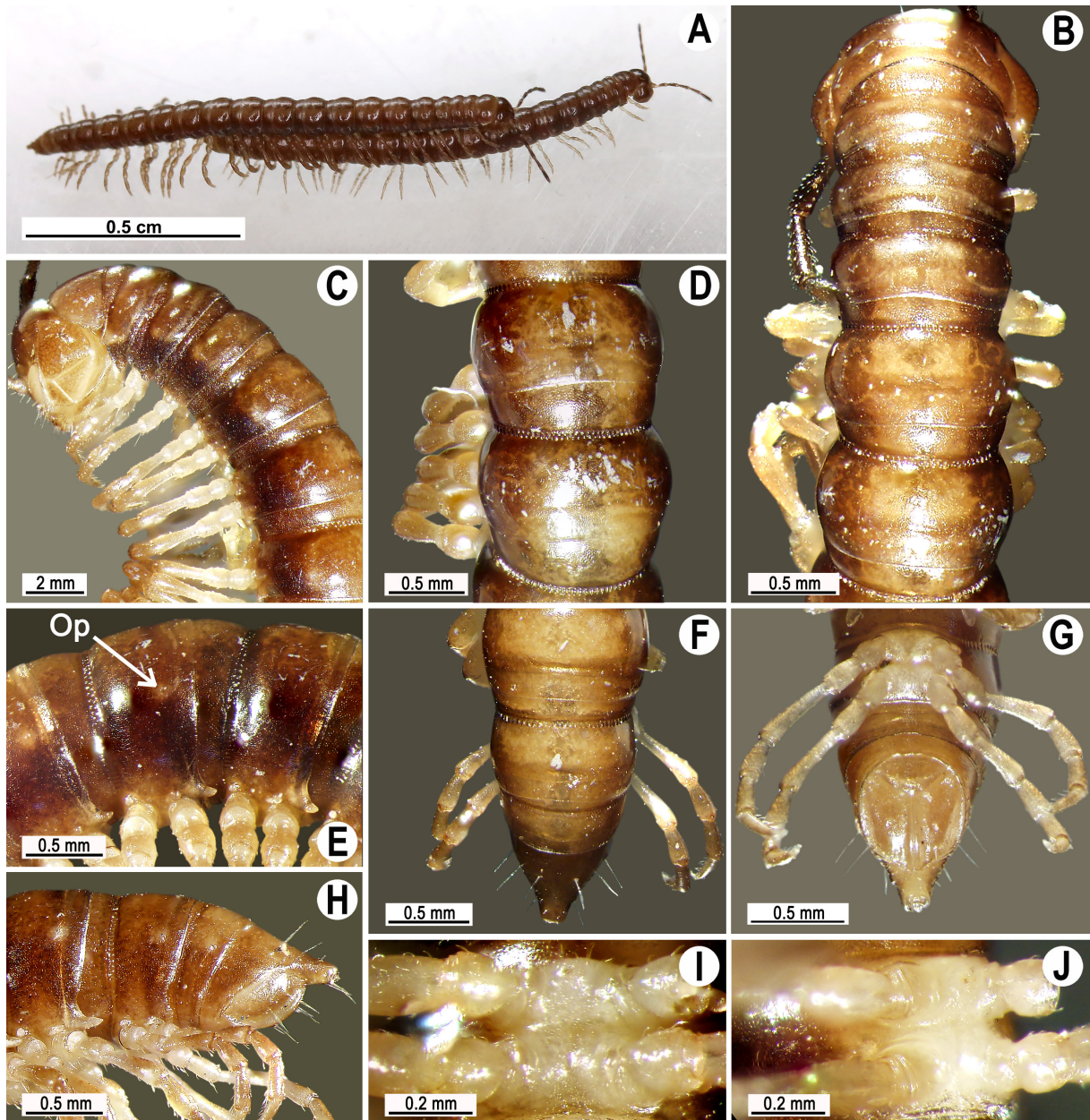
*Tylopus hongkhraiensis* sp. nov.

[urn:lsid:zoobank.org:act:E217CF1E-83D8-4EFD-875B-7C3845D01580](https://zoobank.org/urn:lsid:zoobank.org:act:E217CF1E-83D8-4EFD-875B-7C3845D01580)

Figs 4–6, 26

**Diagnosis**

Differs from all known congeners in the almost missing paraterga, coupled with the gonopod being especially similar to that of *T. magicus* Golovatch, 1984, but differs in process **h** being strong and



**Fig. 4.** *Tylopus hongkhraiensis* sp. nov., holotype, ♂ (B–J), paratypes, ♂, ♀ (A). A. Habitus, live coloration. B–C. Anterior part of body, dorsal and lateral views, respectively. D–E. Segments 10 and 11, dorsal and lateral views, respectively. F–H. Posterior part of body, dorsal, ventral and lateral views, respectively. I–J. Sternal cones between coxae 4, subcaudal and sublateral views, respectively. Abbreviations are explained in the text.

pointed, while process z long, slender and pointed.

### Etymology

The species is named to emphasize the type locality; adjective.

### Material examined

#### Holotype

THAILAND: ♂, Huai Hong Khrai Royal Development Study Centre, Doi Saket, Chiang Mai, 18°52'45" N, 99°12'40" E, ca 420 m a.s.l., 29 Jul. 2015, leg. N. Likhitrakarn (CUMZ).

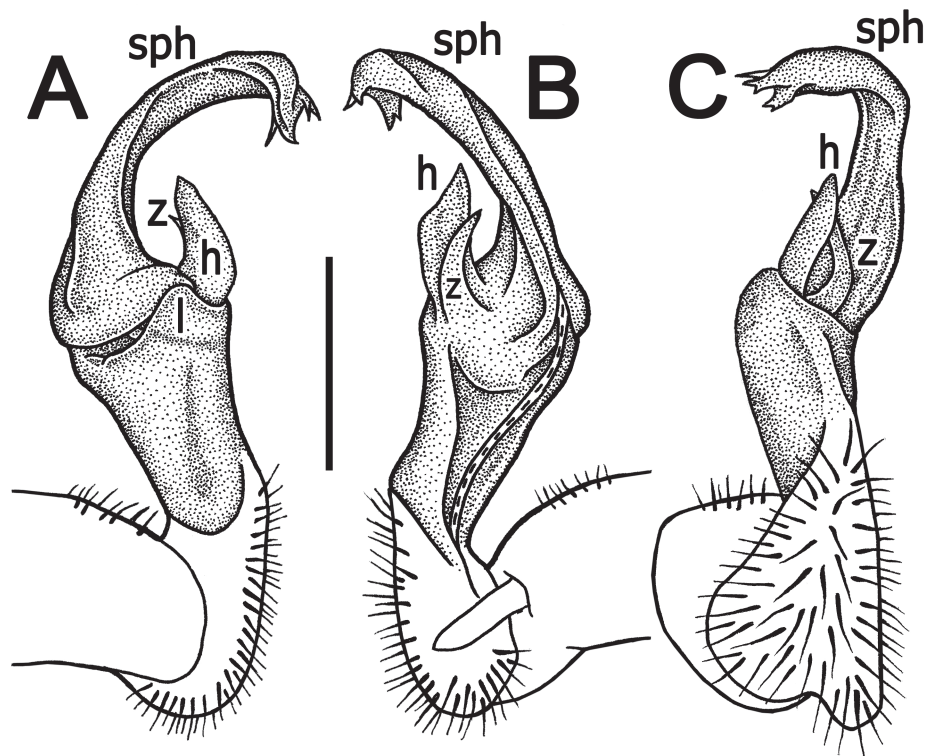
#### Paratypes

THAILAND: 4 ♂♂, 4 ♀♀ (CUMZ); 1 ♂, 1 ♀ (ZMUM ρ3060); 1 ♂, 1 ♀ (ZMUC); 1 ♂, 1 ♀ (NHMW), all same data as for holotype.

### Description

MEASUREMENTS AND COLOUR. Length 11.2–12.8 (♂) or 11.5–12.6 mm (♀), width of midbody pro- and metazonae 0.85–0.96 and 1.04–1.2 mm (♂) or 0.85–1.05 and 1.05–1.32 mm (♀), respectively. Coloration of live animals dark brown (Fig. 4A); legs light brown, venter and a few basal podomeres light brown to yellow-brown. Coloration in alcohol after three months of preservation faded to light brown; antennae and epiproct light brown to pallid, venter and a few basal podomeres light brown to pallid (Fig. 4B–J).

HEAD. Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae rather short (Fig. 4A), surpassing body segment 2 (♂, ♀) when stretched dorsally. In width, segment 3 < 2 < collum < segment 4 < 5 < 6 < 7 < head < 8–17 (♂) or segment 2 < 3 < collum < segment 4 < 5 = 6 < 7 < head <

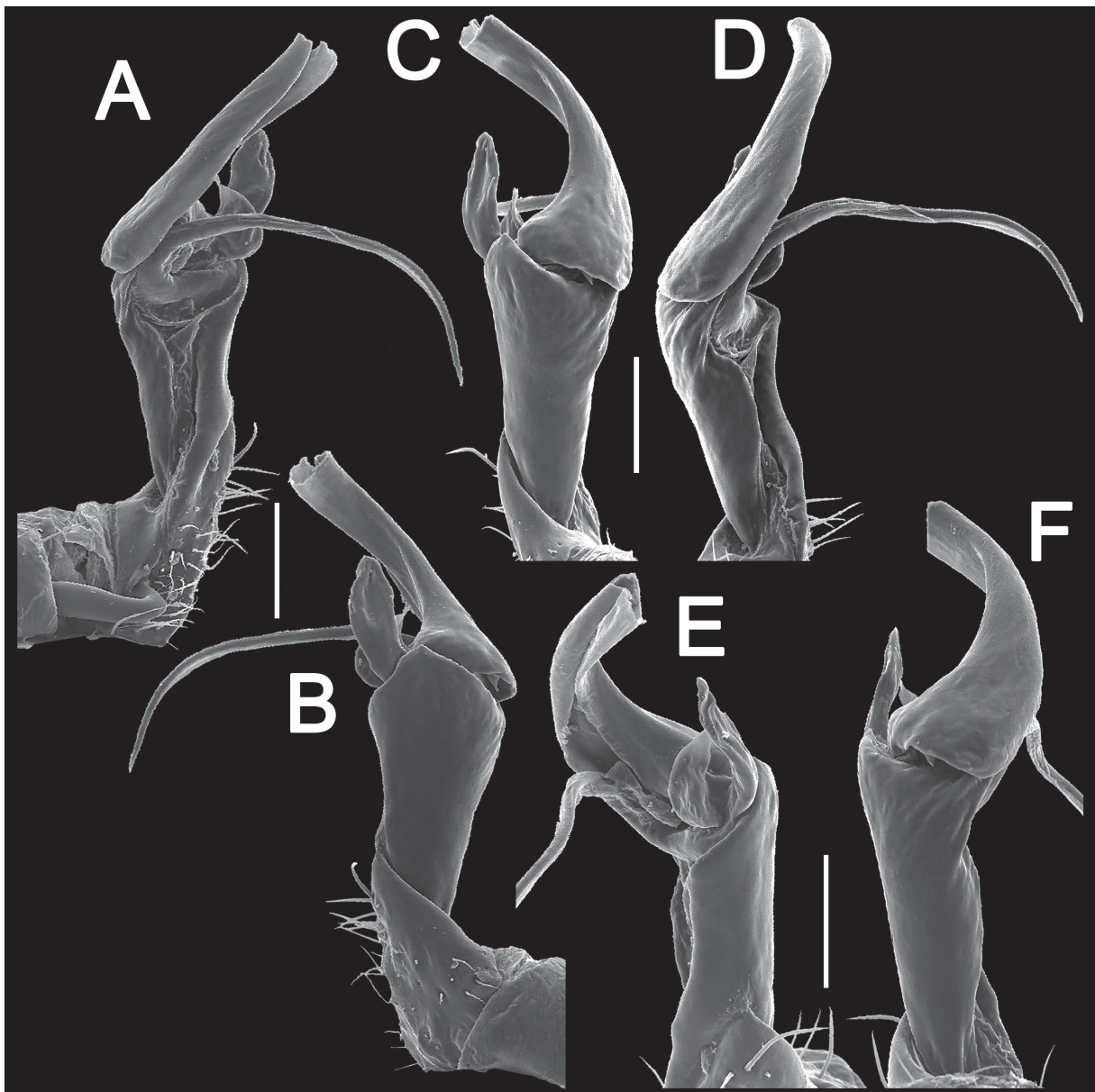


**Fig. 5.** *Tylopus hongkhraiensis* sp. nov., holotype, ♂, right gonopod. A–C. Lateral, mesal and suboral views, respectively. Scale bar = 0.2 mm. Abbreviations are explained in the text.



8–17 (♀); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 3+3 anterior, 2+2 intermediate and 3+3 posterior; caudal corner very narrowly rounded, not surpassing rear tergal margin (Fig. 4B–C).

BODY. Tegument smooth and shining, prozonae very finely shagreened, metaterga nearly smooth, faintly rugulose and leathery (Fig. 4B–F, H). Postcollum metaterga with two transverse rows of setae: 2+2 anterior and 2+2 posterior, traceable at least as insertion points when setae broken off. Tergal setae simple, slender, rather short, about  $\frac{1}{5}$  of metatergal length. Axial line visible, traceable only on metazonae. Postcollum paraterga virtually missing, in pore-bearing segments lateral bulges with ozopores set at about half of midbody height. Ozopores (**Op**) evident (Fig. 4E), lateral, located at about  $\frac{1}{3}$  of metatergal



**Fig. 6.** *Tylopus hongkhraiensis* sp. nov., holotype, ♂, left gonopod. **A–B.** Mesal and lateral views, respectively. **C–F.** Distal part, sublateral, submesal, subboral and subcaudal views, respectively. Scale bars = 0.1 mm.

length in front of posterior edge of metaterga. Transverse sulcus complete on segments 6–16, incomplete on segments 7 and 18 (♂, ♀), very narrow, shallow, not reaching bases of paraterga (Fig. 4B–F, H). Stricture between pro- and metazonae wide, deep, evidently ribbed at bottom down to base of paraterga (Fig. 4B–F, H). Pleurosternal carinae complete crests with a very sharp median tooth on segment 2, increasingly reduced to a rounded caudal crest bulged on segments 2 and 3 (♂, ♀), retained only as an evident, sharp, caudal tooth on segments 5 and 6, thereafter increasingly reduced in size until segment 17, remaining as a small caudal tooth on segment 18 (♂) (Fig. 4C, E, H), or increasingly reduced to caudally roughly granulated bulges on segments 5 and 6, thereafter missing (♀). Epiproct (Fig. 4F–H) conical, flattened dorsoventrally, with two small, but evident, rounded apical papillae; tip subtruncate; lateral pre-apical papillae very small, lying close to tip. Hypoproct roundly subtrapeziform, setigerous knobs at caudal edge small and well-separated (Fig. 4G).

STERNA. Sparsely setose, without modifications; a small, rounded, densely setose sternal cone between ♂ coxae 4 (Fig. 4I, J). A paramedian pair of small tubercles in front of gonopod aperture. Legs rather short, slightly incrassate in ♂, midbody ones ca 1.1–1.3 (♂) or 0.8–0.9 times (♀) as long as body height, prefemora without modifications, ♂ tarsal brushes absent.

GONOPOD. Simple (Figs 5, 6); femorite faintly curved, stout, slightly expanded distad, showing a strong mesal groove; process **h** prominent, slightly curved, pointed; process **z** long and rather slender, evident, likewise curved and pointed; solenophore (**sph**) expanded distally and flattened, typically coiled, clearly bifid, with a pair of small spines.

### Remarks

The millipedes were found mating on bamboo logs on the soil surface during rain. The male was observed walking along the female's back and stimulating her with rhythmic pulses of his legs. The tips of the solenophore and solenomere in Fig. 6 are broken off.

*Tylopus moniliformis* sp. nov.

[urn:lsid:zoobank.org:act:A510843C-08CC-4818-A45F-E35AFDE80E71](https://doi.org/10.21203/rs.3.rs-108433/v1)

Figs 7–9, 26

### Diagnosis

Differs from all known congeners by the almost missing paraterga, much like in *T. hongkhraiensis* sp. nov., coupled with the gonopod structure being similar to that of *T. reductus* Golovatch, 2013, but it differs in the solenophore being more strongly twisted and thicker.

### Etymology

To emphasize the body being strongly bead-shaped, or moniliform; adjective.

### Material examined

#### Holotype

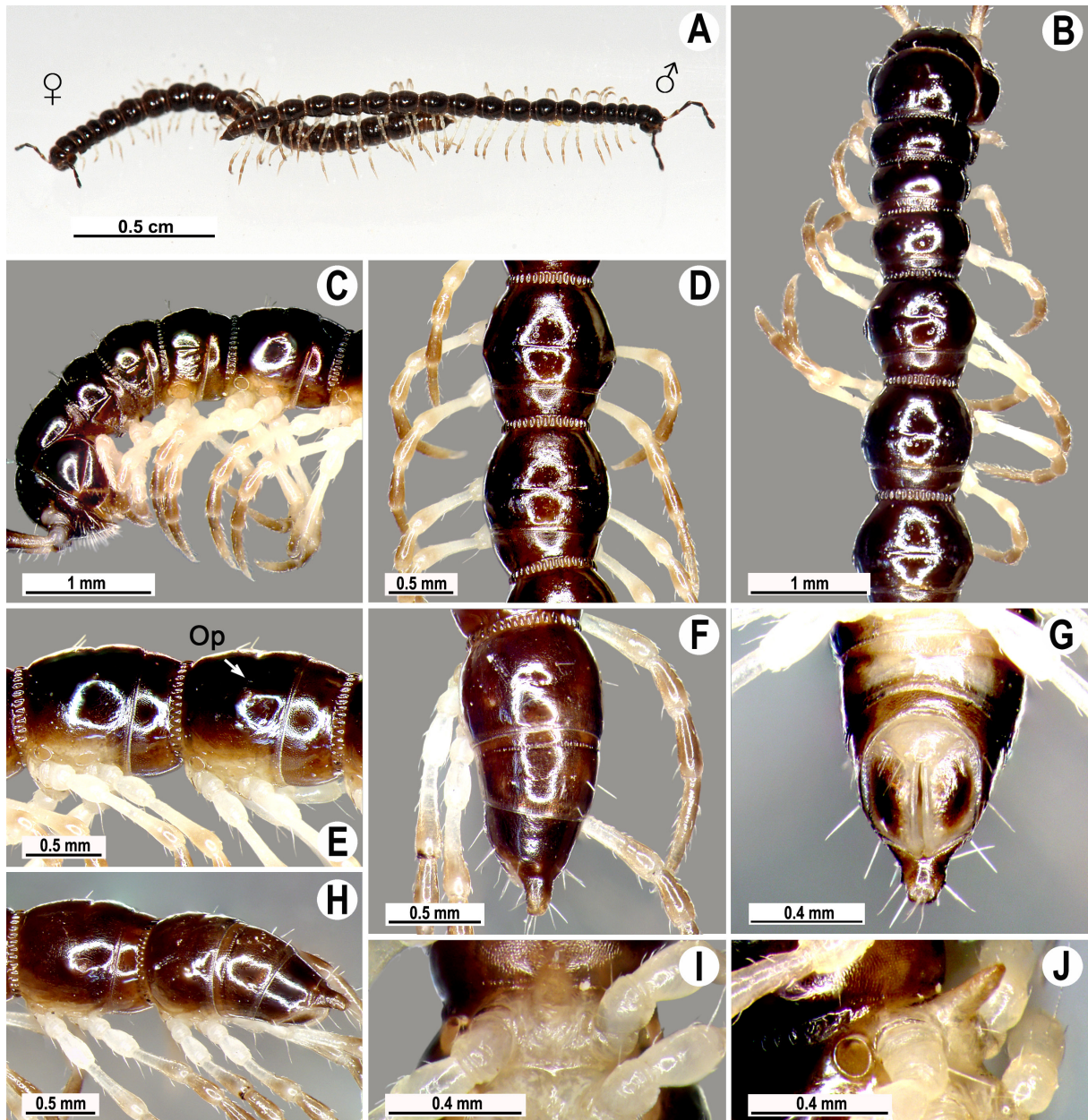
LAOS: ♂, Tad Fane Waterfall, Paksong, Champasak, 15°10'50" N, 106°08'20" E, ca 970 m a.s.l., 20 Jul. 2013, leg. S. Panha, C. Sutcharit, W. Siriwut (CUMZ).

#### Paratypes

LAOS: 2 ♂♂, 8 ♀♀ (CUMZ); 1 ♂, 1 ♀ (ZMUM ρ3061); 1 ♂, 1 ♀ (ZMUC); 1 ♂, 1 ♀ (NHMW), all same data as for holotype.

**Description**

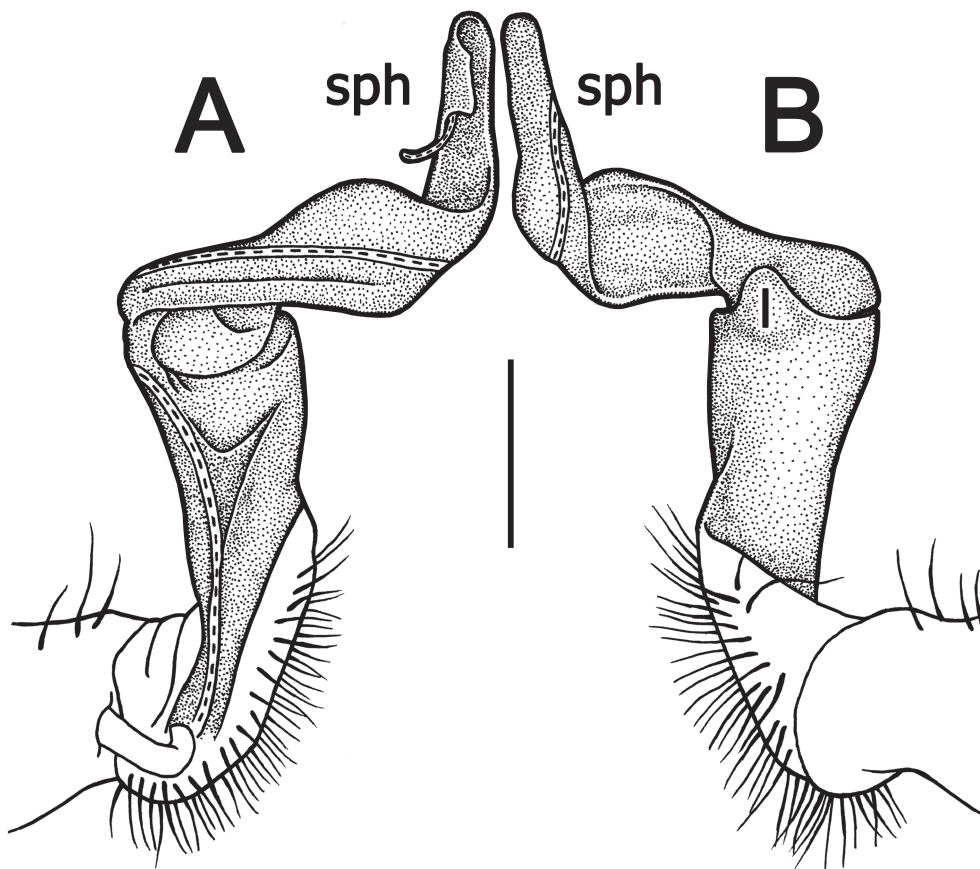
MEASUREMENTS AND COLOUR. Length 14–16 (♂) or 16–18 mm (♀), width of midbody pro- and metazonae 0.6–0.9 and 0.9–1.1 mm (♂) or 0.9–1.2 and 1.2–1.3 mm (♀), respectively. Coloration of live animals dark castaneous brown (Fig. 7A); legs light brown, venter and a few basal podomeres light brown to yellow-brown. Coloration of alcohol material after three months of preservation faded to light brown; antennae and epiproct light brown to pallid, venter and a few basal podomeres light brown to pallid (Fig. 7B–J).



**Fig. 7.** *Tylopus moniliformis* sp. nov., holotype, ♂ (B–J), paratypes, ♂, ♀ (A). A. Habitus, live coloration. B–C. Anterior part of body, dorsal and lateral views, respectively. D–E. Segments 10 and 11, dorsal and lateral views, respectively. F–H. Posterior part of body, subdorsal, ventral and sublateral views, respectively. I–J. Sternal cones between coxae 4, subcaudal and sublateral views, respectively. Abbreviations are explained in the text.

**HEAD.** Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae moderately long (Fig. 7A), surpassing body segment 5 (♂) or reaching body segment 4 (♀) when stretched dorsally. In width, head < segment 4 < 2 = 3 < collum < segment 5 < 6–17 (♂, ♀); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 5+5 anterior, 2+2 intermediate and 1+1 posterior; a very faint marginal incision laterally in posterior 1/3; caudal corner very narrowly rounded, not surpassing rear tergal margin (Fig. 7B–C).

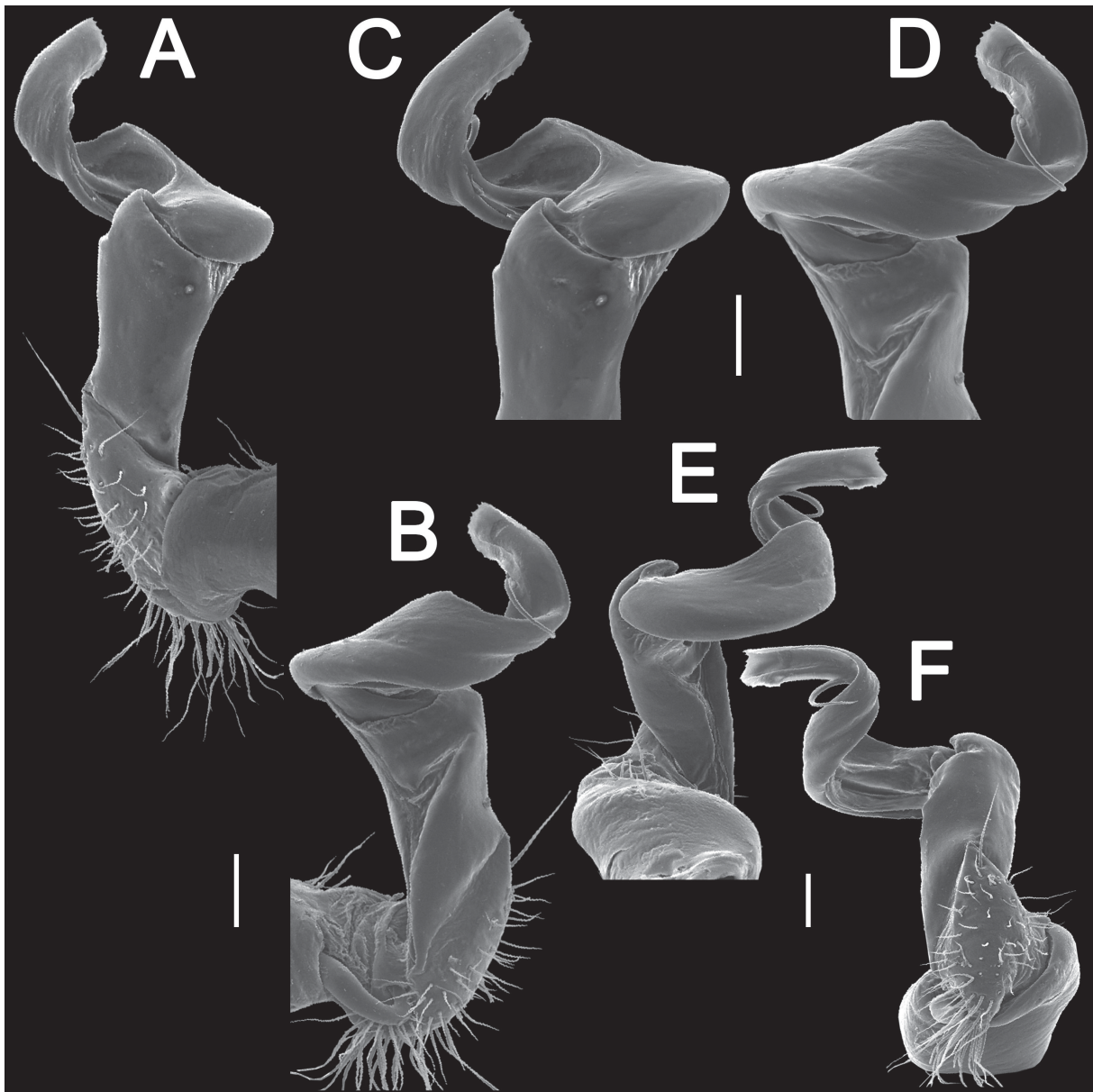
**BODY.** Tegument smooth and shining, prozonae very finely shagreened, metaterga almost smooth, delicately rugulose, leathery (Fig. 7B–F, H). Postcollum metaterga with two transverse rows of setae: 2+2 anterior, always abraded, and 1+1 posterior row, setae traceable at least as insertion points. Tergal setae simple, strong, slender, about 1/3 of metatergal length. Axial line visible, but barely traceable on prozonae (♂). Paraterga 2 well-developed (Fig. 7B, C), horizontal, anterior edges protruded anteriorly, fore corner bent ventrad, pointed; lateral edge with two minute incisions in anterior half; caudal corner very narrowly rounded. Paraterga 3 and 4 rounded, expanded laterally, with two minute incisions only in segment 3. Following paraterga virtually missing (♂) or traceable as small, rounded, laterally expanded bulges (♀), in pore-bearing segments with ozopores set at about half of midbody height. Ozopores (**Op**) evident (Fig. 7E), lateral, lying in an ovoid groove at about 1/3 of metatergal length in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 7B–F, H), slightly incomplete on segment 3, complete on segments 4–18 (♂) or complete on segments 5–18 (♀), always incomplete on segment 19 (♂, ♀), narrow, not reaching bases of paraterga, at most faintly beaded at bottom. Stricture between pro- and metazonae wide, evidently ribbed at bottom down to base of paraterga (Fig. 7B–



**Fig. 8.** *Tylopus moniliformis* sp. nov., paratype, ♂, left gonopod. A–B. Mesal and lateral views, respectively. Scale bar = 0.2 mm. Abbreviations are explained in the text.

F, H). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2 and 3, reduced and remaining a sharp caudal tooth on segment 4, thereafter missing (♂) (Fig. 7C), or thereafter increasingly reduced and remaining a front bulge until segment 18 (♀). Epiproct (Fig. 7F–H) rather short, flattened dorsoventrally, tip subtruncate, subapical lateral papillae small, but visible, lying close to tip. Hypoproct roundly subtriangular, setigerous knobs at caudal edge well-separated and evident.

STERNA. Moderately setose, without modifications; an entire, high, inverted funnel-shaped, sternal lobe each between ♂ coxae 3 and 4 (Fig. 7I–J), lobe being larger between coxae 4. A paramedian pair of evident tubercles in front of gonopod aperture. Legs very long and slender, slightly incrassate



**Fig. 9.** *Tylopus moniliformis* sp. nov., holotype, ♂, left gonopod. **A–B.** Lateral and mesal views, respectively. **C–F.** Distal part, lateral, mesal, subcaudal and suboral views, respectively. Scale bars = 0.1 mm.

in ♂, midbody ones ca 1.5–1.8 (♂) or 1.1–1.4 times (♀) as long as body height, prefemora without modifications, ♂ tarsal brushes absent.

**GONPOD.** Very simple (Figs 8, 9); femorite straight and rather stout, slightly expanded distad, showing a distinct mesal groove, without outgrowths except for a low, sometimes poorly delimited lobe I; solenophore (**sph**) expanded and flattened, typically coiled, suberect distally, devoid of processes.

### Remarks

This species shows the gonopod with lobe **I** separated from the femorite by a rather indistinct sulcus, the presence of the latter lobe being one of the main characteristics of *Tylopus*. Since this locality also yielded the holotype of *Desmoxytes rhinoceros* Likhitrakarn, Golovatch & Panha, 2014 (cf. Likhitrakarn *et al.* 2014b), Tad Fane Waterfall becomes a site quite important for nature conservation, being the type locality of these two millipede species.

### *Tylopus retusus* sp. nov.

[urn:lsid:zoobank.org:act:40D74A7C-61D7-442B-B388-3868C47102C5](https://doi.org/10.2301/40D74A7C-61D7-442B-B388-3868C47102C5)

Figs 10–11, 26

### Diagnosis

Distinguished by its relatively small body with four transverse rows of setae forming no regular pattern of setation; in gonopod structure it is similar to *T. haplorugosus* Golovatch & Enghoff, 1993, but differs in process **h** being rather short, slightly flattened, blunt, coupled with the solenophore being strongly coiled.

### Etymology

To emphasize the blunt tip of process **h**; adjective.

### Material examined

#### Holotype

LAOS: ♂, Muang Xay City, Xay, Oudomxai, 20°41'00" N, 101°59'05" E, ca 640 m a.s.l., mango garden, 14 Oct. 2014, leg. C. Sutcharit & R. Srisonchai (CUMZ).

#### Paratype

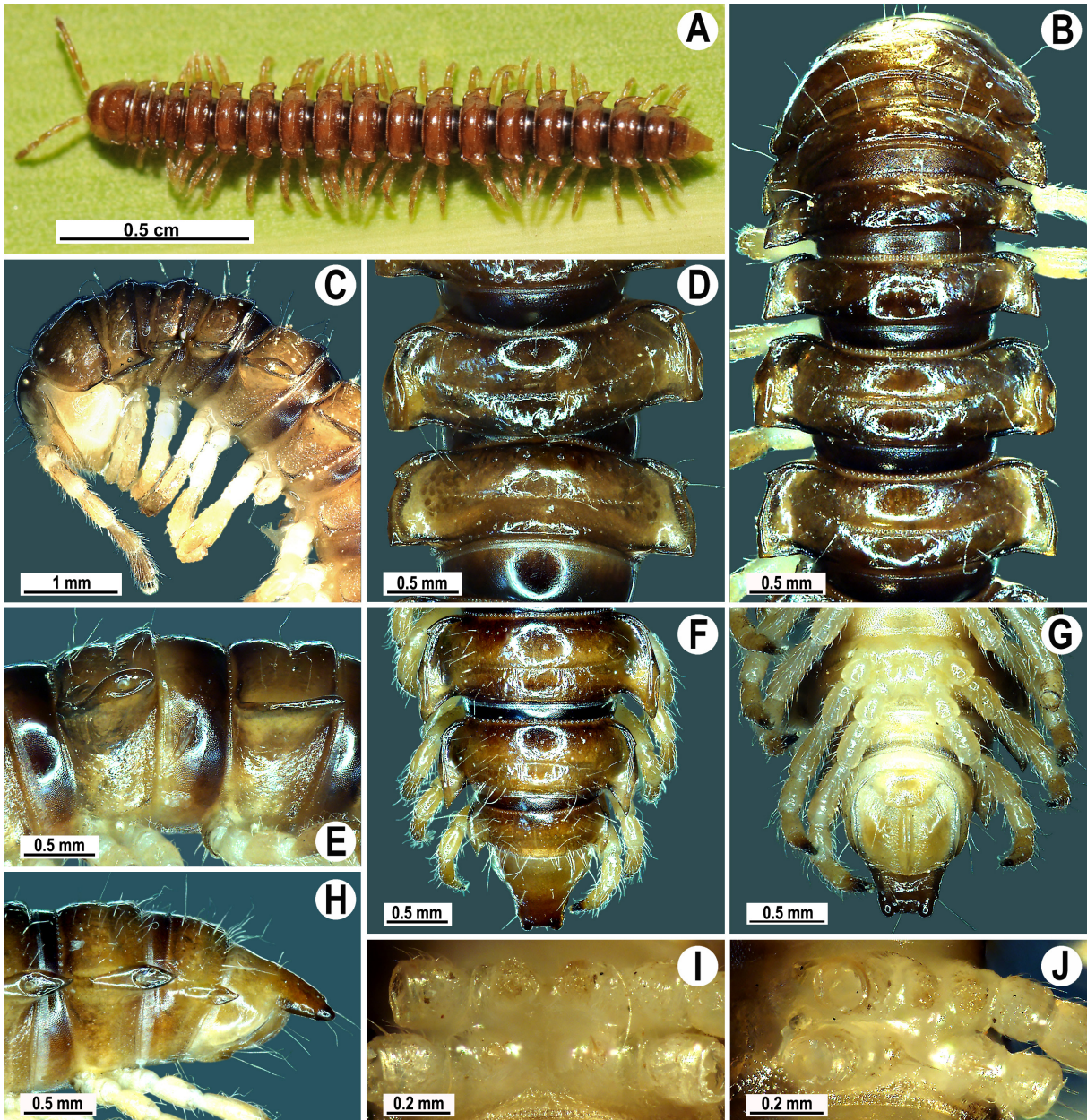
LAOS: 1 ♀, Khoua, Phongsaly, ca 835 m a.s.l., 21°11'55" N, 102°06'40" E, forest near road, 15 Oct. 2014, leg. C. Sutcharit & R. Srisonchai (CUMZ).

### Description

**MEASUREMENTS AND COLOUR.** Length 16.3 (♂) or 20.4 mm (♀), width of midbody pro- and metazonae 1.12 and 2.07 mm (♂) or 2.7 and 3.7 mm (♀), respectively. Live coloration light brown (Fig. 10A); prozonae dark brown; paraterga, antennae, head and legs light brown to yellow-brown. Coloration of alcohol material after one year of preservation faded to light brown to yellow-brown; paraterga, antennae, head, legs and venter light brown to light yellow (Fig. 10B–J).

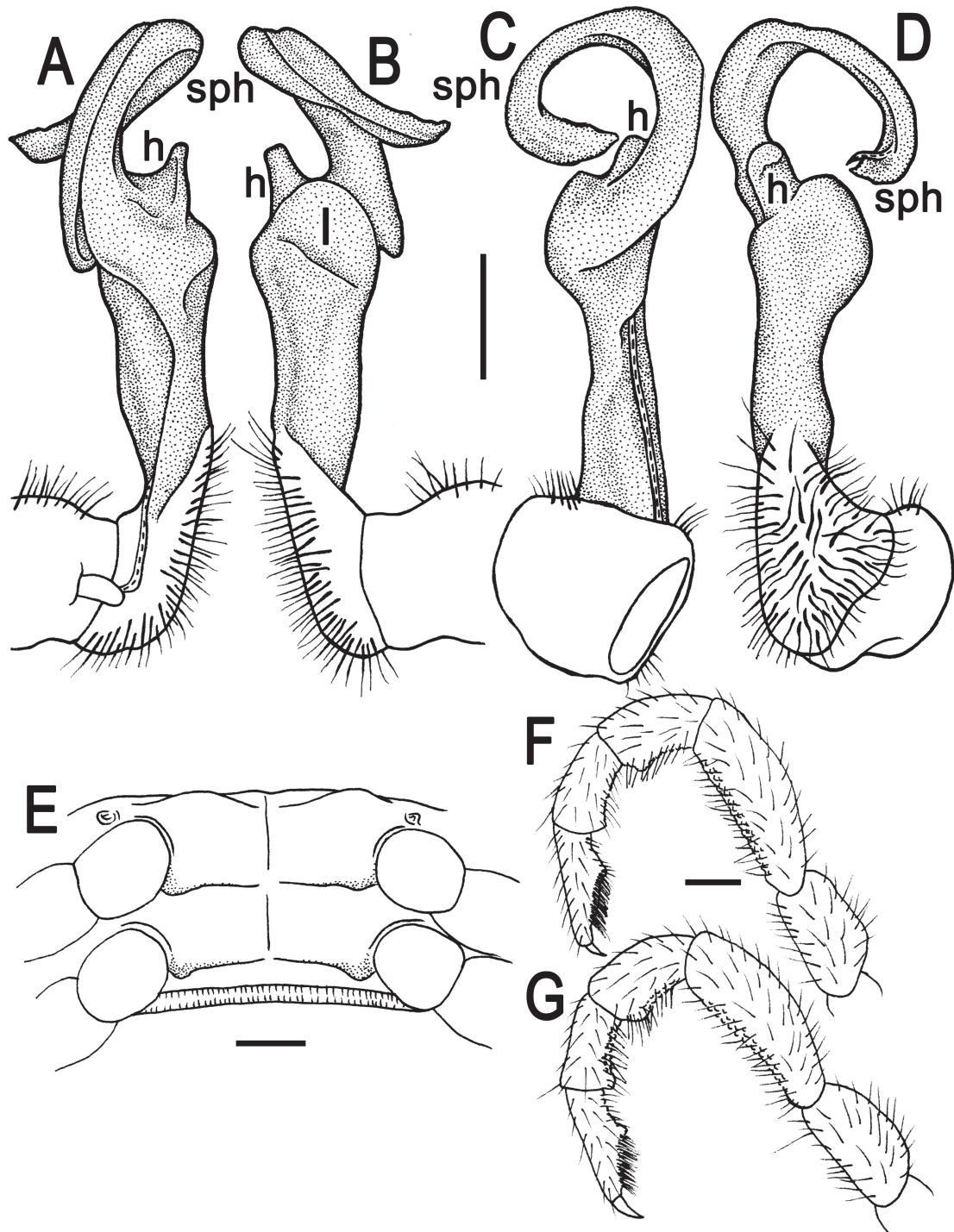
**HEAD.** Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae (Fig. 10A, B) rather short and stout, antennomeres 2–6 subequal in length, reaching body segment 3 (♂, ♀) when stretched dorsally. In width, head < segment 3 < 4 < collum < segments 5–15; thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 6+6 anterior, 4+4 intermediate and 6+6 posterior; a small lateral incision at about midway; caudal corner very broadly rounded, paraterga declined ventrad, slightly produced behind rear tergal margin.

**BODY.** Tegument smooth and shining, prozonae finely shagreened, metaterga leathery, finely rugulose (Fig. 10B, D, F); surface below paraterga roughly microgranulate (Fig. 10C, E, H). Postcollum metaterga with four transverse rows of setae forming no regulated pattern of setation, anterior row with the most dense setae growing increasingly dense towards segment 19 (Fig. 10B, D, F). Tergal setae long and slender, about  $\frac{2}{3}$  as long as metaterga. Axial line well visible on metazonae, traceable also on prozonae. Paraterga strongly developed (Fig. 10B–H), especially so in ♂, set rather high (at upper  $\frac{1}{3}$  of body height), slightly upturned, but lying below dorsum; anterior edge broadly rounded and narrowly bordered, fused to callus; caudal corner very narrowly rounded, starting with segment 16 extending



**Fig. 10.** *Tylopus retusus* sp. nov., holotype, ♂. **A.** Habitus, live coloration. **B–C.** Anterior part of body, dorsal and lateral views, respectively. **D–E.** Segments 10 and 11, dorsal and lateral views, respectively. **F–H.** Posterior part of body, dorsal, ventral and lateral views, respectively. **I–J.** Sternal cones between coxae 4, caudal and sublateral views, respectively.

increasingly behind rear tergal margin (Fig. 10F, H). Paraterga 2 and 3 with two evident incisions at lateral edge (Fig. 10B). Following poreless segments with two similar incisions; pore-boring segments with one, often setigerous incision lying in front of pore (Fig. 10D, E). Calluses of paraterga delimited



**Fig. 11.** *Tylopus retusus* sp. nov., holotype, ♂, left gonopod. **A–D.** Mesal, lateral, subcaudal and suboral views, respectively. **E.** Sterna of segment 10. **F.** Leg 6. **G.** Leg 10. Scale bars = 0.2 mm. Abbreviations are explained in the text.



by a sulcus both dorsally and ventrally. Ozopores evident, lateral, lying in an ovoid groove at about  $\frac{1}{3}$  of metatergal length in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 10B, D, F), slightly incomplete on segment 19, complete on segments 5–18, narrow, undulate, shallow, not reaching bases of paraterga, beaded at bottom. Stricture between pro- and metazonae evident, wide and deep, beaded at bottom down to base of paraterga (Fig. 10B, D–F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–7 (♂) or 2–4 (♀), thereafter increasingly reduced to a small tooth until segment 15 (♂) or 13 (♀), missing more caudally. Epiproct (Fig. 10F–H) conical, flattened dorsoventrally, with two evident, large, rounded apical papillae; tip subtruncate; lateral pre-apical papillae small, lying close to tip. Hypoproct (Fig. 10G) roundly subtrapeziform, setigerous knobs at caudal edge small and well-separated.

**STERNA.** Densely setose, with a small cone caudally near each coxa, rear cones being a little larger than fore ones (Fig. 11E); two small, rough, fully separated, setose cones between ♂ coxae 4 (Fig. 10I, J). Legs rather long and slender, midbody ones ca 1.2–1.3 (♂) or 0.9–1.0 (♀) as long as body height; all male legs until segment 16 with tarsal brushes, prefemora not swollen; prefemora, femora and tibiae with ventral microgranulations; femora, tibiae and tarsi each with an evident adenostyle (tubercle) medially (Fig. 11F–G).

**GONOPOD.** Rather simple (Fig. 11A–D); coxa a little curved caudad, sparsely setose distoventrally. Femorite slightly curved and stout, with an evident mesal groove and a clear distolateral sulcus demarcating a postfemoral part; lobe **l** evident, rounded, with process **h** rather short, slightly flattened, blunt; solenophore (**sph**) strongly coiled, devoid of processes, pointed.

### Remark

This species was found in a mango plantation in Muang Xay City.

*Tylopus acuminatus* sp. nov.

[urn:lsid:zoobank.org:act:C0DB482F-EE58-4385-9733-7D2E724DEFED](https://zoobank.org/urn:lsid:zoobank.org:act:C0DB482F-EE58-4385-9733-7D2E724DEFED)

Figs 12–15, 26

### Diagnosis

Very similar to *T. jeekeli* Golovatch & Enghoff, 1993 and *T. parajeekeli* Likhitrakarn, Golovatch, Pratepasen & Panha, 2010, especially in its gonopod conformation, but differs in process **h** being higher and more strongly flattened, pointed, while the sternal lobe between ♂ coxae 4 linguiform and larger.

### Etymology

To emphasize the acuminate processes **h** on the gonopod; adjective.

### Material examined

#### Holotype

LAOS: ♂, Ban Sin Chai, Boun Neua, Phongsali, 21°31'50" N, 101°51'45" E, ca 820 m a.s.l., 15 Oct. 2014, leg. C. Sutcharit & R. Srisonchai (CUMZ).

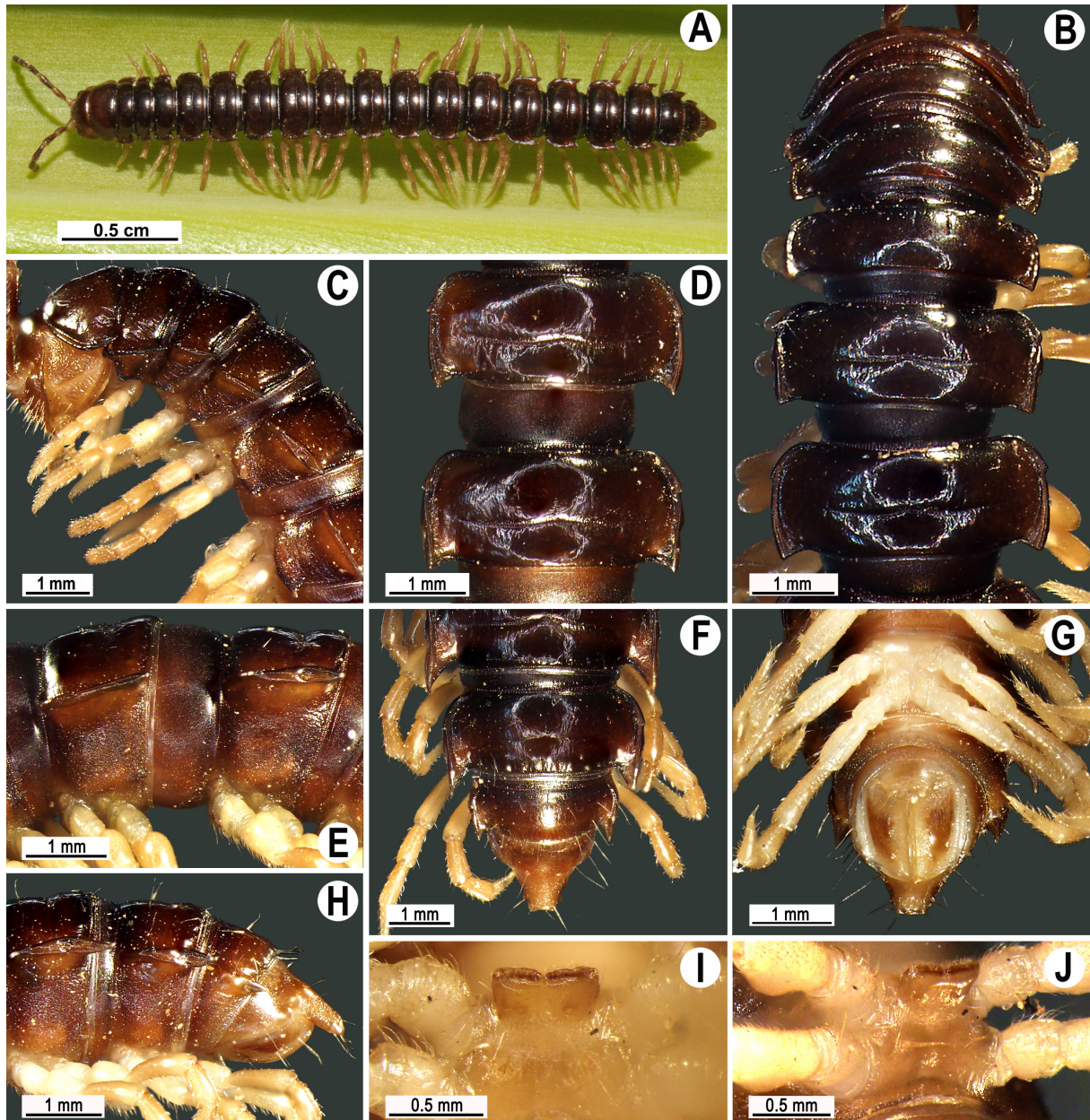
#### Paratypes

LAOS: 1 ♂, 1 ♀, Phuthalang forest protected area, Boun Neua, Phongsali, 21°37'30" N, 101°55'55" E, ca 1125 m a.s.l., 16 Oct. 2014 (CUMZ); 1 ♂, 2 ♀♀, Phufa, Boun Neua, Phongsali, 21°41'05" N, 102°06'35" E, ca 1470 m a.s.l., 16 Oct. 2014 (CUMZ); 1 ♀, near Ban Borkhun, Boun Neua, Phongsali, 21°27'57" N, 101°47'20" E, ca 880 m a.s.l., 18 Oct. 2014 (CUMZ); 1 ♀, Khoua, Phongsali, 21°11'55" N, 102°06'40" E, ca 840 m a.s.l., 15 Oct. 2014 (CUMZ); 1 ♂, 1 ♀ (NHMW), 1 ♂ (ZMUM ρ3059), Ban Na

Thong, Namo, Oudomxay, 20°52'25" N, 101°47'00" E, ca 650 m a.s.l., 14 Oct. 2014; 1 ♂, Phagneung Phoukulom Waterfall, Sing, Luang Namtha, 21°07'15" N, 101°14'40" E, ca 900 m a.s.l., 13 Oct. 2014, all leg. C. Sutcharit & R. Srisonchai (ZMUC).

### Description

MEASUREMENTS AND COLOUR. Length 24.5–31.6 (♂) or 24.3–31.5 mm (♀), width of midbody pro- and metazonae 1.98–2.6 and 2.95–3.6 mm (♂) or 2.7–2.9 and 3.1–4.2 mm (♀), respectively. Live coloration dark brown (Fig. 12A); antennae and epiproct light brown; legs yellow-brown. Coloration of alcohol

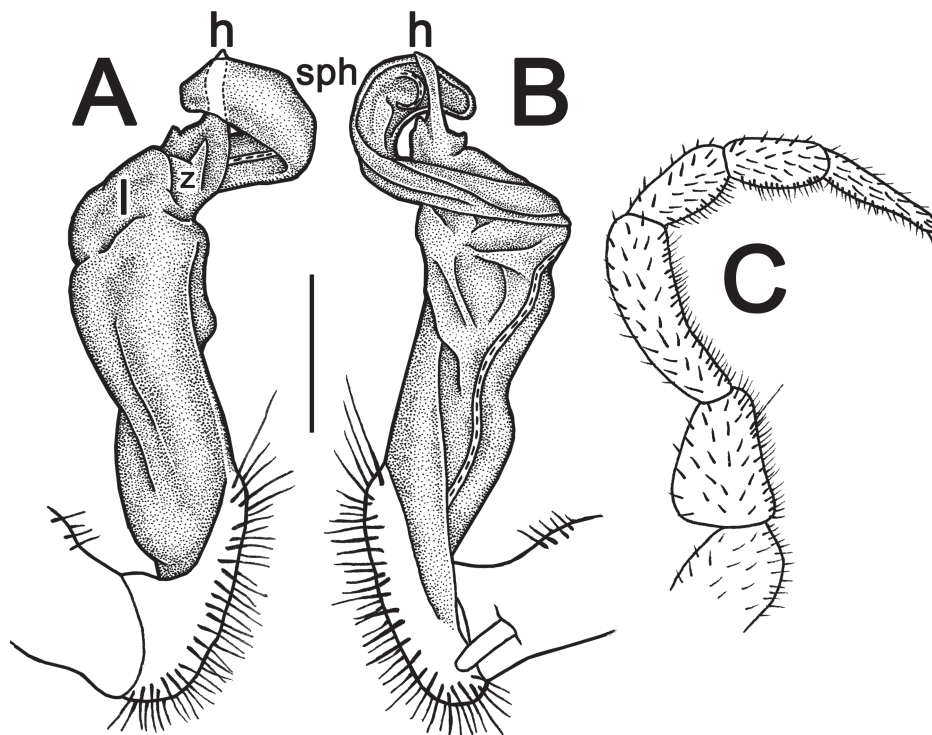


**Fig. 12.** *Tylopus acuminatus* sp. nov., holotype, ♂. **A.** Habitus, live coloration. **B–C.** Anterior part of body, dorsal and lateral views, respectively. **D–E.** Segments 10 and 11, dorsal and lateral views, respectively. **F–H.** Posterior part of body, dorsal, ventral and lateral views, respectively. **I–J.** Sternal cones between coxae 4, caudal and sublateral views, respectively.

material after one year of preservation faded to brown to yellow-brown; head, antennae, epiproct light brown to yellow-brown, legs and venter yellow-brown to light yellow (Fig. 12B–J).

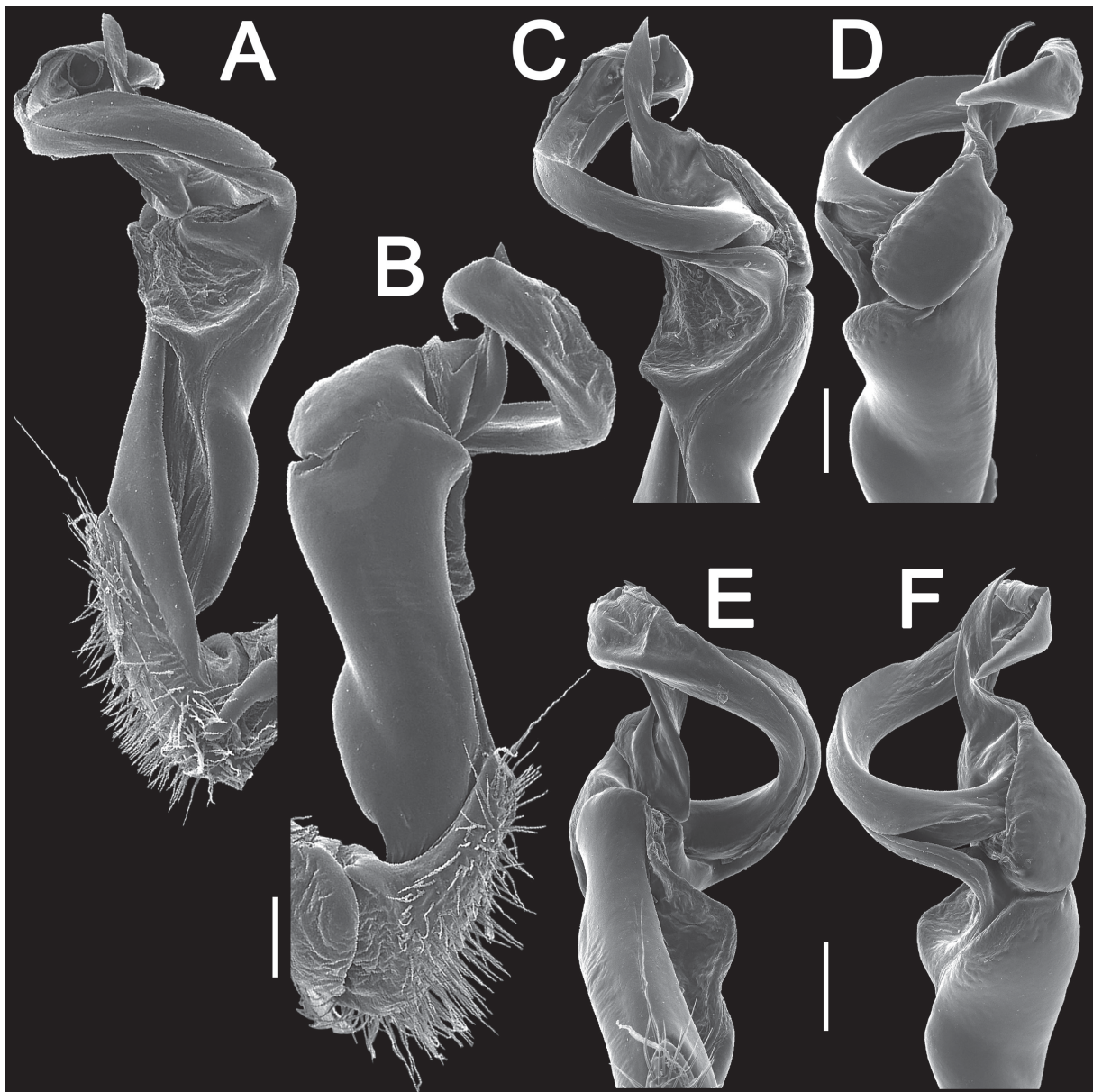
**HEAD.** Clypeolabral region densely, vertex sparsely, setose; epicranial suture distinct. Antennae (Fig. 12A) short, surpassing body segment 2 (♂, ♀) when stretched dorsally. In width, head < segment 3 < collum < segment 4 < 2 < 5–16 (♂), or head < segment 3 < 4 < collum < segment 2 < 5–16 (♀); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 4+4 anterior, 1+1 intermediate and 2+2 posterior paraterga declined ventrad, with a small lateral incision at about midway; caudal corner very broadly rounded, not surpassing rear tergal margin (Fig. 12C).

**BODY.** Tegument smooth and shining, prozonae finely shagreened, metaterga smooth and leathery (Fig. 12B, D, F); surface below paraterga microgranulate (Fig. 12C, E, H). Postcollum metaterga with an anterior transverse row of 2+2, mostly abraded setae; posterior row barely traceable as 4+4 insertion points, these being better visible on segments 17–19 (Fig. 12F). Tergal setae simple and slender, about  $\frac{2}{3}$  as long as metaterga. Axial line traceable on prozonae and anterior halves of metazonae. Paraterga well-developed (Fig. 12B–F, H), especially so in ♂, set rather high (at upper  $\frac{1}{3}$  of body height), slightly upturned, but lying below dorsum; anterior edge broadly rounded and narrowly bordered, fused to callus; caudal corner very narrowly rounded, drawn behind tergal margin, increasingly protruding and pointed starting with segment 16 (Fig. 12F, H). Paraterga 2 with two evident incisions at lateral edge in anterior  $\frac{1}{3}$ . Paraterga 3 and 4 each with two similar incisions at lateral edge, one in anterior  $\frac{1}{3}$ , the other about the middle. Following paraterga each with one evident lateral incision in anterior  $\frac{1}{3}$  and, in pore-bearing segments, a very small denticle in the middle (Fig. 12B, D, F). Calluses on paraterga delimited by a sulcus both dorsally and ventrally. Ozopores evident, lateral, lying in an ovoid groove



**Fig. 13.** *Tylopus acuminatus* sp. nov., holotype, ♂, right gonopod. **A–B.** Lateral and mesal views, respectively. **C.** Leg 13. Scale bar: A–B. 0.5 mm; C = no scale bar. Abbreviations are explained in the text.

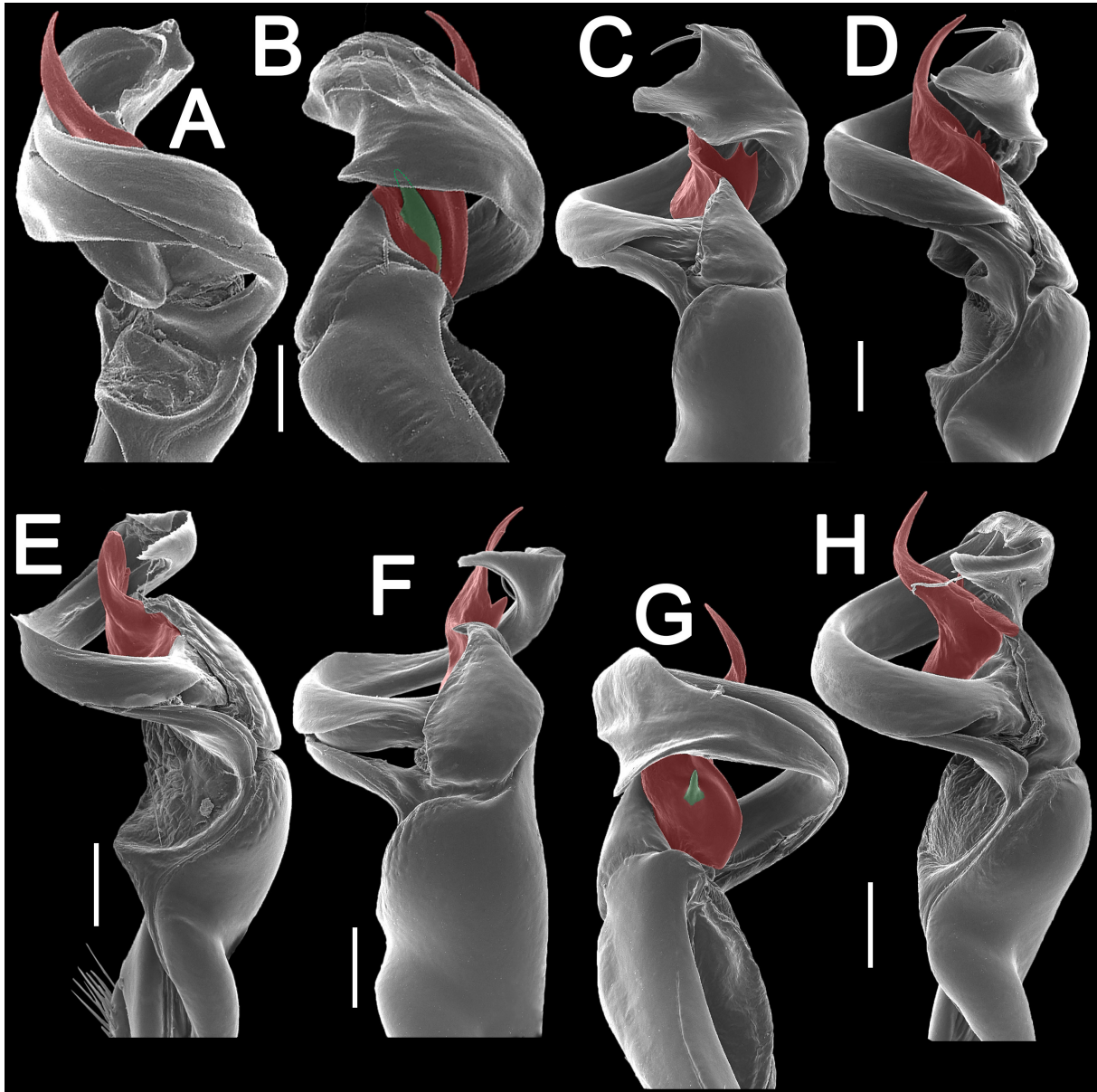
at about  $\frac{1}{3}$  of metatergal length in front of posterior edge of metaterga. Transverse sulcus evident on metaterga 5–17, incomplete on metaterga 18, narrow, line-shaped, rather deep, ribbed at bottom, not reaching bases of paraterga (Fig. 12B, D, F). Stricture between pro- and metazonae evident, wide and deep, ribbed at bottom down to base of paraterga (Fig. 12B, D–F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2 and 3 (♂, ♀), increasingly reduced and remaining a strong, sharp, caudal tooth on segments 4–8, retained as a small sharp tooth on segments 9–16, a minute tooth on segment 17 (♂), or an evident, sharp, caudal tooth on segments 4–15, then remaining a small rounded tooth on segment 16, thereafter missing (♀) (Fig. 12C, E, H). Epiproct (Fig. 12F–H) conical, flattened dorsoventrally, with two evident, rounded, apical papillae; tip subtruncate; lateral pre-apical papillae



**Fig. 14.** *Tylopus acuminatus* sp. nov., holotype, ♂, right gonopod. **A–B.** Mesal and lateral views, respectively. **C–F.** Distal part, sublateral, submesal, subcaudal and suboral views, respectively. Scale bars = 0.2 mm.

evident, lying close to tip. Hypoproct (Fig. 12G) roundly subtrapeziform, setigerous knobs at caudal edge small and well-separated.

STERNA. Moderately setose and densely microtuberculate; cross-impressing shallow; an entire, linguiform, sternal lobe between ♂ coxae 4 (Fig. 12I–J). A paramedian pair of conspicuous ridges in front of gonopod aperture. Legs rather long and slender, midbody ones ca 1.2–1.3 (♂) or 1.0–1.1 (♀) as long as body height; ♂ legs with prefemora distinctly swollen laterally, acropodites with particularly dense setae ventrally (Fig. 13C), but tarsal brushes absent.



**Fig. 15.** *Tylopus acuminatus* sp. nov., paratype, ♂, from Phufa (A–B), paratype, ♂, from Phuthalang forest protected area (C–D), paratype, ♂, from forest near road (E), paratype, ♂, from Ban Na Thong (F), paratype, ♂, from Phagneung Phoukulom waterfall (G–H). A–H. Distal part, sublateral, submesal, dorsal, subdorsal, dorsal, subdorsal, ventral and dorsal views, respectively. Scale bars = 0.2 mm. Red colour shows process **h**. Green colour shows spine **z**.

GONOPOD. Rather simple (Figs 13A–B, 14–15); coxa slightly curved caudad, sparsely setose distoventrally. Femorite slightly curved and stout, with an evident mesal groove and a clear distolateral sulcus demarcating a postfemoral part; process **h** prominent, evidently curved, pointed, with a small, but evident dorsal tooth and sometimes with a small ventral denticle (Fig. 13A–B); spine **z** pointed, sometimes small (Fig. 15G); solenophore (**sph**) large, expanded, flattened and typically coiled.

### Remark

This species shows slight variations in gonopod structure, process **h** often being rather narrow to slightly broader, while spine **z** small to slightly broader (Fig. 15).

*Tylopus dorsalis* sp. nov.

[urn:lsid:zoobank.org:act:EDC8D353-BE43-4D79-8BA4-E23D0FD57CE7](https://doi.org/10.2307/23072307)

Figs 16–17, 26

### Diagnosis

The live coloration is similar to that of *T. trigonum*, but the new species differs in the head and collum being light brown (versus blackish), and the pattern not contrasting (versus contrasting); the gonopod structure is similar to that of *T. crassipes* Golovatch, 1984, but the new species differs in process **x** being longer and its tip rounded dorsally.

### Etymology

To emphasize process **x** on the solenophore arising dorsally; adjective.

### Material examined

#### Holotype

LAOS: ♂, Phuthalang forest protected area, Boun Neua, Phongsali, 21°37'30" N, 101°55'55" E, ca 1125 m a.s.l., 16 Oct. 2014, leg. C. Sutcharit & R. Srisonchai (CUMZ).

#### Paratype

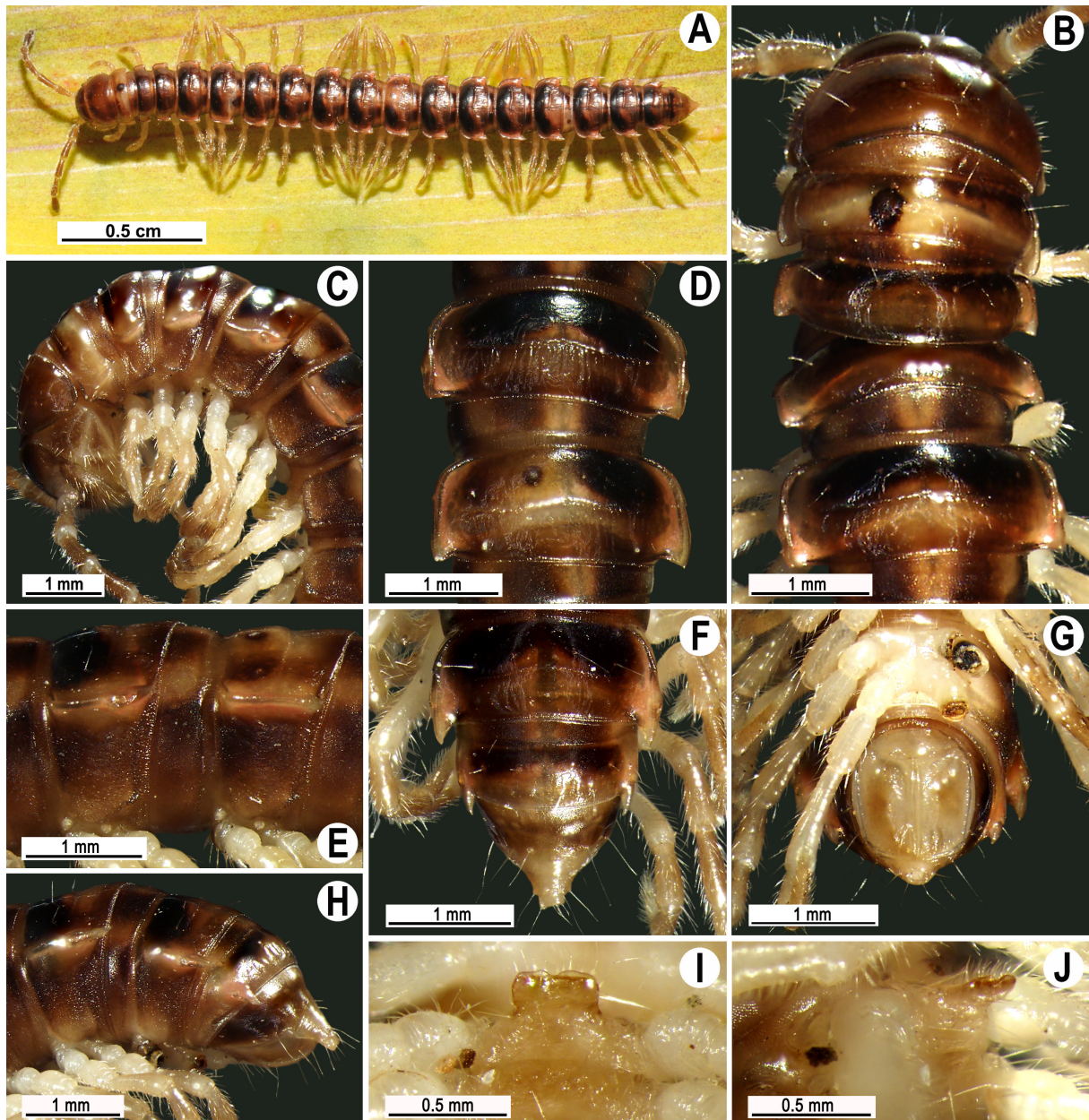
LAOS: 1 ♀, same data as for holotype (CUMZ).

### Description

MEASUREMENTS AND COLOUR. Length 22.1 (♂) or 22.3 mm (♀), width of midbody pro- and metazonae 2.5 and 3.6 mm (♂) or 1.97 and 2.55 mm (♀), respectively. Live coloration light brown (Fig. 16A); paraterga, legs and epiproct light yellow-brown, head and collum light brown, antennomere 7 blackish, collum and following terga each with a light brown triangle and a dark brown collar covering both pro- and metazonae. Coloration of alcohol material faded after one year of preservation to light brown, with a pattern of a dark brown band in pre-sulcus area on metazonae and a pair of paramedian, longitudinal, brown stripes dorsally both on pro- and metaterga; paraterga light red-brown, head brown, antennae, legs, venter and epiproct light yellow-brown (Fig. 16B–J).

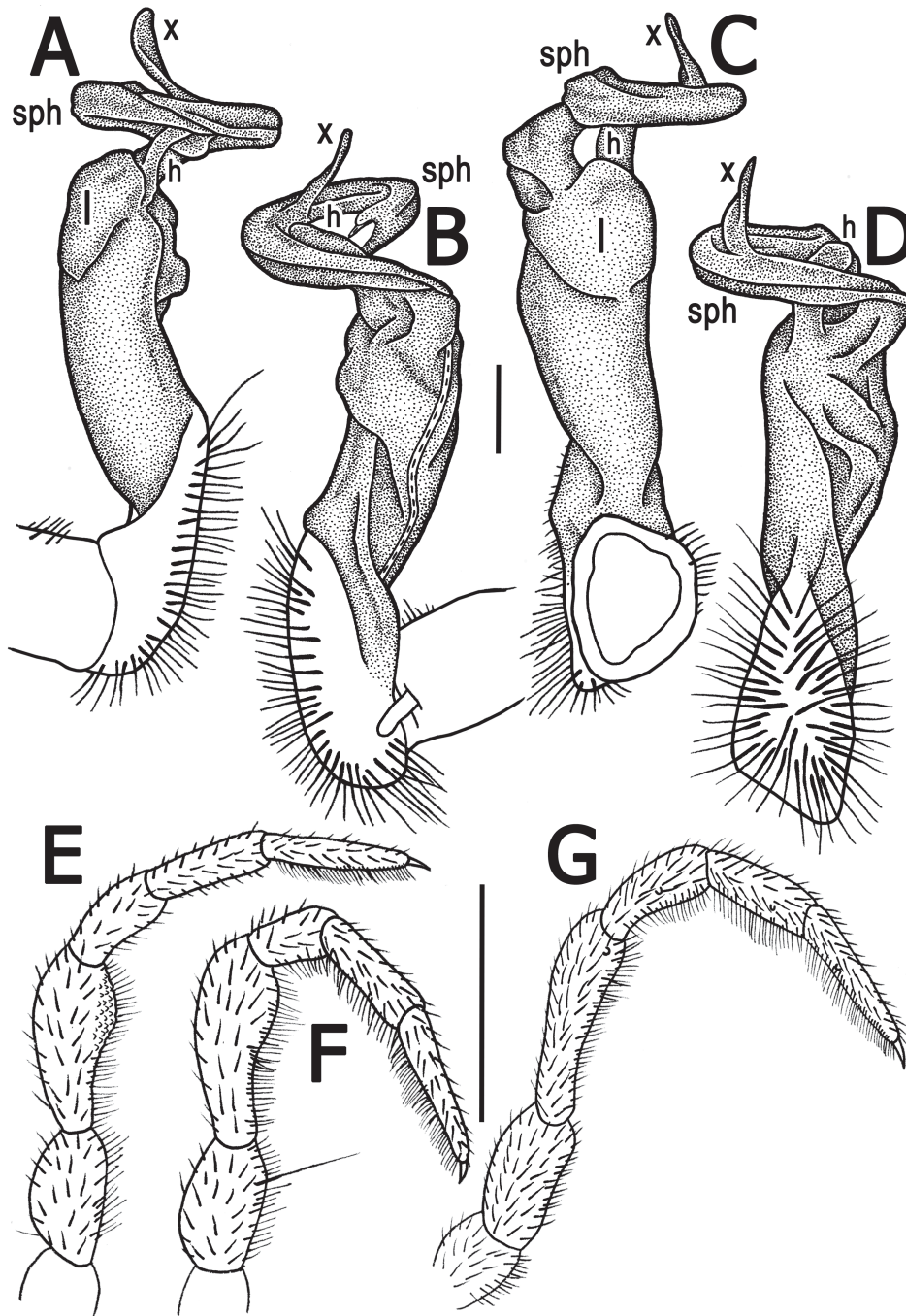
HEAD. Clypeolabral region densely, vertex sparsely, setose; epicranial suture distinct. Antennae rather short (Fig. 16A), extending behind body segment 3 (♂) or 2 (♀) when stretched dorsally. In width, head < segment 3 < 2 = 4 < collum < segments 5–17 (♂, ♀); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 3+3 anterior, 1+1 intermediate and 2+2 posterior; a small lateral denticle at about anterior 1/3 (Fig. 16B, D); caudal corner of paraterga very broadly rounded, declined ventrad, not surpassing rear tergal margin.

**BODY.** Tegument smooth and shining, prozonae finely shagreened, metaterga smooth and leathery, posterior halves rugulose, surface below paraterga microgranulate (Fig. 16B–F, H). Postcollum metaterga with two transverse rows of setae: 2+2 in anterior (pre-sulcus) row, also 2+2 in posterior (post-sulcus) row. Tergal setae long, strong, slender, about  $\frac{2}{3}$  of metatergal length. Axial line traceable both on pro- and metazonae. Paraterga well-developed (Fig. 16B, D, F), especially so in ♂, set rather high (at upper  $\frac{1}{3}$  of body height), anterior edge rounded and narrowly bordered, fused to callus; caudal corner very narrowly rounded, extending increasingly behind rear tergal margin, posterior edge slightly oblique. Calluses on paraterga delimited by a sulcus only dorsally. Paraterga 2 broad, anterior edge angular, lateral edge with



**Fig. 16.** *Tylopus dorsalis* sp. nov., holotype, ♂. **A.** Habitus, live coloration. **B–C.** Anterior part of body, dorsal and lateral views, respectively. **D–E.** Segments 10 and 11, dorsal and lateral views, respectively. **F–H.** Posterior part of body, dorsal, ventral and lateral views, respectively. **I–J.** Sternal cones between coxae 4, caudal and sublateral views, respectively.

three evident incisions. Lateral edge of following paraterga with a clear incision in anterior  $\frac{1}{3}$  (Fig. 16B, D). Paraterga 14–19 with caudal corner extending increasingly behind, with tip evidently curved mesad (Fig. 16F). Ozopores distinct, lateral, lying in an ovoid groove at about  $\frac{1}{3}$  of metatergal length in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 16B, D, F), slightly incomplete on segment 3, complete on segments 4–18, narrow, line-shaped, deep, not reaching bases of paraterga, beaded at bottom. Stricture between pro- and metazona evident, wide, rather deep, clearly ribbed at bottom down to base of paraterga (Fig. 16B, D–G). Pleurosternal carinae complete crests with a sharp



**Fig. 17.** *Tylopus dorsalis* sp. nov., holotype, ♂. A–D. Right gonopod, lateral, mesal, caudal and oral views, respectively. Scale bars = 0.2 mm. Abbreviations are explained in the text.



caudal tooth on segments 2–7, reduced and remaining only a sharp caudal tooth on segment 8, reduced to a small, delicately denticulate, caudal crest on segments 9–15, retained as a minute tooth on segment 16, thereafter missing (♂), or with complete crests and a sharp caudal tooth on segments 2–4, remaining only an evident caudal tooth on segments 5–12, a rounded caudal crest on segments 13–17, thereafter missing (♀) (Fig. 16C, E, H). Epiproct (Fig. 16E–G) conical, flattened dorsoventrally, with two evident, rounded, apical papillae; tip subtruncate; lateral pre-apical papillae evident, lying close to tip. Hypoproct roundly subtriangular, setigerous knobs at caudal edge small and well-separated (Fig. 16G).

STERNA. Sparsely setose, without modifications; cross-impressions shallow; an entire, linguiform, sternal lobe between ♂ coxae 4 (Fig. 16I–J). Legs long and slender, midbody ones ca 1.3–1.4 (♂) or 0.9–1.1 (♀) as long as body height; ♂ femora 6 bulged and microtuberculate ventrally (Fig. 17E); ♂ femora 7 also bulged ventrally (Fig. 17F), but following femora not swollen; legs of segments 7–16 each with femur, postfemur, tibia and tarsus carrying a small adenostyle (tubercle) medially (Fig. 17G), telopodites particularly densely setose ventrally (Fig. 17G), tarsal brushes present until ♂ segment 6.

GONPOD. Rather simple (Fig. 17A–D); coxa slightly curved caudad, sparsely setose distoventrally. Femorite slightly curved and stout, with an evident mesal groove and a clear distolateral sulcus demarcating a postfemoral part; process **h** rather high, directed anterodorsally, flattened, tip rounded; solenophore (**sph**) rather slender, strongly coiled, flattened and evidently bifid, with process **x** being slim and directed dorsally.

*Tylopus thunghaihin* sp. nov.

[urn:lsid:zoobank.org:act:D8C75297-3063-4B15-ADA6-D86AD5796B96](https://zoobank.org/act:D8C75297-3063-4B15-ADA6-D86AD5796B96)

Figs 18–20, 26

**Diagnosis**

The new species seems to be especially similar to *T. nodulipes* (Attems, 1953), but differs in the body tegument being dull, coupled with gonopodal process **m** smaller, process **z** high and rounded, and process **x** pointed.

**Etymology**

To emphasize the type locality, in Lao “Thung Hai Hin”, commonly translated as the famous Plain of Jars, a noun in apposition.

**Material examined**

**Holotype**

LAOS: ♂, Plain of Jars, Xieng Khouang, 19°25'50" N, 103°09'15" E, ca 1100 m a.s.l., 26 Nov. 2014, leg. S.I. Golovatch, C. Sutcharit, N. Likhitrakarn (CUMZ).

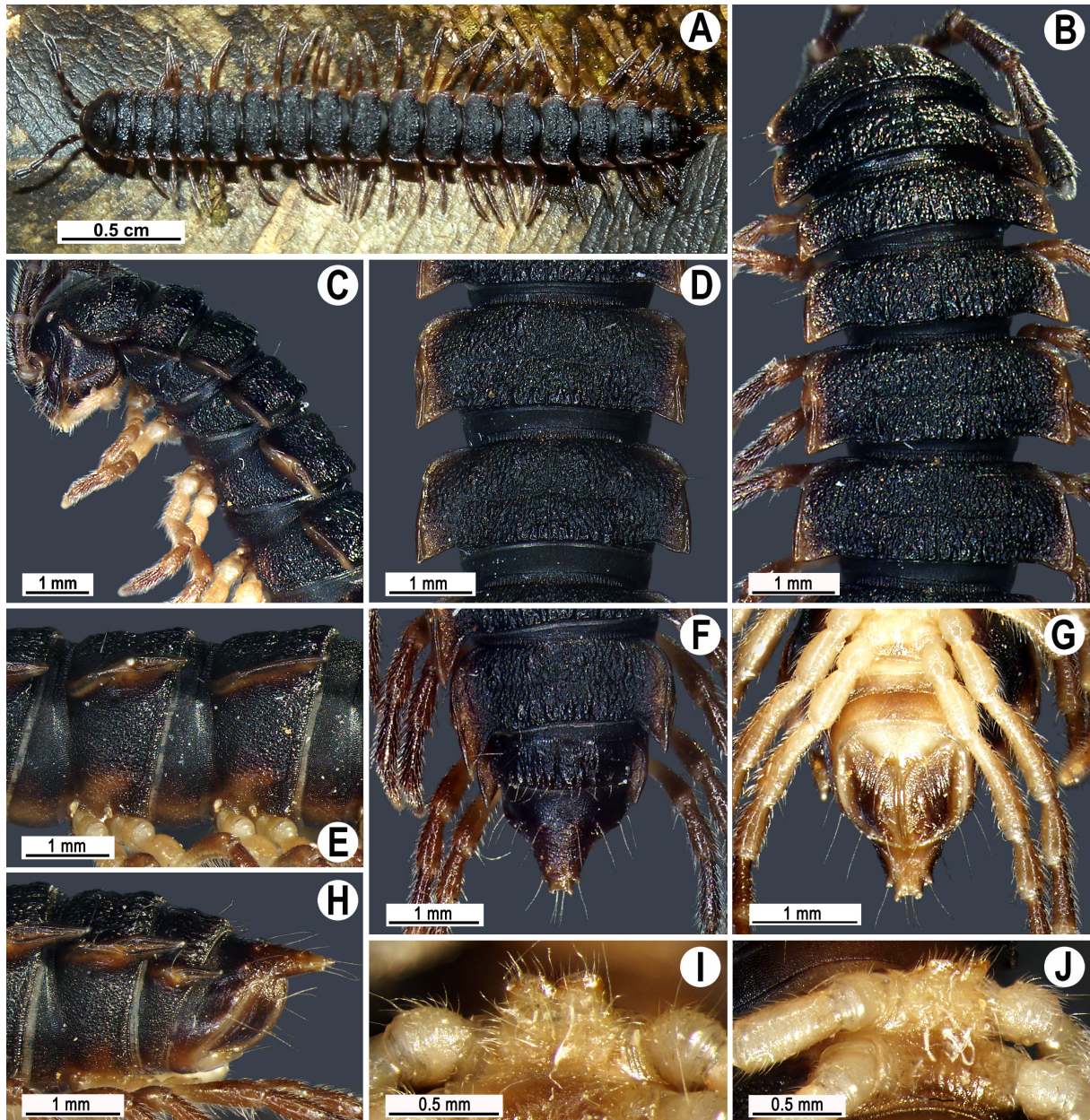
**Paratype**

LAOS: 1 ♀, same data as for holotype (CUMZ).

**Description**

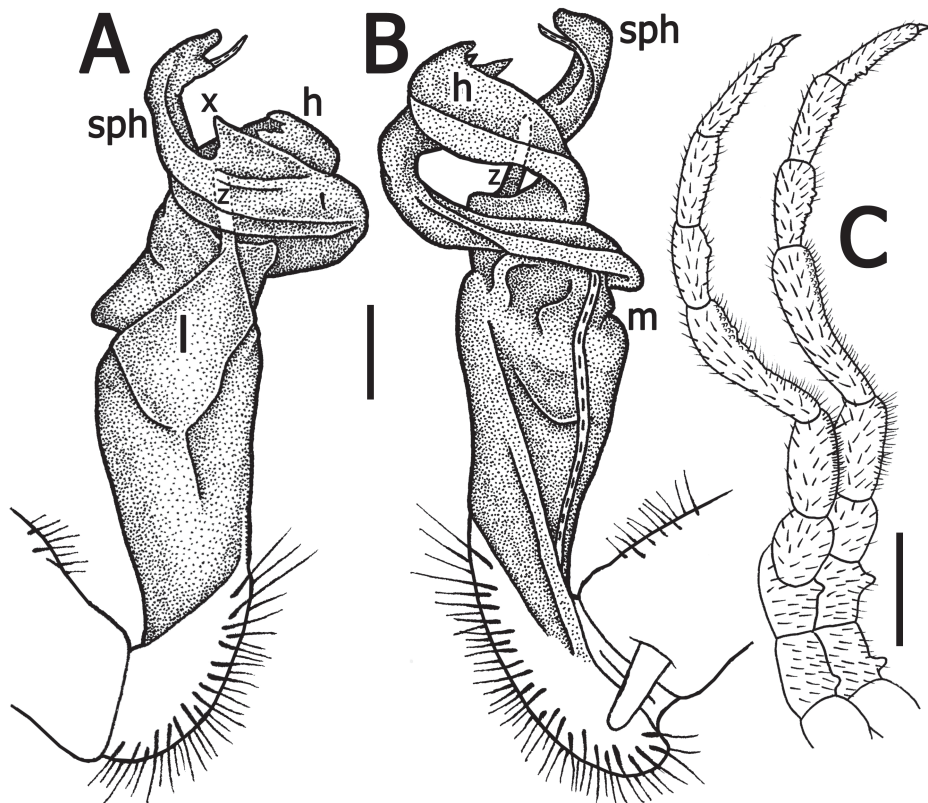
MEASUREMENTS AND COLOUR. Length 26.1 (♂) or 26.2 mm (♀), width of midbody pro- and metazonae 2.02 and 3.02 mm (♂) or 2.04 and 3.04 mm (♀), respectively. Live coloration brown black (Fig. 18A); antennae, paraterga and legs dark brown. Coloration in alcohol after one year of preservation blackish, paraterga dark brown; venter and a few basal podomeres light brown to yellow-brown, legs increasingly darker brown distally (Fig. 18B–J).

HEAD. Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae rather short (Fig. 18A), extending behind body segment 3 ( $\sigma$ ) or 2 ( $\text{♀}$ ) when stretched dorsally. In width, head < segment 3 < 4 < 5 < collum < segment 2 < 6–16 ( $\sigma$ ,  $\text{♀}$ ); thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 4+4 anterior, 1+1 intermediate and 3+3 posterior; with a small lateral incision near midway (Fig. 18B, D); caudal corner of paraterga very broadly rounded, declined ventrad, not surpassing rear tergal margin.



**Fig. 18.** *Tylopus thunghaihin* sp. nov., holotype,  $\sigma$ . **A.** Habitus, live coloration **B–C.** Anterior part of body, dorsal and lateral views, respectively. **D–E.** Segments 10 and 11, dorsal and lateral views, respectively. **F–H.** Posterior part of body, dorsal, ventral and lateral views, respectively. **I–J.** Sternal cones between coxae 4, caudal and sublateral views, respectively.

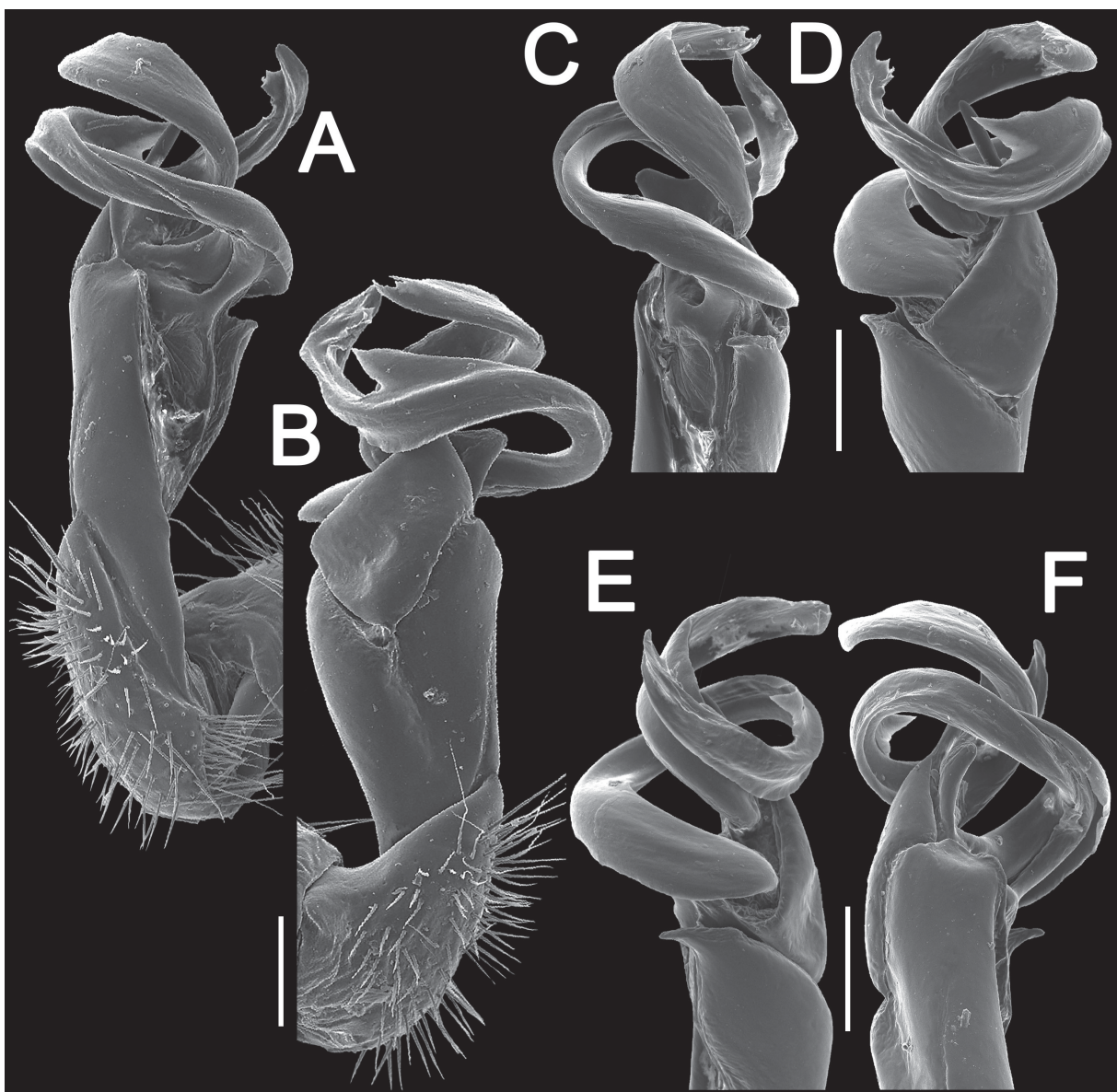
**BODY.** Tegument dull, shining, prozonae finely shagreened; metaterga often roughly microgranulate and rugulose, leathery; surface below paraterga more delicately, but still sufficiently clearly microgranulate and rugulose (Fig. 18A–F, H). Metaterga with two transverse rows of small setigerous cones: 2+2 in anterior (pre-sulcus) row and 3+3 setae usually borne on low, oblong, rounded tubercles in posterior (post-sulcus) row, except for metaterga 17–19, these latter bearing 3(2)+3(2) setae in anterior row and 4+4 in posterior row. Tergal setae simple, slender, often abraded, about as long as  $\frac{1}{3}$  of metazonite. Axial line visible both on pro- and metazonae. Paraterga strongly developed (Fig. 18B, D, F), especially so in ♂, set high (at upper  $\frac{1}{4}$  of body height), anterior edge rounded and narrowly bordered, fused to callus; caudal corner very narrowly rounded, extending increasingly behind rear tergal margin, posterior edge slightly oblique. Calluses on paraterga delimited by a sulcus only dorsally. Paraterga 2 broad, anterior edge angular, lateral edge with three evident incisions. Lateral edge of following paraterga with a clear incision in anterior  $\frac{1}{3}$  (Fig. 18B, D, F). Paraterga 16–19 with caudal corner extending increasingly caudally, tip clearly curved mesad (Fig. 18F). Ozopores evident, lateral, lying in an ovoid groove at about  $\frac{1}{3}$  in front of posterior edge of metaterga. Transverse sulcus distinct (Fig. 18B, D, F), slightly incomplete on segments 4 and 18, complete on segments 5–17, narrow, wave-shaped, rather deep, not reaching bases of paraterga, ribbed at bottom. Stricture between pro- and metazonae evident, wide, deep, ribbed at bottom down to base of paraterga (Fig. 18B–G). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–4 (♂, ♀), increasingly reduced to a front bulge and a caudal tooth until segment 7, retained only as a sharp caudal tooth until segment 16, thereafter missing (♂), or increasingly reduced and remaining only a sharp caudal tooth until segment 15, thereafter missing (♀) (Fig. 18C, E, H). Epiproct (Fig. 18F–H) conical, flattened dorsoventrally, with two evident, rounded,



**Fig. 19.** *Tylopus thunghaihin* sp. nov., holotype, ♂. A–B. Right gonopod, lateral and mesal views, respectively. C. Leg of segment 9. Scale bars: A–B = 0.2 mm; C = 1 mm. Abbreviations are explained in the text.

apical papillae; tip subtruncate; lateral pre-apical papillae large, lying close to tip. Hypoproct roundly subtriangular, setigerous knobs at caudal edge small and well-separated (Fig. 18G).

STERNA. Sparsely setose, with a small, but evident cone caudally near each coxa, rear cones being a little larger than fore ones (Fig. 19C); cross-impressions shallow; a large, central, slightly bifid, setose lobe between ♂ coxae 4 (Fig. 18I–J). Legs long and slender, midbody ones ca 1.2–1.4 (♂) or 1.1–1.2 (♀) as long as body height; legs of ♂ segments 5–17 with femur showing a field of ventral microgranulations, while postfemur, tibia and tarsus each with 1–3 minute adenostyles (tubercles), prefemora not swollen (Fig. 19G), ♂ telopodites with particularly dense short setae ventrally (Fig. 19G), tarsal brushes present until body segment 8.



**Fig. 20.** *Tylopus thunghaihin* sp. nov., holotype, ♂, right gonopod. **A–B.** Mesal and lateral views, respectively. **C–F.** Distal part, submesal, sublateral, subcaudal and suboral views, respectively. Scale bars = 0.2 mm.

GONOPOD. Rather complex (Figs 19A–B, 20); coxa slightly curved caudad, sparsely setose distoventrally. Femorite slightly curved and stout, with an evident mesal groove and a clear distolateral sulcus demarcating a postfemoral part; process **h** high, strongly twisted, tip evidently bifid; process **m** short; process **z** rather long, sausage-shaped; solenophore (**sph**) large, strongly coiled, expanded distally, flattened and clearly bifid; process **x** large, dentiform and pointed dorsally.

### Remarks

This species has been found under stones, each specimen located in its own burrow of ca 30 cm long under its own stone and forming a kind of small cavern, all in the Plain of Jars, Laos.

### *Tylopus punctus* sp. nov.

[urn:lsid:zoobank.org:act:35585ACA-8490-49EE-8DA5-73EB3EB04A5C](https://doi.org/10.3896/BI.2020.35585ACA-8490-49EE-8DA5-73EB3EB04A5C)

Figs 21–22, 26

### Diagnosis

Very similar to *T. silvestris* (Pocock, 1895), but differs in the smaller size, the width of midbody being 2.1–2.5 mm (versus 3.0 mm); the caudal corner of midbody paraterga very narrowly rounded and not drawn behind the rear tergal margin (versus nearly pointed and produced behind the rear tergal margin), and gonopod process **h** small and pointed (versus absent).

### Etymology

To emphasize gonopod process **h** being small and pointed; adjective.

### Material examined

#### Holotype

MYANMAR: ♂, Mintaingbin Forest Camp, ca 35 km north of Aungban, Chan State, 20°55'20" N, 96°33'60" E, ca 1300 m a.s.l., 11–23 Jun. 2004, leg. H. Schillhammer & H.V. Shaverdo (NHMW-8248).

#### Paratype

MYANMAR: 1 ♀, same data as for holotype (NHMW-8249).

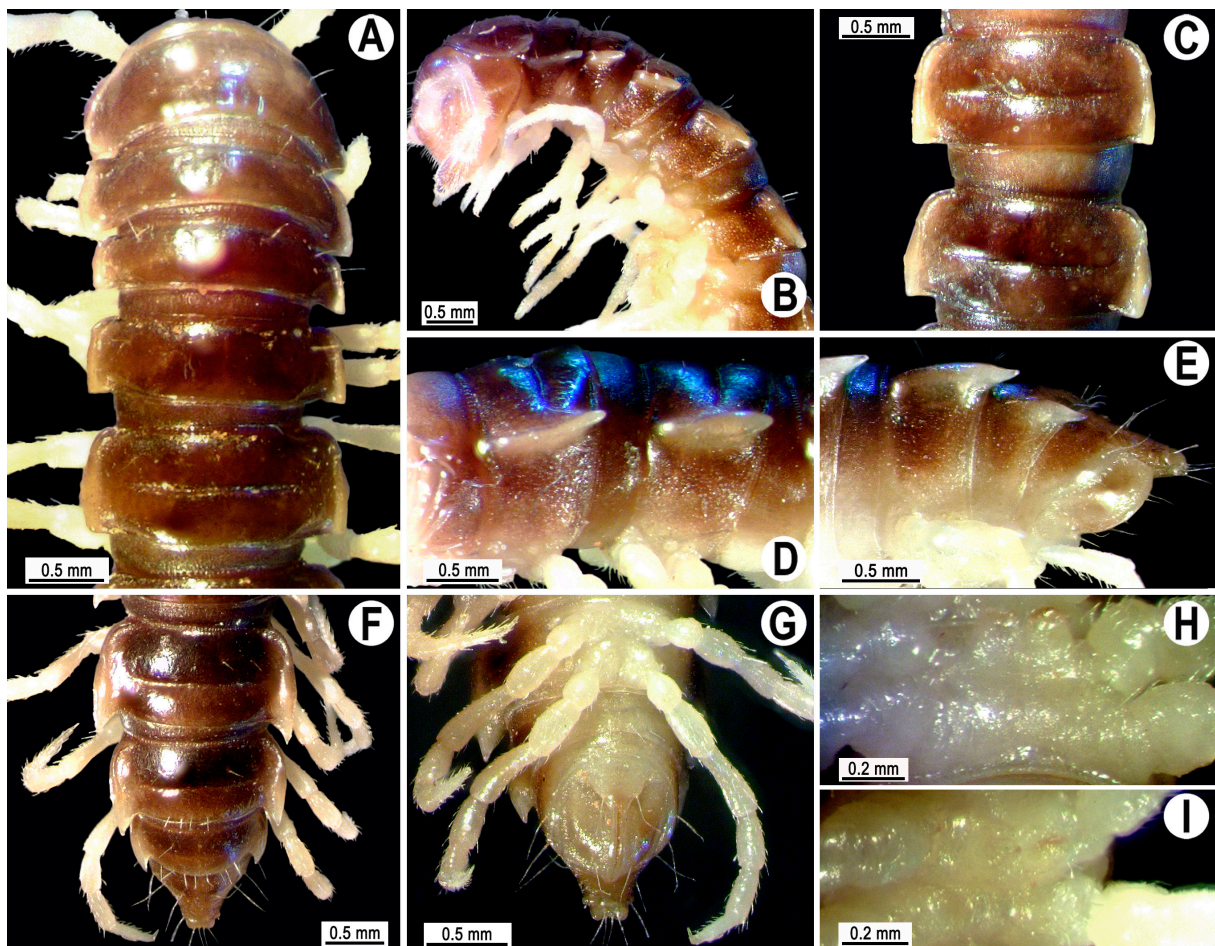
### Description

MEASUREMENTS AND COLOUR. Length 27.5 (♂) or 29 mm (♀), width of midbody pro- and metazonae 1.56 and 2.1 mm (♂) or 1.98 and 2.5 mm (♀), respectively. Coloration of alcohol material upon long-term preservation rather uniformly light brown to brown, with light yellow paraterga, antennae, venter and legs (Fig. 21A–I).

HEAD. Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae rather short (Fig. 21B), reaching only in front of body segment 3 (♂, ♀) when stretched dorsally. In width, segment 3 < 4 < head < collum < segment 2 < 5–15; thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 4+4 anterior, 2+2 intermediate and 3+3 posterior; an evident lateral incision at about anterior 1/3; caudal corner of paraterga very broadly rounded, declined ventrad, not drawn behind rear tergal margin.

BODY. Tegument smooth and shining, prozonae very finely shagreened, metaterga rather smooth and leathery, with posterior halves faintly rugulose, surface below paraterga finely microgranulate (Fig. 21A–F). Postcollum metaterga with two transverse rows of setae: 2+2 in anterior (pre-sulcus) row, mostly abraded, and 2+2 in posterior (post-sulcus) row, mostly traceable as insertion points, except

for segments 18 and 19, each latter with 4+4 setae in posterior row. Tergal setae simple, slender, about  $\frac{1}{3}$  of metatergal length (Fig. 21A, F). Axial line visible both on pro- and metazonae. Paraterga well-developed (Fig. 21A–G), especially so in ♂, set high (at upper  $\frac{1}{4}$  of body height), anterior edge rounded and narrowly bordered, fused to callus; caudal corner very narrowly rounded, segments 2 and 3 slightly extending behind rear tergal margin, thereafter not surpassing rear tergal margin until segment 15 (Fig. 21A–D). Paraterga 2 broad, anterior edge angular, lateral edge with two small, but evident incisions in anterior half. Following paraterga with an evident incision in anterior  $\frac{1}{3}$  of lateral edge (Fig. 21A, C, F). Calluses on paraterga delimited by a sulcus only dorsally, rather narrow, a little wider on pore-bearing segments. Ozopores distinct, lying at about  $\frac{1}{4}$  of metatergal length in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 21A, D, F), slightly incomplete on segment 19, complete on segments 5–18, narrow, line-shaped, rather deep, reaching bases of paraterga, beaded at bottom. Stricture between pro- and metazonae evident, rather wide and deep, beaded at bottom down to base of paraterga (Fig. 21A, C–F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2 and 3, thereafter increasingly reduced and remaining a sharp caudal tooth until segment 9 (♂) or 6 (♀), retained as a small caudal tooth and increasingly reduced until segment 17, absent from segment 18 (♂) or 7 (♀). Epiproct (Fig. 21E–G) conical, flattened dorsoventrally, with two evident,



**Fig. 21.** *Tylopus punctus* sp. nov., holotype, ♂. A–B. Anterior part of body, dorsal and lateral views, respectively. C–D. Segments 11–12, dorsal and lateral views, respectively. E–G. Posterior part of body, lateral, subdorsal and subventral views, respectively. H–I. Sternal cones between coxae 4, subcaudal and sublateral views, respectively.

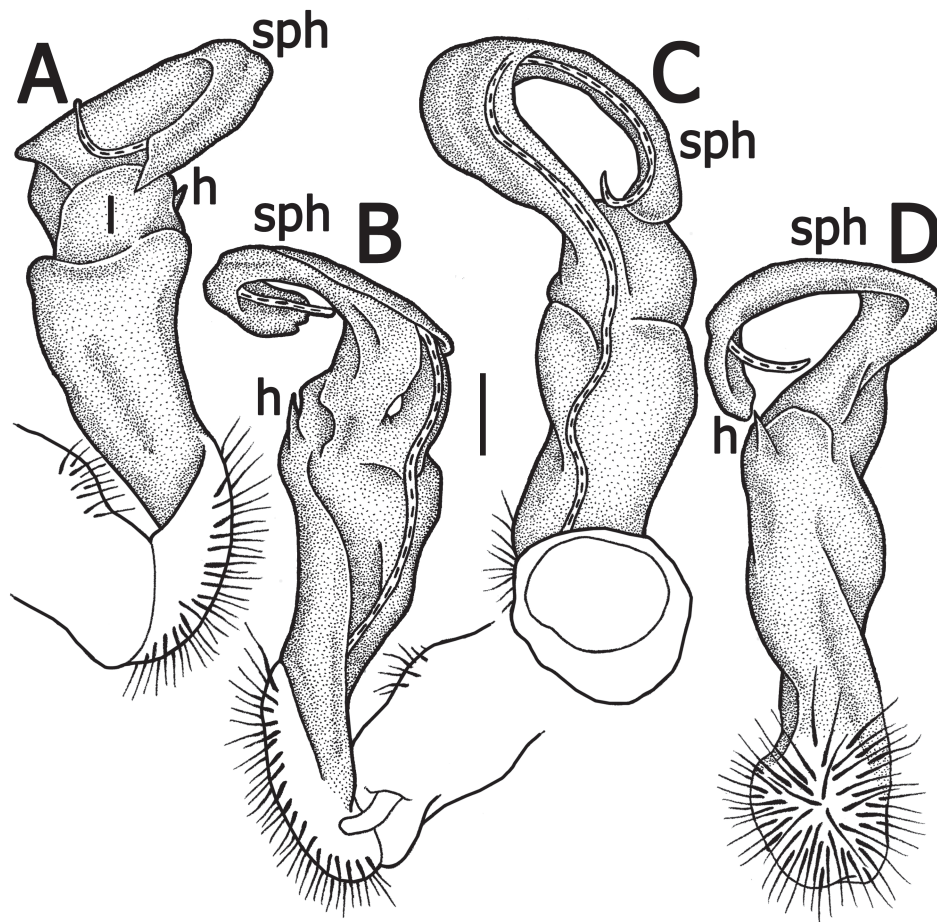
rather large, rounded, apical papillae; tip subtruncate; lateral pre-apical papillae clear, lying close to tip. Hypoproct roundly subtriangular, setigerous knobs at caudal edge small and well-separated (Fig. 21G).

STERNA. Sparsely setose, without modifications, but with a pair of small, blunt, fully separated cones between ♂ coxae 4 (Fig. 21H, I). Legs rather short and slender, midbody ones ca 1.1–1.2 (♂) or 0.8–0.9 (♀) as long as body height, ♂ prefemora not swollen, ♂ tarsal brushes present only on legs 1 and 2.

GONOPOD. Rather simple (Fig. 22); coxa slightly curved caudad, sparsely setose distoventrally. Prefemur sparsely setose, about 1/3 as long as femorite + postfemoral part. Femorite curved and stout, with an evident mesal groove and a strong distolateral sulcus demarcating a postfemoral part; process **h** small, slender and pointed; solenophore (**sph**) clearly coiled, long and flattened.

#### Remark

Pocock (1895) described only *T. doriae* (Pocock, 1895) and *T. silvestris* from northern Myanmar, the above being a third species of this genus also occurring in northern Myanmar.



**Fig. 22.** *Tylopus punctus* sp. nov., holotype, ♂. **A–D.** Left gonopod, lateral, mesal, subcaudal and suboral views, respectively. Scale bar = 0.2 mm. Abbreviations are explained in the text.

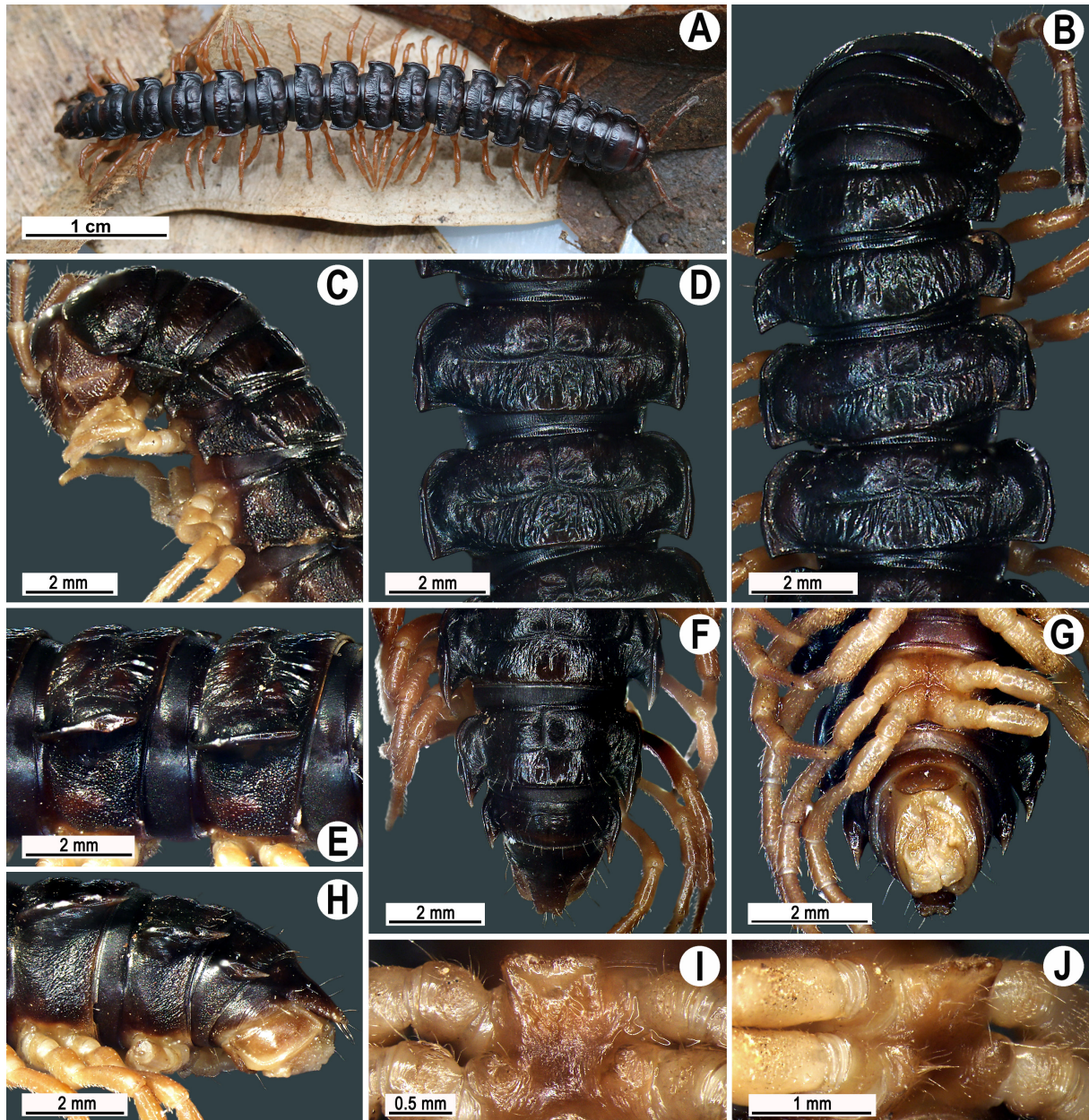
*New faunistic record*

*Tylopus baenzigeri* Golovatch & Enghoff, 1993

Figs 23–26

*Tylopus baenzigeri* Golovatch & Enghoff, 1993: 101, figs 50–51 (Type locality, Doi Suthep National Park).

*Tylopus baenzigeri* – Enghoff 2005: 99. — Likhitrakarn *et al.* 2010: 25; 2014a: 65.



**Fig. 23.** *Tylopus baenzigeri* Golovatch & Enghoff, 1993, ♂. **A.** Habitus, live coloration. **B–C.** Anterior part of body, dorsal and lateral views, respectively. **D–E.** Segments 10 and 11, dorsal and lateral views, respectively. **F–H.** Posterior part of body, dorsal, ventral and lateral views, respectively. **I–J.** Sternal cones between coxae 4, subcaudal and sublateral views, respectively.



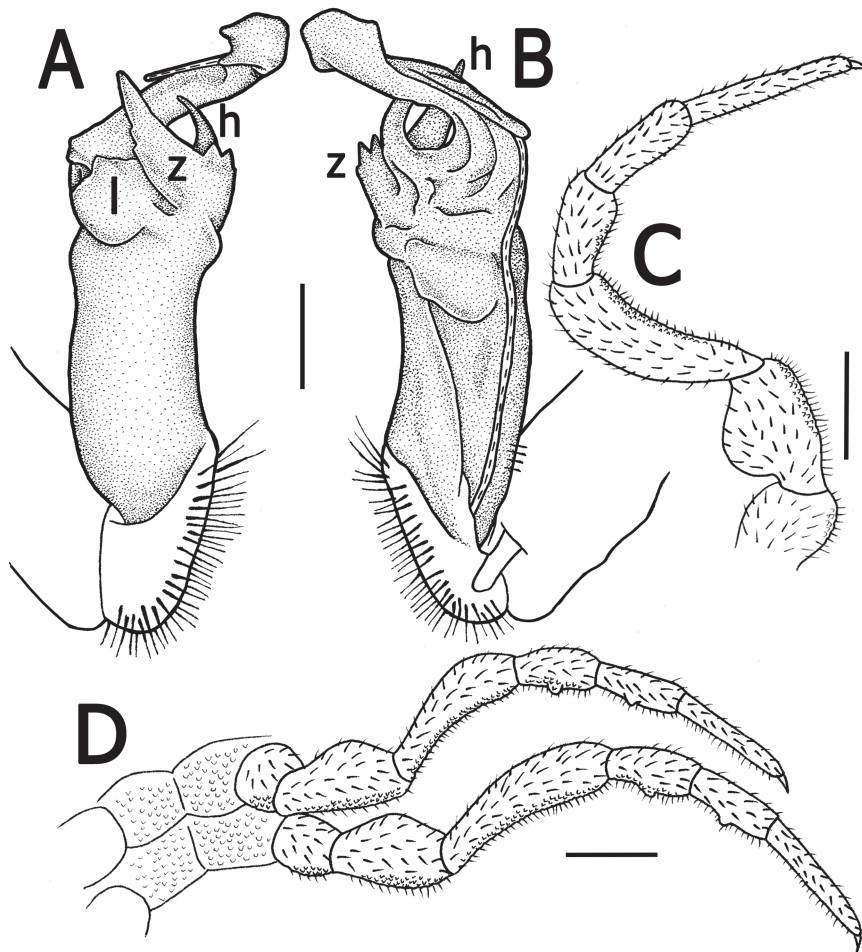
**Material examined**

THAILAND: ♂, Royal Agricultural Station Angkhang, Fang, Chiang Mai, 19°54'05"N, 99° 2'25"E, ca 1420 m a.s.l., 12 August 2014, leg. N. Likhitrakarn (CUMZ).

**Descriptive notes**

**MEASUREMENTS AND COLOUR.** Length 43.8 mm, width of midbody pro- and metazonae 3.51 and 5.04 mm, respectively. Coloration of live animal, as well as of alcohol material black-brown (Fig. 23A–G), head and venter dark to light brown, legs and antennae yellowish brown to light yellowish.

**BODY.** Antennae rather short (Fig. 23B), extending behind body segment 3 (♂) when stretched dorsally. In width, segment 3 < 4 < 5 < collum < segment 2 < 6–17; thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 4+4 anterior, 1+1 intermediate and 4+4 posterior; a very faint incision laterally in posterior 1/3; caudal corner of paraterga very broadly rounded, not drawn behind rear tergal margin (Fig. 23B–C). Paraterga 2 well-developed (Fig. 23B–C), horizontal, lateral edge with two minute incisions in anterior half, caudal corner very narrowly rounded. Paraterga 3 and 4 each nearly pointed, expanded laterally, with two minute incisions in the middle. Sterna densely setose and finely microtuberculate (Fig. 24D); with a large, subtrapeziform, ventrally slightly concave, sternal lobe between ♂ coxae 4 (Fig. 23I–J). Legs rather long and slender, midbody ones ca 1.2–1.3 (♂) as long as



**Fig. 24.** *Tylopus baenzigeri* Golovatch & Enghoff, 1993, ♂. **A–B.** Right gonopod, lateral and mesal views, respectively. **C.** Leg 8. **D.** Legs of segment 11. Scale bars = 0.5 mm. Abbreviations are explained in the text.

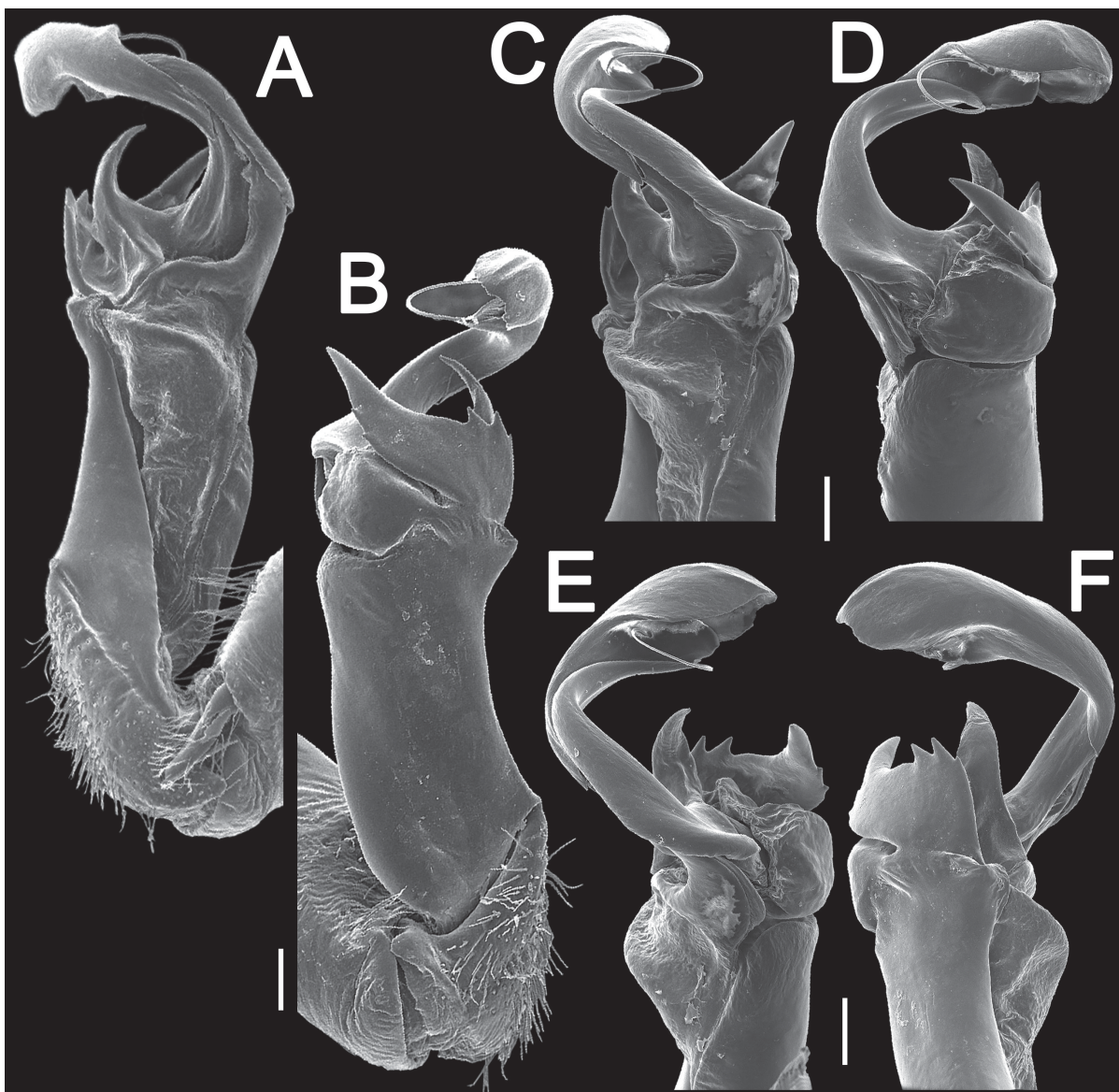
body height; ♂ legs without tarsal brushes; ♂ postfemora and tibiae each with an adenostyle (tubercle) on segments 8–17; ♂ coxae, prefemora, femora and postfemora microtuberculate ventrally (Fig. 24C–D).

### Remarks

This new specimen agrees in most details with the original description (Golovatch & Enghoff 1993), especially in gonopod structure which shows a huge spine *z* serrate on both sides (Figs 24A–B, 3), and in a large body. Thus, to document its identity the new specimen has been illustrated in detail for comparative purposes (Figs 23–25). The type locality of *T. baenzigeri*, Doi Suthep National Park, is located quite far away (about 120 km) from this new place.

### Checklist

Table 1 presents a checklist of the known or new *Tylopus* species, all arranged in alphabetic order. Data on their distribution are also provided.



**Fig. 25.** *Tylopus baenzigeri* Golovatch & Enghoff, 1993, ♂, right gonopod. A–B. Mesal and lateral views, respectively. C–F. Distal part, submesal, sublateral, subcaudal and suboral views, respectively. Scale bar = 0.2 mm.

**Table 1.** Records of *Tylopus* species.

No.	Species	Localities
1	<i>Tylopus acuminatus</i> sp. nov.	Ban Sin Chai; Phuthalang forest protected area; Phufa; Ban Borkhun; Khoua; Ban Na Thong, Phongsali Province, Phagneung Phoukulom waterfall, Luang Namtha Province, Laos (see details above).
2	<i>Tylopus affinis</i> Golovatch & Enghoff, 1993	Doi Suthep National Park (Golovatch & Enghoff 1993); Doi Inthanon National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993; Enghoff 2005).
3	<i>Tylopus allorugosus</i> Golovatch & Enghoff, 1993	Doi Inthanon National Park; Doi Suthep National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993; Likhitrakarn <i>et al.</i> 2010).
4	<i>Tylopus amicus</i> Golovatch & Enghoff, 1993	Doi Pha Hom Pok National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
5	<i>Tylopus asper</i> Golovatch & Enghoff, 1993	Doi Inthanon National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
6	<i>Tylopus baenzigeri</i> Golovatch & Enghoff, 1993	Doi Suthep National Park (Golovatch & Enghoff 1993); Royal Agricultural Station, Angkhang Chiang Mai Province, Thailand (see above).
7	<i>Tylopus bispinosus</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Umphang, Tak Province, Thailand (Likhitrakarn <i>et al.</i> 2010).
8	<i>Tylopus coriaceus</i> Golovatch & Enghoff, 1993	Phu Kheio, Chaiyapum Province, Thailand (Golovatch & Enghoff 1993).
9	<i>Tylopus corrugatus</i> Likhitrakarn, Golovatch & Panha, 2014	Doi Inthanon National Park, Chiang Mai Province, Thailand (Likhitrakarn <i>et al.</i> 2014a).
10	<i>Tylopus crassipes</i> Golovatch, 1984	Oquyho (Golovatch 1984); Nam Xay commune; Hoang Lien National Park, Lao cai Province, Vietnam (Nguyen 2012).
11	<i>Tylopus degerboelae</i> Golovatch & Enghoff, 1993	Doi Inthanon National Park; Doi Chiang Dao National Park (Golovatch & Enghoff 1993); Doi Suthep National Park (Golovatch & Enghoff 1993, Likhitrakarn <i>et al.</i> 2010); Doi Phatang, Chiang Mai Province, Thailand (Likhitrakarn <i>et al.</i> 2010).
12	<i>Tylopus deharvengi</i> Liu & Luo, 2013	Yaonan Dong, Guangxi, China (Liu & Luo 2013).
13	<i>Tylopus doriae</i> (Pocock, 1895)	Yado; Bia-po; Meteleo; Puepoli, Myanmar (Pocock 1895); Doi Suthep National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).

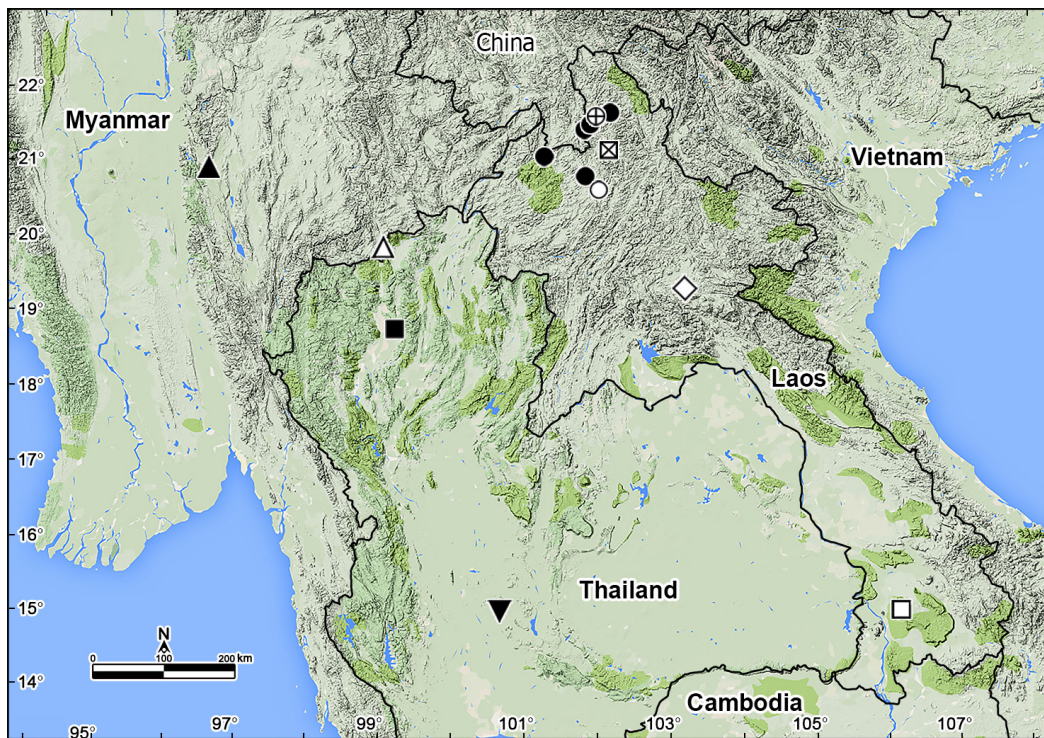
No.	Species	Localities
14	<i>Tylopus dorsalis</i> sp. nov.	Phuthalang forest protected area, Phongsali Province, Laos (see above)
15	<i>Tylopus extremus</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Doi Phahom Pok National Park, Fang District, Chiang Mai Province, Thailand (Likhitrakarn <i>et al.</i> 2010).
16	<i>Tylopus flavolineatus</i> sp. nov.	Wat Tham Santisuk, Lopburi Province Thailand (see above)
17	<i>Tylopus golovatchi</i> Nguyen, 2012	Xuan Son National Park, Phu Tho Province, Vietnam (Nguyen 2012).
18	<i>Tylopus grandis</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Pha Mon Cave; Mae Lana, Pangmapha District, Mae Hong Son Province (Likhitrakarn <i>et al.</i> 2010).
19	<i>Tylopus granulatus</i> Golovatch, 1984	Cuc Phuong Nature Reserve, Ninh binh Province, Vietnam (Golovatch 1984).
20	<i>Tylopus haplorugosus</i> Golovatch & Enghoff, 1993	Doi Inthanon National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993, Likhitrakarn <i>et al.</i> 2010).
21	<i>Tylopus hilaris</i> (Attems, 1937)	Bana, Danang Province (Attems 1937); Bach Ma National Park, Thua Thien Hue Province; Ngoc Linh Mountain, Kon Tum Province, Vietnam (Nguyen 2012).
22	<i>Tylopus hilaroides</i> Golovatch, 1984	Cuc Phuong Nature Reserve Ninh binh Province (Golovatch 1984); Cuc Phuong National Park, Ninh Binh Province, Vietnam (Nguyen 2012).
23	<i>Tylopus hoffmani</i> Golovatch & Enghoff, 1993	Doi Suthep National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
24	<i>Tylopus hongkhraiensis</i> sp. nov.	Huai Hong Khrai Royal Development Study Centre, Chiang Mai Province, Thailand (see above)
25	<i>Tylopus jeekeli</i> Golovatch & Enghoff, 1993	Doi Inthanon National park (Golovatch & Enghoff 1993); Doi Suthep National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993; Likhitrakarn <i>et al.</i> 2010).
26	<i>Tylopus kabaki</i> Golovatch, 2014	Dêqên, Yunnan Province, China (Golovatch 2014).
27	<i>Tylopus maculatus</i> Golovatch, 1984	Oquyho, Lao cai Province, Vietnam (Golovatch 1984).
28	<i>Tylopus magicus</i> Golovatch, 1984	Oquyho, Lao cai Province, Vietnam (Golovatch 1984).
29	<i>Tylopus moniliformis</i> sp. nov.	Tad Fane Waterfall, Champasak Province, Laos (see above)
30	<i>Tylopus mutilatus</i> (Attems, 1953)	Langbiang mountain, Lam Dong Province, Vietnam (Attems 1953).

No.	Species	Localities
31	<i>Tylopus nodulipes</i> (Attems, 1953)	Luang Prabang, Laos; Mt Fan-Si-Pan (Attems 1953); Nam Xay commune, Lao Cai Province; Son Tay commune, Ha Tinh Province; Pu Mat National Park, Nghe An Province, Vietnam (Nguyen 2012).
32	<i>Tylopus pallidus</i> Golovatch & Enghoff, 1993	Doi Pha Hom Pok, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
33	<i>Tylopus parahilaroides</i> Likhitrakarn, Golovatch & Panha, 2014	Phuluang Wildlife Sanctuary, Phuluang District, Loei Province, Thailand (Likhitrakarn <i>et al.</i> 2014a).
34	<i>Tylopus parajeekeli</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Doi Inthanon National Park, Chiang Mai Province, Thailand (Likhitrakarn <i>et al.</i> 2010).
35	<i>Tylopus perarmatus</i> Hoffman, 1973	Doi Suthep National Park (Hoffman 1973; Golovatch & Enghoff 1993); Doi Inthanon National Park (Golovatch & Enghoff 1993; Likhitrakarn <i>et al.</i> 2010); Doi Chiang Dao (Golovatch & Enghoff 1993); Doi Phatang, Chiang Mai Province (Likhitrakarn <i>et al.</i> 2010); Ban Huai Kaeo (Golovatch & Enghoff 1993); Thum Pha Thai, Lampang Province; Ban Pang Rim Kon; Phucheefah; Doi Pha Tang, Chiang Rai Province; Nam Min Waterfall, Phayao Province; Tham Pha Nang Khoi, Phrae Province; Ton Tong Waterfall, Nan Province, Thailand (Likhitrakarn <i>et al.</i> 2010).
36	<i>Tylopus perplexus</i> Golovatch & Enghoff, 1993	Doi Pha Hom Pok, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
37	<i>Tylopus phanluongi</i> Nguyen, 2012	Ngoc Linh Mountain, Kon Tun Province, Vietnam (Nguyen 2012).
38	<i>Tylopus poolpermorum</i> Golovatch & Enghoff, 1993	Doi Pha Hom Pok, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
39	<i>Tylopus procurvus</i> Golovatch, 1984	Oquyho (Golovatch 1984); Hoang Lien National Park, Lao cai Province, Vietnam (Nguyen 2012).
40	<i>Tylopus prosperus</i> Golovatch & Enghoff, 1993	Doi Inthanon National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993; Likhitrakarn <i>et al.</i> 2010).
41	<i>Tylopus pulvinipes</i> Golovatch & Enghoff, 1993	Phu Kheio, Chaiyaphum Province, Thailand (Golovatch & Enghoff 1993).
42	<i>Tylopus punctus</i> sp. nov.	Mintaingbin Forest Camp, Chan State, Myanmar (see above).
43	<i>Tylopus reductus</i> Golovatch, 2013	Gaoligong Shan Mountain, Yunnan Province, China (Golovatch 2013).
44	<i>Tylopus retusus</i> sp. nov.	Xay city, Oudomxai Province, Laos (see below).
45	<i>Tylopus roseiparaterga</i> Nguyen, 2012	Tam Dao National Park, Vinh Phuc Province, Vietnam (Nguyen 2012).

No.	Species	Localities
46	<i>Tylopus rugosus</i> Golovatch & Enghoff, 1993	Chiang Dao (Golovatch & Enghoff, 1993); Buathong Waterfall forest park, Chiang Mai Province, Thailand (Likhitrakarn <i>et al.</i> 2010).
47	<i>Tylopus sapaensis</i> Nguyen, 2012	Hoang Lien National Park, Lao Cai Province, Vietnam (Nguyen 2012).
48	<i>Tylopus schawalleri</i> Golovatch, 2013	Diancang Shan Mountain, Yunnan Province, China (Golovatch 2013).
49	<i>Tylopus semirugosus</i> Golovatch & Enghoff, 1993	Ban Mussoe, Mae Sot District, Tak Province, Thailand (Golovatch & Enghoff 1993).
50	<i>Tylopus sigma</i> (Attems, 1953)	Sapa, Lao Cai Province, Vietnam (Attems 1953).
51	<i>Tylopus silvestris</i> (Pocock, 1895)	village of Thao, Myanmar (Pocock 1895).
52	<i>Tylopus similirugosus</i> Golovatch & Enghoff, 1993	Doi Suthep National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
53	<i>Tylopus similis</i> Golovatch, 2014	Between Lijiang and Shangrila, Yunnan Province, China (Golovatch 2014).
54	<i>Tylopus sinensis</i> Golovatch, 1995	Mengzi County, Yunnan Province, China (Golovatch 1995).
55	<i>Tylopus spinisterna</i> Nguyen, 2012	Bi Doup-Nui Ba National Park, Lam Dong Province, Vietnam (Nguyen 2012).
56	<i>Tylopus strongylosomoides</i> (Korsós & Golovatch, 1989)	Tam Dao National Park, Vinh Phu Province (Korsós & Golovatch 1989); Xuan Son national Park, Phu Tho Province, Vietnam (Nguyen 2012).
57	<i>Tylopus subcoriaceus</i> Golovatch & Enghoff, 1993	Doi Suthep National Park, Chiang Mai Province, Thailand (Golovatch & Enghoff 1993).
58	<i>Tylopus tamdaoensis</i> Korsós & Golovatch, 1989	Tam Dao National Park, Vinh Phu Province, Vietnam (Korsós & Golovatch 1989; Nguyen 2012).
59	<i>Tylopus thunghaihin</i> sp. nov.	Plain of Jars, Xieng Khouang Province, Laos (see above).
60	<i>Tylopus topali</i> Golovatch, 1984	Cuc Phuong Nature Reserve, Ninh binh Province (Golovatch 1984; Nguyen 2012); Xuan Son National Park, Phu Tho Province, Vietnam (Nguyen 2012).
61	<i>Tylopus trigonum</i> Likhitrakarn, Golovatch & Panha, 2014	Pa Wai waterfall, Tak Province, Thailand (Likhitrakarn <i>et al.</i> 2014a).
62	<i>Tylopus veliger</i> Likhitrakarn, Golovatch, Prateepasen & Panha, 2010	Ton Tong Waterfall, Nan Province, Thailand (Likhitrakarn <i>et al.</i> 2010).

**Key to the known species of *Tylopus* (based chiefly on ♂), modified after Likhitrakarn *et al.* (2010):**

1. Most of ♂ prefemora evidently swollen laterally (Figs 13C, 24C) .....2
  - All ♂ prefemora normal, not bulged laterally (Figs 2G, 11F, G, 17E–G, 19C) .....29
2. Surface of metaterga virtually smooth, at best extremely faintly rugulose in certain places and/or with a few barely traceable (setigerous) tubercles near caudal margin (setae mostly broken off) (Figs 7B, D, 12A–B, D, 21A, C) .....3
  - Surface of metaterga mostly rugulose to coarsely rugose/tuberculate (Figs 18A–B, D, 23B, D) .....9
3. Paraterga moderately developed (Figs 1A, C, 21A, C), ratio of ♂ midbody prozonite to metazonite width below 1:1.2 .....4
  - Paraterga relatively well-developed (Figs 10B, D, 11B, D, 18B, D), ratio of ♂ midbody prozonite to metazonite width over 1:1.2 .....5
4. Transverse sulcus on metaterga starting with segment 5. Calluses without incisions. Gonopod with process small and dentiform. Thailand ..... *T. prosperus* Golovatch & Enghoff, 1993
  - Transverse sulcus on metaterga starting with segment 4. Calluses with faint one or two denticles on poreless and poriferous paraterga, respectively. Gonopod very simple, without processes. Southern China ..... *T. reductus* Golovatch, 2013



**Fig. 26.** Distribution of the new eight species of *Tylopus*. **Filled triangle.** *T. punctus* sp. nov. **Filled circle.** *T. acuminatus* sp. nov. **Crossed circle.** *T. acuminatus* sp. nov., *T. dorsalis* sp. nov. **Crossed square.** *T. acuminatus* sp. nov. *T. retusus* sp. nov. **Open circle.** *T. retusus* sp. nov. **Open triangle.** *T. baenzigeri* Golovatch & Enghoff, 1993. **Filled square.** *T. hongkhraiensis* sp. nov. **Open diamond.** *T. thunghaihin* sp. nov. **Inverted filled triangle.** *T. flavolineatus* sp. nov. **Open square.** *T. moniliformis* sp. nov.

5. Calluses without incisions. Gonopod postfemoral lobe **I** much broader than long; area basal to **I** delimited by a distinct cingulum .....6
  - Calluses mostly with 1–2 incisions. Gonopod postfemoral lobe **I** either as long as broad or longer; no cingulum basal to **I** .....7
6. Body smaller: length up to ca 19–30 mm. Gonopod with a broadly coiled solenophore and a small finger-shaped process on lobe **I**. China .....*T. kabaki* Golovatch, 2014
  - Body larger: length ca 33–35 mm. Gonopod with a slender and coiled solenophore, but without processes on lobe **I**. Vietnam .....*T. magicus* Golovatch, 1984
7. Metaterga at best only very faintly rugulose near stricture, near sulcus and/or at base of paraterga, with 2–3 weak, oblong tubercles near rear margin. ♂ postfemora and tibiae tuberculiferous. Gonopods with process **z** serrate, with 3 spines. Thailand .....*T. similirugosus* Golovatch & Enghoff, 1993
  - Metatergal surface entirely smooth, polished, without tubercles. ♂ legs without adenostyles (= tubercles). Gonopods with process **z** pointed, without spines .....8
8. Midline wanting. Gonopods with process **h** without additional tooth, while process **z** very high. Vietnam .....*T. mutilatus* (Attems, 1953)
  - Midline mostly traceable on prozonae and anterior halves of metaterga. Gonopods with process **h** higher with an evident dorsal tooth, while process **z** small (Figs 13A–B, 14–15). Laos .....*T. acuminatus* sp. nov.
9. Body larger: 37–42 mm long, 2.8–3.8 and 4.1–5.0 mm wide on pro- and metaterga, respectively ..... 10
  - Body smaller ..... 15
10. Sterna between ♂ coxae 4 with a pair of separated cones. Gonopod with a short spiniform process **h**, a basally only poorly delimited lobe **I** and a small lobe-shaped process **z**. Thailand .....*T. grandis* Likhitrakarn, Golovatch, Prateepasen & Panha, 2010
  - Sterna between ♂ coxae 4 with a slightly notched sternal lobe. Gonopod with a rather long process **h** carrying two branches, plus a basally evidently delimited lobe **I** and a large, serrated process **z**. Vietnam .....*T. phanluongi* Nguyen, 2012
11. Both processes **h** and **z** of gonopod spiniform. Thailand .....
  - .....*T. bispinosus* Likhitrakarn, Golovatch, Prateepasen & Panha, 2010
  - Gonopod otherwise ..... 12
12. Gonopod process **h** subflagelliform, process **m** extremely long and prominent. Thailand.....
  - .....*T. extremus* Likhitrakarn, Golovatch, Prateepasen & Panha, 2010
  - Gonopod otherwise ..... 13
13. Gonopod process **h** prominent, spine **s** high, rather slender, curved, nearly pointed. Vietnam .....*T. sapaensis* Nguyen, 2012
  - Gonopod otherwise ..... 14
14. ♂ legs shorter, ca 1.2–1.3 times as long as midbody height. Gonopod lobe **I** velum-shaped and supplied with two denticles; spine **z** short and knife-shaped, while spine **h** rudimentary. Thailand .....*T. veliger* Likhitrakarn, Golovatch, Prateepasen & Panha, 2010
  - ♂ legs longer, ca 1.6–1.7 times as long as midbody height. Gonopod spine **z** small, placed closer to base of spine **h**. Thailand .....*T. parajeekeli* Likhitrakarn, Golovatch, Prateepasen & Panha, 2010



15. Most of metaterga with a pattern of 2+2 and 2+2 setigerous tubercles in two rows, rear row somewhat less strongly developed than fore one. Myanmar and Thailand ... *T. doriae* (Pocock, 1895)  
 – Most of metaterga with rear row of setigerous tubercles or wrinkles more strongly developed than fore row, the latter (next to) wanting .....16
16. Transverse sulcus on metaterga starting with segment 4, either fully or almost fully developed there, always fully developed starting with segment 5 .....17  
 – Transverse sulcus on metaterga starting only with segment 5 .....20
17. Transverse sulcus fully developed and reaching base of paraterga already starting with segment 4. Gonopod tooth **z** at base of lobe **I** coarsely serrate along proximal margin. Vietnam .....  
 ..... *T. hilaris* (Attems, 1937)  
 – Transverse sulcus fully developed only starting with segment 5. Gonopod tooth **z** either devoid of serration or serrate along distal margin .....18
18. Paraterga 2 rather broadly rounded caudolaterally. Gonopod relatively simple, process **h** poorly developed, no additional outgrowths near base. Thailand .....  
 ..... *T. affinis* Golovatch & Enghoff, 1993  
 – Paraterga 2 pointed caudally. Gonopods more complex .....19
19. Coloration dark brown, without a cingulate pattern. Sternal lamina between ♂ coxae 4 low and distinctly bimodal. Gonopod tooth **z** prominent and serrate along distal margin. Thailand .....  
 ..... *T. rugosus* Golovatch & Enghoff, 1993  
 – Coloration pale, with a cingulate pattern. Sternal lamina between ♂ coxae 4 high, subquadrate. Gonopod tooth **z** smaller and spiniform. Thailand ..... *T. semirugosus* Golovatch & Enghoff, 1993
20. Paratergal corner protruding caudad behind rear margin only starting with segment 15, being obtuse-angled or subrectangular and lying more or less within the margin until segment 14. Vietnam .....  
 ..... *T. hilaroides* Golovatch, 1984  
 – Paratergal corner protruding caudad behind rear margin before segment 14, mostly pointed ...21
21. Pattern of tergal setation on segments 18 and/or 19: 2+2 and 5+5 in two rows .....22  
 – Pattern of tergal setation at least on segments 5–19: 2+2 and 4+4 in two rows .....25
22. Pattern of tergal setation 2+2 and 5+5 on both segments 18 and 19. Paraterga 2 pointed caudally. Epiproct with pre-apical incisions very close to apical knobs. Sternal lamina between ♂ coxae 4 an unusually low and even ridge. Adenostyles on midbody ♂ postfemora and, to a lesser extent, tibiae exceptionally prominent. Thailand .....  
 ..... *T. poolpermorum* Golovatch & Enghoff, 1993  
 – Pattern of tergal setation 2+2 and 5+5 on segment 19. Paraterga 2 more or less narrowly rounded. Pre-apical incisions on epiproct more strongly removed from tip. Sternal lamina between ♂ coxae 4 concave medially. Ventral adenostyles on ♂ legs less prominent .....23
23. Body smaller: width ca 2.0 mm. Sternal lamina between ♂ coxae 4 a pair of separated setigerous tubercles. Ventral adenostyles on ♂ legs almost missing. Gonopods without any outgrowths near base of process **h**. Thailand .....  
 ..... *T. haplorugosus* Golovatch & Enghoff, 1993  
 – Body larger: width over 3.0 mm. Sternal lamina between ♂ coxae 4 single. Ventral adenostyles on ♂ legs more prominent. Gonopod with a spine near base of process **h** .....24
24. Sternal lamina between ♂ coxae 4 high, emarginated. Adenostyles on ♂ postfemora and tibiae well-developed. Gonopods rather simple, spine **z** inconspicuous. Thailand .....  
 ..... *T. allorugosus* Golovatch & Enghoff, 1993

- Sternal lamina between ♂ coxae lower, slightly concave. Adenostyles on ♂ postfemora and tibiae less strongly developed. Gonopods more complex, spine **z** long and large. Thailand ..... *T. perarmatus* Hoffman, 1973
- 25. Paraterga 2 pointed caudally. Sternal lamina between ♂ coxae 4 exceptionally densely setose, low and concave ventrally. Gonopods with a medium-sized process **h** and a smaller lobular **z** at base of **h**. Thailand ..... *T. jeekeli* Golovatch & Enghoff, 1993
- Paraterga 2 more or less narrowly rounded caudally. Sternal lamina between ♂ coxae 4 higher and less strongly setose. Gonopod outgrowths **h** and **z** either almost wanting or very large ...26
- 26. Sternal lamina between ♂ coxae 4 with a straight ventral margin. Pleurosternal carinae poorly developed, in ♂ slightly drawn behind rear margin only until segments 8–10 .....27
- Sternal lamina between ♂ coxae 4 slightly concave ventrally. Pleurosternal carinae better developed, in ♂ slightly drawn behind rear margin at least until segment 15 .....28
- 27. Body smaller: width up to 3.1–3.2 mm. Mid-dorsal line very clear on both halves of metaterga. Gonopods relatively simple, with both **h** and **z** almost wanting. Thailand ..... *T. hoffmani* Golovatch & Enghoff, 1993
- Body larger: width 4.0–5.3 mm. Mid-dorsal line not so well-developed at least on rear halves of metaterga. Gonopods more complex, with both **h** and **z** very conspicuous (Figs 24A–B, 25). Thailand ..... *T. baenzigeri* Golovatch & Enghoff, 1993
- 28. Metatergum 19 slightly rugulose posteriorly. Calluses on segment 2 with three, on following paraterga with two, incisions. Gonopods extremely complex, with numerous spiniform outgrowths. Thailand ..... *T. perplexus* Golovatch & Enghoff, 1993
- Metatergum 19 entirely smooth. Calluses with two or three incisions on poreless and poriferous paraterga, respectively. Gonopod less strongly differentiated. Thailand ..... *T. amicus* Golovatch & Enghoff, 1993
- 29. Either most of ♂ sterna with an oblique tubercle or spine, or only anterior sterna with a small cone, near coxae .....30
- Neither spines nor tubercles on ♂ sterna .....37
- 30. Calluses virtually devoid of incisions .....31
- Calluses always at least with one lateral incision .....32
- 31. ♂ coxae 4 with a pair of separated cones. Gonopod process **h** small, while solenophore slender and short. China ..... *T. sinensis* Golovatch, 1995
- ♂ coxae 4 with an entire, subtrapeziform, sternal lobe. Gonopod process **h** larger, while solenophore stout and long. Vietnam ..... *T. golovatchi* Nguyen, 2012
- 32. A pair of small, fully separated, setose cones between ♂ coxae 4 (Fig. 10I–J). Gonopod with process **h** rather short, slightly flattened, blunt (Fig. 11A–D). Laos ..... *T. retusus* sp. nov.
- An entire lobe between ♂ coxae 4. Gonopod otherwise .....33
- 33. Metaterga strongly rugose/tuberculate/granulate (Fig. 18A–F, H) .....34
- Metaterga entirely smooth and polished, devoid of evident tubercles, at best extremely faintly rugulose near transverse sulcus (Fig. 1A–F) .....35

34. Calluses mostly with one lateral, clear incision. Pleurosternal carinae missing after segment 17. Gonopod processes **h**, **z**, **m** and spine **x** present (Fig. 19A–B). Laos ...*T. thunghaihin* sp. nov.  
 – Calluses with two lateral setigerous incisions. Pleurosternal carinae missing after segment 12. Only gonopod process **h** present. Vietnam .....*T. spinisterna* Nguyen, 2012
35. Only rear sternum on most of ♂ segments with a pair of small spines. Metaterga mostly with 2+2 and 3+3 setigerous tubercles in two transverse rows. Pleurosternal carinae missing after segment 9. Myanmar .....*T. silvestris* (Pocock, 1895)  
 – Fore and rear sterna of most of ♂ segments with a pair of small tubercles and spines, respectively. Pleurosternal carinae present until segment 18 .....36
36. Metaterga with four transverse rows of very small setigerous tubercles or setae. ♂ tarsal brushes present until leg 6. ♂ femora 5 with a very strong, distoventral, densely pilose adenostyle (Fig. 2F). Gonopod process **h** higher and pointed (Fig. 2A–D). (Fig. 26). Thailand .....*T. flavolineatus* sp. nov.  
 – Metaterga with two transverse rows of small tubercles or spines, respectively ♂ tarsal brushes missing. ♂ legs normal. Gonopod process **h** very small. Vietnam .....*T. maculatus* Golovatch, 1984
37. Paraterga virtually missing (Figs 4A–H, 7A–H) .....38  
 – Paraterga well- or strongly developed (Figs 1A, C, 10B, D, 12B, D, 16B, D, 18B, D, 23B, D) ...39
38. Antennae shorter (Fig. 4A), drawn behind only body segment 2 when stretched dorsally. A small, rounded, densely setose, sternal cone between ♂ coxae 4 (Fig. 4I–J). Gonopod process **h** prominent, while process **z** long and rather slender (Figs 5–6). Thailand .....*T. hongkhraiensis* sp. nov.  
 – Antennae longer (Fig. 7A), reaching behind body segment 3. An entire, high, inverted funnel-shaped, sternal lobe between each of ♂ coxae 3 and 4 (Fig. 7I–J). Gonopod without processes (Figs 8–9). Laos .....*T. moniliformis* sp. nov.
39. Metaterga entirely smooth and polished, devoid of evident tubercles, at best extremely faintly rugulose near transverse sulcus .....40  
 – Metaterga rather clearly rugose/tuberculate/granulate, posterior row of setae at least partly borne on tubercles .....46
40. Transverse sulcus on metaterga starting with segment 3 or 4, but fully developed and reaching bases of paraterga starting with segment 4 or 5. Gonopod process **h** large (Fig. 17A–D) .....41  
 – Transverse sulcus on metaterga starting only with segment 5. Gonopod process **h** small (Fig. 22) ...44
41. Gonopod with a distinct sharp process on lobe **I**. Ventral adenostyles on ♂ legs absent. Southern China .....*T. similis* Golovatch, 2014  
 – Gonopod without processes on lobe **I**. Ventral adenostyles on ♂ legs: a distal knob on femur, a distomedial knob on postfemur, and a parabaasal knob on both tibia and tarsus .....42
42. Head wider than collum and subequal in width to segment 3. Gonopod process **h** at about midlength with a strong ventral outgrowth, while solenophore without processes. Vietnam .....*T. procurvus* Golovatch, 1984  
 – Head narrower than collum. Gonopod process **h** without outgrowths, while process **x** present on solenophore .....43
43. Antennae shorter (Fig. 16A), extending only behind body segment 2 when stretched dorsally. ♂ tarsal brushes present until segment 6. Gonopod process **x** longer, the latter's tip rounded dorsally (Fig. 17A–D). Laos .....*T. dorsalis* sp. nov.

- Antennae longer, reaching until body segment 5. ♂ tarsal brushes present on all segments. Gonopod process **x** shorter, its tip pointed. Vietnam ..... *T. crassipes* Golovatch, 1984
- 44. Small species: width 1.6 mm. Only a single row of 2+2 tergal setae. Metaterga entirely smooth. Adenostyles on ♂ legs present. Vietnam ..... *T. sigma* (Attems, 1953)
  - Body wider than 2.0 mm. Metaterga with two transverse rows of setae or traceable insertion points. Metaterga very finely rugulose only near transverse sulcus. Adenostyles on ♂ legs absent or represented by pads in their stead .....45
- 45. Paraterga broader: 3.1 mm wide. Pleurosternal carinae present until segment 13 or 14. Pads present on ♂ femora, postfemora, tibiae (all distally) and tarsi (almost entirely). Thailand .....
  - ..... *T. pulvinipes* Golovatch & Enghoff, 1993
  - Paraterga narrower: 2.1–2.5 mm wide. Pleurosternal carinae present until segment 17. ♂ legs without pads. Myanmar ..... *T. punctus* sp. nov.
- 46. Metatergal surface polished and smooth except for two rows of conspicuous tubercles .....47
  - Metaterga at least partly rugulose/rugose to granular; at most one row of tubercles .....52
- 47. ♂ legs without adenostyles (= tubercles). Gonopods with process **h** higher than solenophore, strongly twisted, pointed apically. Southern China ..... *T. schawalleri* Golovatch, 2013
  - ♂ legs with adenostyles (= tubercles) at least on segment 6. Gonopods otherwise. Vietnam ...48
- 48. Paraterga very poorly developed, rounded, low, projecting slightly behind rear margin like small knobs only on segments 18 and 19. Calluses virtually devoid of incisions. Transverse sulcus on metaterga poorly developed, starting already with segment 2, although fully developed only starting with segment 5. A paramedian pair of denticles between ♂ coxae 5 behind a prominent, subquadrate lamina between ♂ coxae 4. Gonopod process **h** entirely missing. Thailand .....
  - ..... *T. strongylosomoides* (Korsós & Golovatch, 1989)
  - Paraterga better developed, protruding behind rear margin at least starting with segment 5. Calluses always at least with one lateral incision. Transverse sulcus starting only with segments 3–5. Dentiform tubercles between ♂ coxae 5 missing. Gonopod process **h** invariably present .....49
- 49. Body larger: more than 25 mm long. ♂ tarsal brushes not present on all legs. Gonopod lobe **I** normal ...50
  - Body smaller: less than 18 mm long. ♂ tarsal brushes present on all legs. Gonopod lobe **I** with a spine apically .....51
- 50. ♂ tarsal brushes present on legs 1–15. Pleurosternal carinae present until segment 9. Gonopod process **h** larger, finger-shaped. Vietnam ..... *T. roseiparaterga* Nguyen, 2012
  - ♂ tarsal brushes present on legs 5–30. Pleurosternal carinae present until segment 17. Gonopod process **h** small, slender and pointed. Southern China ..... *T. deharvengi* Liu & Luo, 2013
- 51. Paraterga acutangular caudally and pointed beak-like already starting with collum. Tergal setigerous tubercles: 3+3 and 5+5 on segments 16–19. Adenostyle pattern on ♂ legs: a distal knob on femora and a parbasal knob on most of postfemora, tibiae and tarsi. Gonopod process **h** large, lamellar and sigmoid. Vietnam ..... *T. granulatus* Golovatch, 1984
  - Paraterga acutangular caudally and pointed beak-like only starting with segment 4. 2+2 and 4+4 tergal setigerous tubercles on segments 16–19. Adenostyle pattern on ♂ legs: a proximal finger-shaped tubercle crowned with a bunch of setae only on femora 6, 8 and 9. Gonopod process **h** smaller, spiniform. Vietnam ..... *T. topali* Golovatch, 1984

52. Transverse sulcus on metaterga starting and fully developed only with segment 5. Ventral adenostyles present on all ♂ podomeres except coxa. Vietnam and/or Laos .....53  
 – Transverse sulcus on metaterga starting with segment 4, but fully developed only starting with segment 5. Ventral tubercles only on some of ♂ telopoditomeres. Thailand .....54
53. Metaterga rugulose also in front of transverse sulcus, at rear margin with several oblong tubercles. Sternal lamina between ♂ coxae 4 a pair of setigerous knobs. Neither gonopod lobe **m** nor lobe **I** spinigerous. Vietnam .....*T. tamdaoensis* Korsós & Golovatch, 1989  
 – Metaterga rugose only behind transverse sulcus, without evident tubercles at rear margin. Sternal lamina between ♂ coxae 4 single. Both gonopod lobe **m** and lobe **I** crowned with a spine. Laos and Vietnam .....*T. nodulipes* (Attems, 1953)
54. Metaterga modestly rugulose only near transverse sulcus, posteriorly neither granular nor microtuberculate. Calluses broad. Gonopod process **h** simple, high, never particularly coiled; lobe **I** very moderately serrate at apex .....55  
 – Metaterga distinctly rugose-granular/microtuberculate even on fore halves. Calluses narrow. Gonopod process **h** better developed and more strongly coiled; lobe **I** apically either bare or with a digitiform outgrowth .....56
55. Caudal corner of paraterga pointed starting with segment 3. Pleurosternal carinae particularly well-developed, drawn behind rear margin until segment 16 or 17. Adenostyles often present on ♂ prefemora .....*T. degerboelae* Golovatch & Enghoff, 1993  
 – Caudal corners of paraterga mainly narrowly rounded, pointed only starting with segment 15. Pleurosternal carinae less strongly developed .....*T. pallidus* Golovatch & Enghoff, 1993
56. Coloration dark, brown. Sternal lamina between ♂ coxae 4 a pair of separated setigerous tubercles preceded by another pair of very small tubercles between coxae 3. Gonopod lobe **I** devoid of an apical process .....*T. asper* Golovatch & Enghoff, 1993  
 – Coloration uniformly pale. Sternal lamina between ♂ coxae 4 single, not accompanied by additional tubercles in front or behind. Gonopod lobe **I** with a strong, apical, finger-shaped process .....57
57. Mostly 3+3 tubercles at rear margin of metaterga. Sternal lamina between ♂ coxae 4 distinctly emarginate. Larger adenostyles close to midlength on ♂ postfemora and tibiae, femora with a distal knob. Gonopod process **h** slenderer and shorter, apex of lobule **m** not developed into a spine .....*T. subcoriaceus* Golovatch & Enghoff, 1993  
 – Mostly 4+4 tubercles at rear margin of metaterga. Sternal lamina between ♂ coxae trapeziform. Larger adenostyles on both postfemora and tibiae more distal, femoral knob missing. Gonopod process **h** unusually prominent, with a hook at base; apex of lobule **m** spiniform .....*T. coriaceus* Golovatch & Enghoff, 1993

## Discussion

At the moment, a total of 62 species of *Tylopus* are known from Indochina and the adjacent parts of southern China and Myanmar, including eight new species described above. Most of the species (31, or > 50%) come from Thailand, followed by Vietnam (18), Laos (6), southern China (6) and Myanmar (3). Country endemism is close to 100%, as only *T. doriae* and *T. nodulipes* have been recorded from two of the countries at once. There is little doubt, however, that the above outlined picture is still far from final.

Having collected millipedes throughout Thailand and Laos, we can state that most of the *Tylopus* species are quite rare and restricted in distribution, even though many occur sympatrically if not syntopically.

Thus, the Doi Inthanon and Doi Suthep mountains, both in northern Thailand, support at least 10 congeners each (Likhitrakarn *et al.* 2014a). It seems that such sympatric assemblages are represented by a number of phenofaunas separated by certain time periods rather than a geographic distance. As a result, the adults of most of the known species have only been collected once and from a single locality, with repeated collecting success being rather an exception than a rule.

An additional factor to be considered, the one that only makes the picture even more complicated, lies in the fact that the bulk of *Tylopus* diversity appears to be confined to montane woodlands exceeding 500 m in elevation. This only exacerbates the situation as too many of such places are difficult to access and thus only contribute to the abundant lacunae to be covered by future collecting efforts. Given the highly mosaic, often relictual distribution of mountainous forests in the regions concerned, against the background of too numerous undercollected to completely unsampled mountainous areas across most of Indochina, as well as southern China and the East Indies, the real diversity of *Tylopus* can still be very generously termed as highly underestimated. Thus, during the past two decades, since the first large review of *Tylopus* which focused on the fauna of Thailand alone (see Golovatch & Enghoff 1993), the number of described congeners known to occur in that country has nearly doubled, whereas the whole generic diversity tripled. Yet Cambodia remains a complete *terra incognita* in this respect (Likhitrakarn *et al.* 2015).

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