



Three new species of the Oriental millipede  
genus *Tylopus* Jeekel, 1968 (Diplopoda,  
Polydesmida, Paradoxosomatidae)  
from China and Laos

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Nam Non cave, inside the cave entrance; in médaillon: *Tylopus namnonensis* Likhitrakarn, n. sp. ♀ paratype, dorsal view in live color pattern.

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# Three new species of the Oriental millipede genus *Tylopus* Jeekel, 1968 (Diplopoda, Polydesmida, Paradoxosomatidae) from China and Laos

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## KEY WORDS

Sulciferini,  
key,  
Indochina,  
endemism,  
new species.

## ABSTRACT

Three new species of *Tylopus* Jeekel, 1968 are described, one from southwestern China, *T. tropicalis* Likhitrakarn, n. sp., and two from Laos, *T. namnonensis* Likhitrakarn, n. sp. and *T. khikheb* Likhitrakarn, n. sp. Keys are compiled to all nine and 15 species of *Tylopus* currently known to occur in China and Laos, respectively.

## RÉSUMÉ

Trois nouvelles espèces du genre oriental de mille-pattes *Tylopus* Jeekel, 1968 (Diplopoda, Polydesmida, Paradoxosomatidae) de Chine et du Laos.

## MOTS CLÉS

Sulciferini,  
clé,  
Indochine,  
endémisme,  
espèces nouvelles.

Trois nouvelles espèces de *Tylopus* Jeekel, 1968 sont décrites, une du sud-ouest de la Chine, *T. tropicalis* Likhitrakarn, n. sp., et deux du Laos, *T. namnonensis* Likhitrakarn, n. sp. et *T. khikheb* Likhitrakarn, n. sp. Des clés sont compilées pour les neuf et 15 espèces de *Tylopus* actuellement connues en Chine et au Laos, respectivement.

## INTRODUCTION

The Oriental millipede genus *Tylopus* Jeekel, 1968 is known to be one of the most species-rich not only within the family Paradoxosomatidae Daday, 1889, but also in the entire class Diplopoda, presently encompassing 80 species that range from southern China in the north (Golovatch & Liu 2020) to Thailand, Myanmar and Indochina in the south (Likhitrakarn *et al.* 2010, 2014, 2016, 2021; Nguyen 2012; Nguyen & Eguchi 2022; Srisonchai *et al.* 2023). Chiefly occurring in montane forests, these millipedes show a remarkable range of ecological adaptations that allows them to live at 350–4025 m a.s.l. (Golovatch & Liu 2020).

This study is devoted to descriptions of another three new species of *Tylopus*, one from southwestern China, *T. tropicalis* Likhitrakarn, n. sp., and two from Laos, *T. namnonensis* Likhitrakarn, n. sp. and *T. khikheb* Likhitrakarn, n. sp. In addition, keys are compiled to all nine and 15 species of *Tylopus* currently known to occur in China and Laos, respectively. The newly discovered species primarily inhabit high-altitude forests and show pronounced short-range endemism (SRE), emphasizing the crucial need for further exploration and documentation in these regions.

Despite several taxonomic revisions and new refined diagnoses (Jeekel 1965, 1968; Golovatch & Enghoff 1993; Likhitrakarn *et al.* 2010, 2016), the focus has primarily been on adding new species descriptions, distribution maps, and identification keys. Over the last decade, there has been a substantial rise in the discovery of new *Tylopus* species. The current record of *Tylopus* species in Indochina and the adjacent areas of southern China has reached 80 (Nguyen 2012; Golovatch 2013, 2014, 2018, 2019, 2020; Liu & Luo 2013; Likhitrakarn *et al.* 2014, 2016, 2021; Golovatch *et al.* 2016; Nguyen & Eguchi 2022; Srisonchai *et al.* 2023), but there can be little doubt this estimate will considerably increase with further explorations of and collections in the regions concerned.

The present study contributes to our knowledge of *Tylopus* diversity by describing a new species from southern China and another two from northern Laos. We also provide updated identification keys to all *Tylopus* species currently known to occur in these countries.

## MATERIAL AND METHODS

New specimens were collected manually in China and Laos between 2015 and 2022. Fieldwork participants included Somsak Panha and members of the Animal Systematics Research Unit at Chulalongkorn University, as well as a team from the Fédération française de Spéléologie, Commission scientifique, Groupe d'Étude de Biospéologie, France, led by Josiane Lips.

All animals were euthanized humanely following the American Veterinary Medical Association's guidelines for animal euthanasia (2020). They were then preserved in a 75% ethanol solution for further morphological examination. The Animal Care and Use Protocol Review No. 1723018 was applied.

Live specimens were photographed in the field using an Olympus Tough 4 digital camera and in the laboratory using a Nikon 700D digital camera with a Nikon AF-S VR 105 mm macro lens. Subsequently, specimens were examined, measured, and photographed under a Nikon SMZ 745T trinocular stereo microscope equipped with a Canon EOS 5DS R digital SLR camera. Images were processed and edited with Adobe Photoshop CS6. Line drawings were created based on photographs and further examination under the stereo microscope equipped with a digital SLR camera. For scanning electron microscopy (SEM), gonopods were coated with an 8 nm gold layer using a CCU-010 high vacuum sputter and a carbon coater (Safematic). Images were captured with a TESCAN VEGA3 scanning electron microscope operated at 5 keV acceleration voltage. Following SEM examination, gonopods were returned to 75% ethanol.

Coordinates and elevations were recorded using Garmin GPSMAP 60 CSx and Garmin eTrex 30 devices with the WGS84 datum. The accuracy of recorded data was subsequently verified using Google Earth Pro ver. 7.3.6.

## ABBREVIATIONS

CUMZ Museum of Zoology, Chulalongkorn University, Bangkok.

## Morphology

The terminology for denoting the gonopodal and somatic structures primarily follows Golovatch & Enghoff (1993) and Likhitrakarn *et al.* (2010, 2016).

## Gonopodal structures

a	adenostyle;
cx	coxite;
fe	femorite;
h	process h;
l	lobe l;
m	process m;
pfe	prefemoral part;
slm	solenomere;
sph	solenophore;
x	process x.

## SYSTEMATICS

Family PARADOXOSOMATIDAE Daday, 1889  
 Subfamily PARADOXOSOMATINAE Daday, 1889  
 Tribe Sulciferini Attems, 1898

Genus *Tylopus* Jeekel, 1968

*Agnesia* Attems, 1953: 174.

*Tylopus* Jeekel, 1968: 60.

*Paratylopus* Korsós & Golovatch, 1989: 215.

TYPE SPECIES. — *Agnesia nodulipes* Attems, 1953, by original designation.

EMENDED DIAGNOSIS. — Body medium-sized to large (c. 10–44 mm long, c. 0.5–5.1 mm wide), with 20 segments. Paraterga from virtually missing to strongly developed, usually with lateral incisions. Transverse metatergal sulcus distinct. Leg relatively long and slender,





FIG. 1. — *Tylopus tropicalis* Likhitrakarn, n. sp., ♂ holotype: **A**, habitus, live coloration; **B, C**, anterior part of body, dorsal and lateral views, respectively; **D, E**, rings 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. Scale bars: A, D, G, 0.5 mm; B, C, E, F, H, 1 mm; I, 0.2 mm; J, 0.3 mm.

most species present adenostyles (= ventral outgrowths) at least on some of the male legs. ♂ tarsal brushes usually present. A sternal lobe between ♂ coxae 4 present.

The gonopod telopodite typically features a prominent transverse ring, or cingulum, demarcating the postfemoral region which starts at the base of a free, flagelliform solenomere. This solenomere is largely sheathed by a slender, sigmoid solenophore that often bears basal outgrowths. The cingulum is rarely incomplete, usually due to a reduced sulcus at the base of a postfemoral lobe l. While lobe l itself is usually simple, sometimes it can be crowned with an additional outgrowth or process. Beyond lobe l, the postfemoral region usually possesses a medially positioned process h. Additional disto- and/or postfemoral outgrowth appearing even more sporadically is process z, more variable, albeit occasionally reduced or even absent. Only a few species show particularly complex gonopods, where not only is the postfemoral region supplied with a long, spiniform process z, but also with a small to elongated, knife- or spine-shaped outgrowth m on the distodorsal portion of the femorite (Golovatch & Enghoff 1993; Likhitrakarn *et al.* 2010).

#### REMARK

Full reviews of this genus were performed by Golovatch & Enghoff (1993) and Likhitrakarn *et al.* (2010).

*Tylopus tropicalis*  
Likhitrakarn, n. sp.  
(Figs 1-3)

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**TYPE MATERIAL.** — **Holotype.** China • ♂; Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Xishuangbanna Tropical Botanical Garden; c. 600 m a.s.l.; 21°55'03.1"N, 101°16'17.2"E; 26.XI.2016; C. Sutcharit leg.; CUMZ-PD0028.



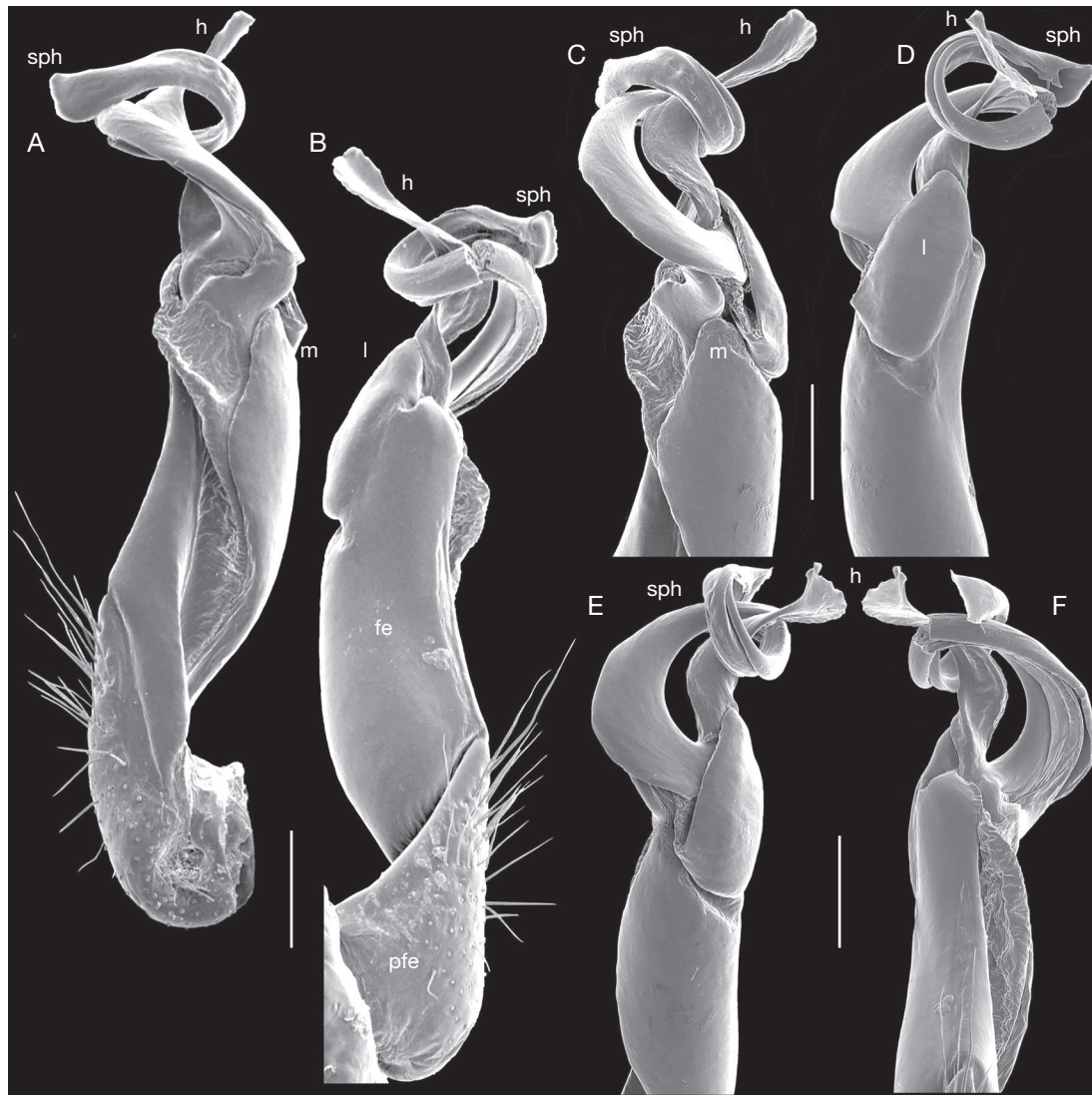


FIG. 2. — *Tylopus tropicalis* Likhitrakarn, n. sp., ♂ holotype, right gonopod: **A, B**, mesal and lateral views, respectively; **C-F**, distal part, submesal, sublateral, subcaudal and suboral views, respectively. Scale bars: 0.2 mm. Abbreviations: **fe**, femur; **h**, process h; **l**, lobe l; **m**, process m; **pfe**, prefemoral part; **sph**, solenophore.

**ETYMOLOGY.** — The species is so named to emphasize the tropical forest habitat of the type locality where the holotype was collected; adjective.

**DIAGNOSIS.** — The new species seems to be particularly similar to both *T. spinisterna* Nguyen, 2012 from Vietnam and *T. schawalleri* Golovatch, 2013 from China, especially in its gonopodal conformation. Indeed, these species share a stout, high and suberect process h. However, the new species differs from *T. spinisterna* by having the solenomere more strongly twisted and longer than process h (Figs 2; 3A, B); the caudal corner of midbody paraterga is pointed and more strongly protruded behind (Fig. 1D), while midbody sterna show no modifications (Fig. 1G). The new species differs from *T. schawalleri* in having longer antennae, in the shape of sternal lobes between ♂ coxae 4, coupled with the pleurosternal carinae being complete crests with evident, sharp, caudal denticles produced past the rear tergal margin on rings 2-8 (Fig. 1C), gradually decreasing in size until ring 15 (Fig. 1H) (vs complete crests only on rings 2-7 and gradually decreasing in size until ring 11) and femora 4-12 each with an adenostyle distally on ventral side (Fig. 3D, C) (vs adenostyles absent).

**DESCRIPTION**

Length *c.* 20 mm, width of midbody pro- and metazona 1.6 and 2.4 mm, respectively (♂).

Coloration of live animals dark castaneous brown (Fig. 1A), with contrasting light brown calluses of paraterga; venter and legs yellowish brown; coloration of alcohol material after five years of preservation faded to dark brown; calluses of paraterga yellowish brown to pallid, venter and legs light brown to light yellowish (Fig. 1B-J).

Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae long (Fig 1A), reaching to ring 4 when stretched dorsally. In width, head < ring 3 < ring 4 < collum < ring 2 < 5 < 6 < 7-16 (Fig. 1B), thereafter body gently and gradually tapering. Collum with three transverse rows of strong setae: 3+3 anterior, 2+2 intermediate, and 3+3 posterior; a small lateral incision near midway; caudal corner very broadly rounded, paraterga declined ventrad, not produced past rear tergal margin (Fig. 1B, C).



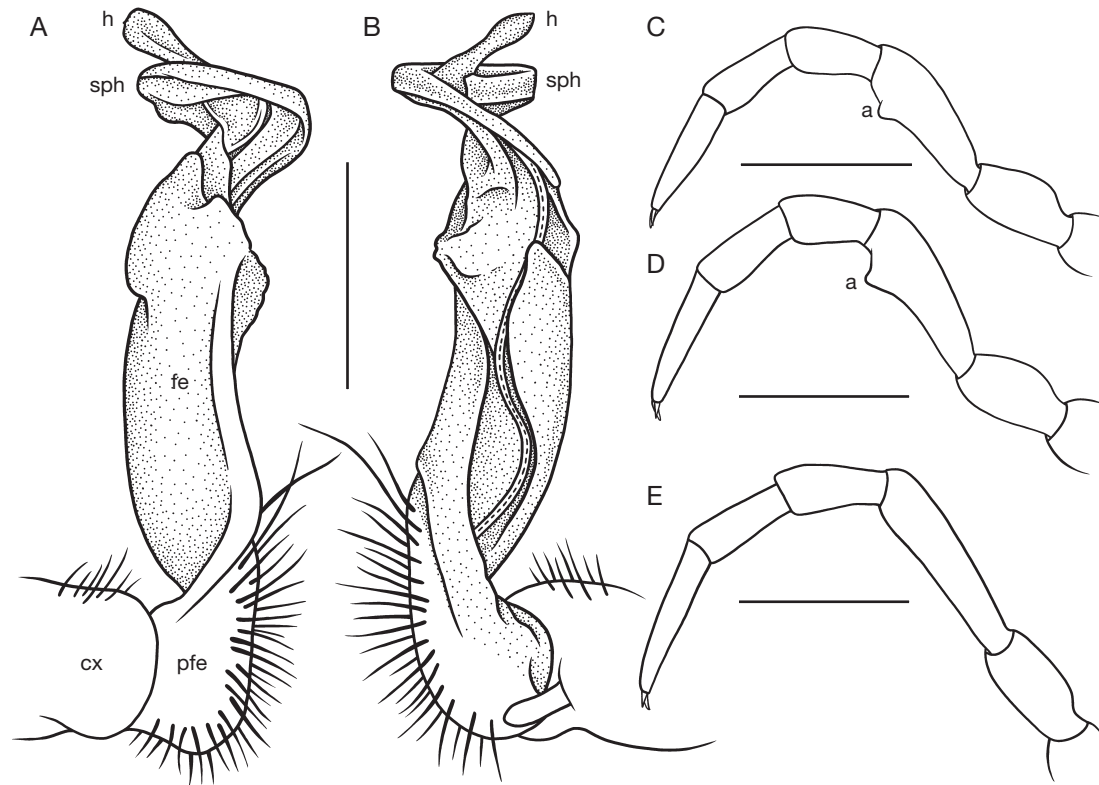


FIG. 3. — *Tylopus tropicalis* Likhitrakarn, n. sp., ♂ holotype: **A, B**, right gonopod, lateral and mesal views, respectively; **C–E**, leg of rings 4, 6 and 10, respectively. Scale bars: 0.5 mm. Abbreviations: **a**, adenostyle; **cx**, coxa; **fe**, femur; **h**, process h; **l**, lobe l; **m**, process m; **pfe**, prefemoral part; **sph**, solenophore.

Tegument smooth and shining, prozona finely shagreened, metaterga smooth and leathery, posterior halves often rugulose, surface below paraterga microgranulate (Fig. 1A–F, H). Postcollum metaterga with two transverse rows of rather long setae: 2 + 2 in anterior and 2 + 2 in posterior row, the latter often abraded, but then readily traceable as insertion points. Tergal setae long, strong, slender, about 1/3 metatergal length. Axial line visible both on pro- and metazona. Paraterga strongly developed (Fig. 1B, D, F), subhorizontal, slightly upturned posteriorly, always lying high, at upper 1/3 midbody height, but remaining below dorsum; anterior edge well-developed, mostly regularly rounded and narrowly bordered, fused to callus; caudal corner narrowly rounded, extending increasingly past rear tergal margin, especially strongly curved mesad on rings 15–19, posterior edge oblique (Fig. 1D, F); paraterga very thin blunt blades in lateral view, a little thicker only on pore-bearing rings (Fig. 1E). Calluses on paraterga delimited by a sulcus only dorsally. Paraterga 2 broad, lateral edge with an evident incision in anterior 1/3 and a small knob in posterior 1/3. Paraterga 3 and 4 with two small incisions at lateral edge (Fig. 1B), one in anterior 1/3, the other at posterior 1/3; anterior incision particularly evident. Lateral edge of following paraterga with two small incisions, one in anterior 1/3, the other at midway, caudal incision being smaller in pore-bearing rings (Fig. 1D). Ozopores evident, lateral, lying in an ovoid groove at about 1/3 metatergal length in front of posterior edge of metaterga (Fig. 1D, E). Transverse sulcus usually distinct (Fig. 1B, D, F), slightly incomplete

on rings 4 and 18, complete and clearly visible on metaterga 5–17, deep, reaching the bases of paraterga, arcuate, ribbed at bottom. Stricture between pro- and metazona rather wide, deep, ribbed at bottom down to base of paraterga (Fig. 1C, D). Pleurosternal carinae complete crests on rings 2–8, thereafter broken into an anterior bulge and a caudal tooth, both growing increasingly reduced until ring 15, thereafter missing (Fig. 1C, E, H).

Epiproct (Fig. 1F–H) conical, flattened dorsoventrally, subtruncate, with two evident apical papillae directed caudally, both pointed at tip; pre-apical papillae small, but evident, lying close to tip. Hypoproct subtrapeziform (Fig. 1G), small setiferous knobs at caudal edge well-separated and evident.

Sterna sparsely setose, without modifications (Fig. 1G); cross-impressions shallow; a single, linguiform, sternal lobe between ♂ coxae 4 (Fig. 1I, J). Legs long and slender, midbody ones *c.* 1.3–1.4 as long as body height (Fig. 3E); femora 5–11 each with a large adenostyle distally on ventral side (Fig. 3D), a smaller adenostyle on each of femora 4 and 12 (Fig. 3C); tarsal brushes present until ring 16 (♂).

Gonopods simple (Figs 2; 3A, B); coxite (cx) a little curved caudad, sparsely setose distoventrally. Prefemorite (pfe) densely setose, as usual, about 1/3 as long as femorite + “postfemoral” part. Femorite (fe) rather slender, expanded distad, slightly curved, showing a mesal groove; lobe l simple; process m evident; solenophore (sph) long and slender, typically coiled, tip subtruncate; process h strongly developed, curved and acute, expanded distad, set higher than solenophore.

KEY TO SPECIES OF *TYLOPUS* JEEKEL, 1968 CURRENTLY KNOWN TO OCCUR IN CHINA,  
CHIEFLY BASED ON ♂ CHARACTERS, MODIFIED AFTER GOLOVATCH (2013)

1. Paraterga moderately developed, never pointed beak-like caudally, ratio of ♂ midbody prozonite to metazonite width < 1:1.2 ..... 2  
— Paraterga relatively well-developed (Fig. 1B, D), pointed beak-like caudally, ratio of ♂ midbody prozonite to metazonite width > 1:1.2 ..... 5
2. Coloration pale yellowish brown. Gonopod relatively simple, process h poorly developed, no additional outgrowths near base. .... *T. sinensis* Golovatch, 1995  
— Coloration light brown to blackish brown. Gonopods more complex ..... 3
3. Body smaller: length 17-20 mm. Coloration light brown. ♂ tarsal brushes present until ring 9. Gonopod process h present, hook-shaped and pointed ..... *T. uncinatus* Golovatch, 2020  
— Body larger: length ca 21-30 mm. Coloration light to blackish brown. ♂ tibial and tarsal brushes present until ring 17. Gonopod process h absent or present and disk-shaped ..... 4
4. Body smaller: length 21-23 mm. ♂ prefemora clearly swollen laterally. Gonopod process h present, while solenophore with two characteristic distal spines (a and s) ..... *T. similis* Golovatch, 2014  
— Body larger: length ca 30 mm. ♂ prefemora only very faintly bulged laterally. Gonopod process h absent, while solenophore without spines ..... *T. kabaki* Golovatch, 2014
5. Gonopod very simple, process h absent ..... *T. reductus* Golovatch, 2013  
— Gonopod process h present (Figs 2; 3A, B) ..... 6
6. Body smaller: length 17 mm. Coloration whitish grey with a light brown pattern on pro- and metazona. ♂ legs without adenostyles ..... *T. schawalleri* Golovatch, 2013  
— Body larger: length ca 20-28 mm. Coloration otherwise. ♂ legs with adenostyles (Fig. 3C, D) ..... 7
7. Antennae longer, reaching until ring 4 when stretched dorsally. Only ♂ femora with tuberculiform adenostyles (Fig. 3C, D) ..... *T. tropicalis* Likhitrakarn, n. sp.  
— Antennae shorter, extending only behind ring 2 or 3 when stretched dorsally. ♂ femora, postfemora, tibiae and tarsi with tuberculiform adenostyles ..... 8
8. Gonopod process h a very sharp tip and shorter than half solenophore height. Pleurosternal carinae present until ring 17 ..... *T. deharvengi* Liu & Luo, 2013  
— Gonopod process h stout and higher than half solenophore height. Pleurosternal carinae present until ring 11 ..... *T. nigromarginatus* Golovatch, 2018

REMARKS ON *TYLOPUS* SPECIES FROM CHINA

*Tylopus sinensis* Golovatch, 1995 was the first species of *Tylopus* to be documented from China. It was so named to emphasize the country of origin (Golovatch 1995).

Seven new species of *Tylopus* have since been described from China (Golovatch 2013, 2014, 2018, 2020; Liu & Luo 2013). The altitudinal distributions of the *Tylopus* species in China vary from lowland to high-montane (350-4025 m a.s.l.). All congeners appear to be confined to the southwestern parts of the country (Golovatch & Liu 2020). As a result, presently the fauna comprises nine species currently documented from China, including the above new one.

*Tylopus namnonensis* Likhitrakarn, n. sp.  
(Figs 4-6)

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TYPE MATERIAL. — **Holotype.** Laos • ♂; Khammouane Province, Konglor, Tham Nam Non; 175 m a.s.l.; 18°01'44"N, 104°41'26"E; 28.II.2023; J. Lips leg.; CUMZ-27205.

**Paratype.** Laos • 1 ♀; same data as the holotype; CUMZ-27205.

ETYMOLOGY. — To emphasize Nam Non cave, the type locality, one of the biggest caves in Khammouane Province; adjective.

DIAGNOSIS. — This new species closely resembles *T. dorsalis* Likhitrakarn, Golovatch & Panha, 2016, particularly in gonopod conformation. However, this new species is distinguished by the metaterga being roughly microgranulate (vs smooth), the distal position of process x on the solenophore (vs median), the pleurosternal carinae in ♂ extending to ring 13 (vs 16), and the tarsal brushes in ♂ present until ring 12 (vs 6).

DESCRIPTION

Length 22.5 mm (♂), 29.3 mm (♀), width of midbody pro- and metazona 2.2 and 2.8 mm (♂) or 2.7 and 3.5 mm (♀), respectively.

Coloration of live animals light brown (Fig. 4B), with contrasting dark brown to blackish collar covering both pro- and metazona, head, collum, rings 2 and 3 dark brown to blackish, antennae and epiproct light brown, antennomere 7 dark brown, paraterga, venter and legs yellowish brown; coloration of alcohol material after one year of preservation dark brown; paraterga, legs, antennae and epiproct light yellow-brown, antennomere 7 dark brown, head and collum brownish, fol-



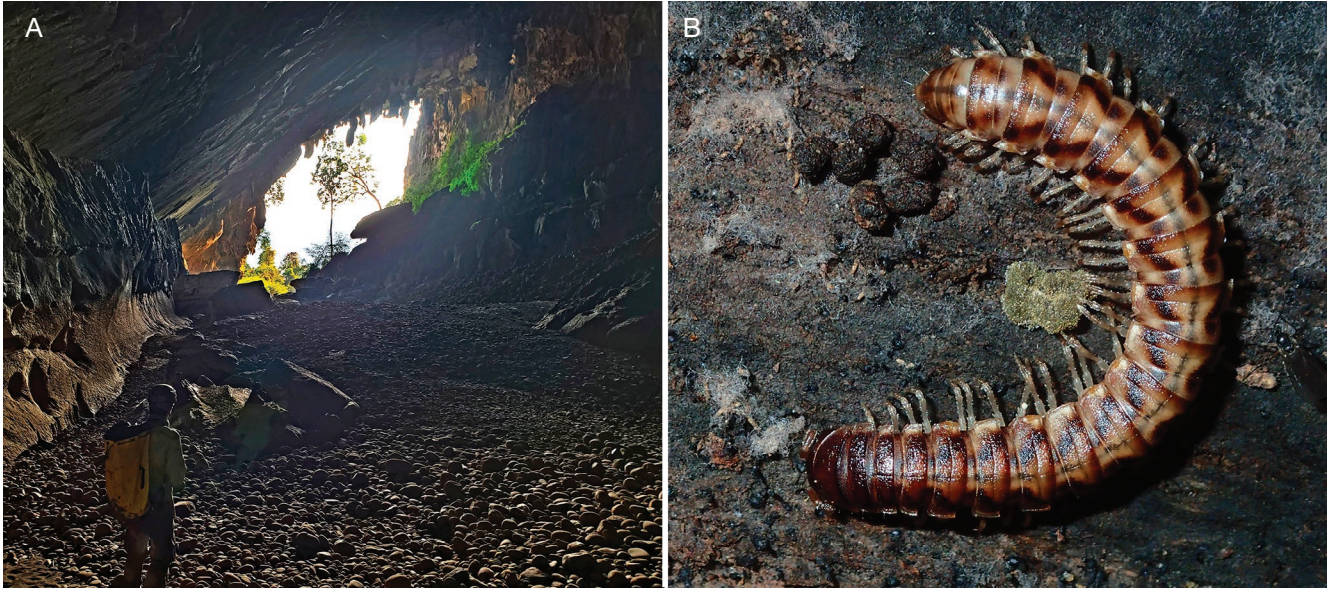


FIG. 4. — *Tylopus namnonensis* Likhitrakarn, n. sp.: **A**, Nam Non cave (the type locality), inside the cave entrance; **B**, ♀ paratype, dorsal view in live color pattern, pictures taken not to scale.



FIG. 5. — *Tylopus namnonensis* Likhitrakarn, n. sp., ♂ holotype: **A**, **B**, anterior part of body, dorsal and lateral views, respectively; **C**, **D**, rings 10 and 11, dorsal and lateral views, respectively; **E**–**G**, posterior part of body, lateral, dorsal and ventral views, respectively; **H**, **I**, sternal cones between coxae 4, subcaudal and sublateral views, respectively. Scale bars: A–G, 0.1 mm; H, I, 0.2 mm.



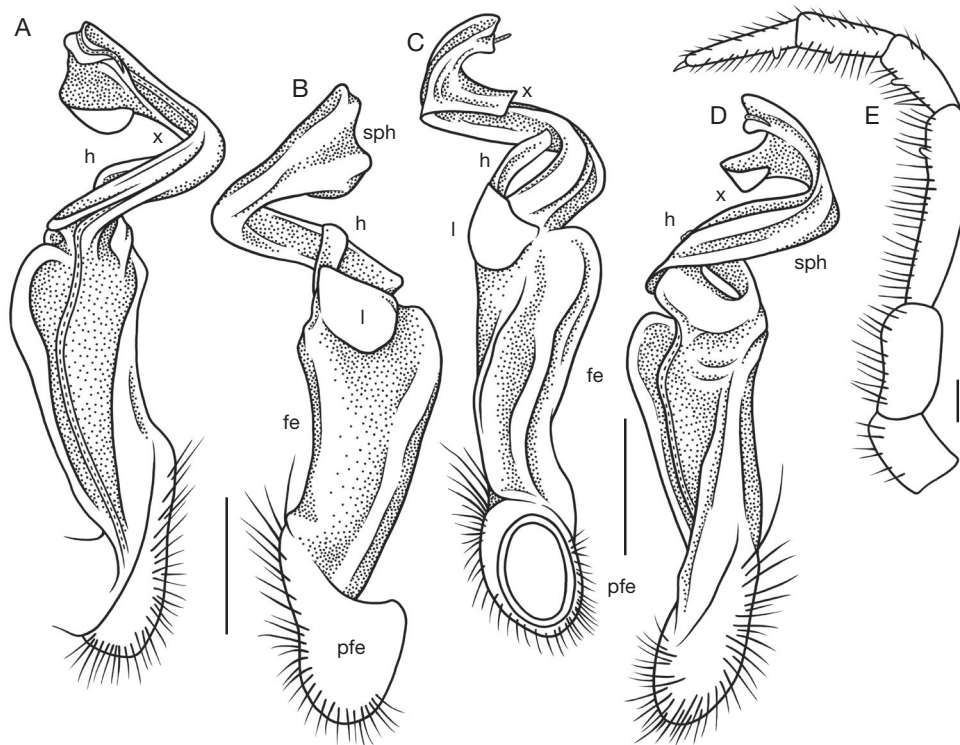


FIG. 6. — *Tylopus namnonensis* Likhitrakarn, n. sp., ♂ holotype, left gonopod: **A-D**, mesal, lateral, caudal and suboral views, respectively; **E**, leg of ring 11. Scale bars: 0.2 mm. Abbreviations: **fe**, femur; **l**, lobe l; **h**, process h; **pfe**, prefemoral part; **slm**, solenomere; **sph**, solenophore; **x**, process x.

lowing terga with a light brown triangle and a blackish collar covering both pro- and metazona (Fig. 5A-F), venter and a few basal podomeres light yellowish to pallid (Fig. 5A, B, E-G).

Clypeolabral region and vertex rather densely setose, epicranial suture distinct. Antennae relatively short (Fig. 5A, B), reaching to body ring 3 when stretched dorsally (♂, ♀). In width, head < ring 3 < 4 < collum < ring 2 < 5 < 6 < 7-16 (♂, ♀), thereafter body gently and gradually tapering towards telson. Collum with three transverse rows of strong setae: 4 + 4 anterior, 1 + 1 intermediate, and 4 + 4 posterior; a small, lateral, setigerous incision near midway; caudal corner very broadly rounded, paraterga declined ventrad, not produced past rear tergal margin (Fig. 5A, B).

Tegument dull and shining, prozona finely shagreened, metaterga often roughly microgranulate and rugulose, leathery, surface below paraterga more delicately, but still sufficiently clearly microgranulate and rugulose (Fig. 5A-F). Postcollum metaterga with two transverse rows of rather long setae: 2 + 2 in anterior and 3 + 3 in posterior row, the latter often abraded, but then readily traceable as insertion points. Tergal setae long, strong, slender, about 1/4 metatergal length. Axial line well visible on metazona, traceable also on prozona. Paraterga strongly developed (Fig. 5A-G), especially so in ♂, set rather high (at upper 1/3 body height), slightly upturned, but lying below dorsum; anterior edge broadly rounded and narrowly bordered, fused to callus; caudal corner rather narrowly rounded, extending increasingly past rear tergal margin, especially well curved mesad on rings 16-19, posterior edge oblique (Fig. 5F, G); paraterga very thin blunt blades in lateral view,

a little thicker only on pore-bearing rings (Fig. 5D). Calluses on paraterga delimited by a sulcus both dorsally and ventrally. Paraterga 2 broad, horizontal, anterior edge angular, lateral edge with three evident incisions: two in anterior 1/3, one at midway, and the smallest one near a very broadly rounded caudal corner. Paraterga 3 and 4 each with two small incisions at lateral edge (Fig. 5A), one in anterior 1/3, the other at posterior 1/3. Following paraterga each with one evident lateral incision in anterior 1/3 (Fig. 5C). Ozopores evident, lateral, lying in an ovoid groove at about 1/3 metatergal length in front of posterior edge of metaterga (Fig. 5B, D). Transverse sulcus usually distinct (Fig. 5A, C, F), slightly incomplete on ring 19, complete and clearly visible on metaterga 5-18, narrow, deep, reaching the bases of paraterga, ribbed at bottom. Stricture between pro- and metazona wide, deep, ribbed at bottom down to base of paraterga (Fig. 5A, C, F). Pleurosternal carinae complete crests on rings 2-4 (♂, ♀), clearly increasing in size on rings 5-7, thereafter broken into an anterior small bulge and a small and sharp caudal tooth, both growing increasingly reduced until ring 13, thereafter missing (♂) (Fig. 5B, D, E), or increasingly reduced and remaining only a small caudal tooth until ring 8, thereafter missing (♀). Epiproct (Fig. 5E-G) conical, flattened dorsoventrally, subtruncate, with two evident apical papillae directed caudally, both pointed at tip; pre-apical papillae small, but evident, lying close to tip. Hypoproct subtrapeziform (Fig. 5G), small setiferous knobs at caudal edge well-separated and evident.

Sterna sparsely setose, without modifications (Fig. 5G); cross-impressions shallow; a large, central, slightly bifid, setose



lobe between ♂ coxae 4 (Fig. 5H, I). Legs long and slender, midbody ones *c.* 1.2-1.4 (♂) or 0.9-1.1 times (♀) as long as body height; prefemora not swollen, legs on rings 6-8 each with a small adenostyle on postfemur and tibia; legs of rings 9-16 each with a small adenostyle on femur, postfemur, tibia and tarsus (Fig. 6E); telopodites particularly densely setose ventrally (Fig. 6E), tarsal brushes present until ring 12.

Gonopods rather simple (Fig. 6A-D). Prefemorite (pfe) densely setose, about 1/3 as long as femorite + “postfemoral” part. Femorite (fe) slightly curved and stout, with an evident mesal groove and a clear distolateral sulcus demarcating a postfemoral part; lobe l simple (Fig. 6B, C); process h rather short, mediodorsal, flattened, tip rounded and with a small notch (Fig. 6B, C); solenophore (sph) long and slender, typically coiled, expanded distad, flattened and evidently bifid, with process x being elongated, apically rounded and directed forward (Fig. 6A, C, D).

#### REMARKS

The specimens were collected inside a cave (Fig. 4A), around 500 meters away from the entrance. In the wet season, an underground river takes up all of the gallery. Big trees and a lot of wood remains are carried inside. The specimens were collected on wood debris. Despite formally coming from a cave, this new species seems to be nothing more than a troglodene.

### *Tylopus khikheb* Likhitrakarn, n. sp. (Figs 7-9)

[urn:lsid:zoobank.org:act:891AC1DA-5662-430E-A530-82BCC718FE0C](https://doi.org/10.21203/rs.3.rs-2911111/v1)

**TYPE MATERIAL.** — **Holotype.** Laos • ♂; Vientiane Prefecture, Muang Fuang District, Ban Thoua Village, near Pha Thor Nor Kham; *c.* 250 m a.s.l.; 18°41'58"N, 102°07'58"E; 29.VI.2023; Sutcharit C. and Jeratthitikul E. leg.; CUMZ-PD0030.

**Paratypes.** Laos • 1 ♂, 3 ♀; same data as the holotype; CUMZ-PD0030.

**ETYMOLOGY.** — “Khikheb” is a vernacular name commonly used in the northeastern regions of Thailand and in Laos to denote a flat-backed millipede (Polydesmida); noun in apposition.

**DIAGNOSIS.** — Differs from all known congeners in showing almost missing to very poorly developed paraterga. This new species resembles *T. hongkhaiensis* Likhitrakarn, Golovatch & Panha, 2016, from northern Thailand, *T. moniliformis* Likhitrakarn, Golovatch & Panha, 2016, from southern Laos, and *T. bokorensis* Srisonchai & Likhitrakarn, 2023, from southern Cambodia, but it differs from both *T. moniliformis* and *T. bokorensis* by having a sternal cone between ♂ coxae 4 (Fig. 7I, J) (*vs* a lobe between each ♂ coxae 3 and 4); the distal part of the solenophore showing a constriction (Figs 8; 9) (*vs* being expanded or wide). *Tylopus khikheb* Likhitrakarn, n. sp. differs from *T. hongkhaiensis* by the postfemoral part of the gonopod showing neither process h nor z (Figs 8; 9) (*vs* with evident processes h and z).

#### DESCRIPTION

Measurements (n = 5; ♂, n = 2; ♀, n = 3). Length 16.3-18.7 mm (♂), 18.5-21.3 mm (♀), width of midbody pro- and metazona 0.8-1.1 and 1.1-1.3 mm (♂) or 0.9-1.2 and 1.1-1.4 mm (♀), respectively.

Coloration of live animals dark brown (Fig. 7A) with lighter brown metaterga; 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 yellow-brown to pallid, venter and a few basal podomeres light yellowish to pallid (Fig. 7B-J).

Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae moderately long (Fig. 7A), extending past ring 3 (♂, ♀) when stretched dorsally. In width, > ring 3 < 4 < collum < ring 2 < 5 < 6-17 < head (♂, ♀); body gently and gradually tapering on rings 18-20. Collum with three transverse rows of setae: 4 + 4 anterior, 2 + 2 intermediate and 3 + 3 posterior; a very faint marginal incision laterally in posterior 1/3; caudal corner very narrowly rounded, not drawn past rear tergal margin (Fig. 7A-C).

Tegument smooth and shining, prozona 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 3 + 3 posterior, pattern traceable at least as insertion points. Tergal setae simple, slender, rather short, about 1/6 metatergal length. Axial line barely traceable on pro- and metazona (♂, ♀). Paraterga 2 well-developed (Fig. 7B, C), horizontal, anterior edges protruded anteriorly, fore corner bent ventrad, pointed; lateral edge with two minute incisions at about 1/3 paratergal length in front of posterior edge of paraterga; caudal corner very narrowly rounded (Fig. 7B). Paraterga 3 and 4 rounded and smooth, expanded laterally. Following paraterga virtually missing, on pore-bearing rings traceable only as small, rounded, laterally expanded bulges (♂) or small, rounded, laterally expanded bulges on all rings, larger on ♀ pore-bearing rings than in ♂.

Ozopores (Op) evident (Fig. 7C, E, H), lateral, each lying in an ovoid groove at about 1/3 metatergal length in front of posterior edge of metaterga. Transverse sulcus usually distinct (Fig. 7C, D, F), incomplete on ring 18, complete on rings 5-17 (♂, ♀), very narrow, not reaching the bases of paraterga, at most faintly beaded at bottom. Stricture between pro- and metazona wide, rather deep, beaded at bottom down to base of paraterga (Fig. 7B-F, H). Pleurosternal carinae complete crests with a sharp caudal tooth on rings 2 and 3, reduced and remaining a sharp caudal tooth on ring 4, thereafter missing (♂, ♀) (Fig. 7C, E, H).

Epiproct (Fig. 7F-H) rather short, flattened dorsoventrally, tip subtruncate, subapical lateral papillae small, but visible, lying close to tip. Hypoproct roundly subtrapeziform, small setigerous knobs at caudal edge well-separated (Fig. 7G).

Sterna sparsely setose, without modifications (Fig. 7G); an entire, high, inverted funnel-shaped, sternal lobe between ♂ coxae 4 (Fig. 7I, J). A paramedian pair of evident tubercles in front of gonopod aperture. Legs very long and slender, slightly thicker in ♂, midbody ones *c.* 1.3-1.5 (♂) or 1.2-1.4 times (♀) as long as body height, prefemora without modifications, ♂ tarsal brushes absent.

Gonopods very simple (Figs 8; 9); coxite (cx) slightly curved caudad and sparsely setose distoventrally. Prefemorite



FIG. 7. — *Tylopus khikheb* Likhitrakarn, n. sp., ♂ holotype: **A**, habitus, live coloration; **B, C**, anterior part of body, dorsal and lateral views, respectively; **D, E**, rings 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. Scale bars: A-H, 0.5 mm; I, 0.2 mm; J, 0.3 mm.

(pfe) densely setose, as usual, about 1/3 as long as femorite + “postfemorite” part. Femorite (fe) straight and rather stout, slightly expanded distad, showing a distinct mesal groove, without outgrowths except for a low, sometimes poorly delimited lobe l; solenophore (sph) clearly coiled, flattened, suberect distally, devoid of processes.

REMARKS ON *TYLOPUS* SPECIES FROM LAOS

*Tylopus nodulipes* (Attems, 1953), the type species of *Tylopus* was originally reported from two localities: Luang Prabang Province, Laos and Mount Fan-Si-Pan, Lao Cai Province,

Vietnam (Attems 1953). The male from Luang Prabang, Laos, was subsequently selected as the lectotype of this species (Likhitrakarn *et al.* 2014). Further records concerned Vietnam (Nguyen 2012), but none Laos.

Later, 11 further species of this genus were described from Laos (Likhitrakarn *et al.* 2016; Golovatch 2018). Finally, a new species, *T. panhai*, has recently been added (Srisonchai *et al.* 2023).

Consequently, a total of 15 species of *Tylopus* have been documented from Laos, including two new ones described above.



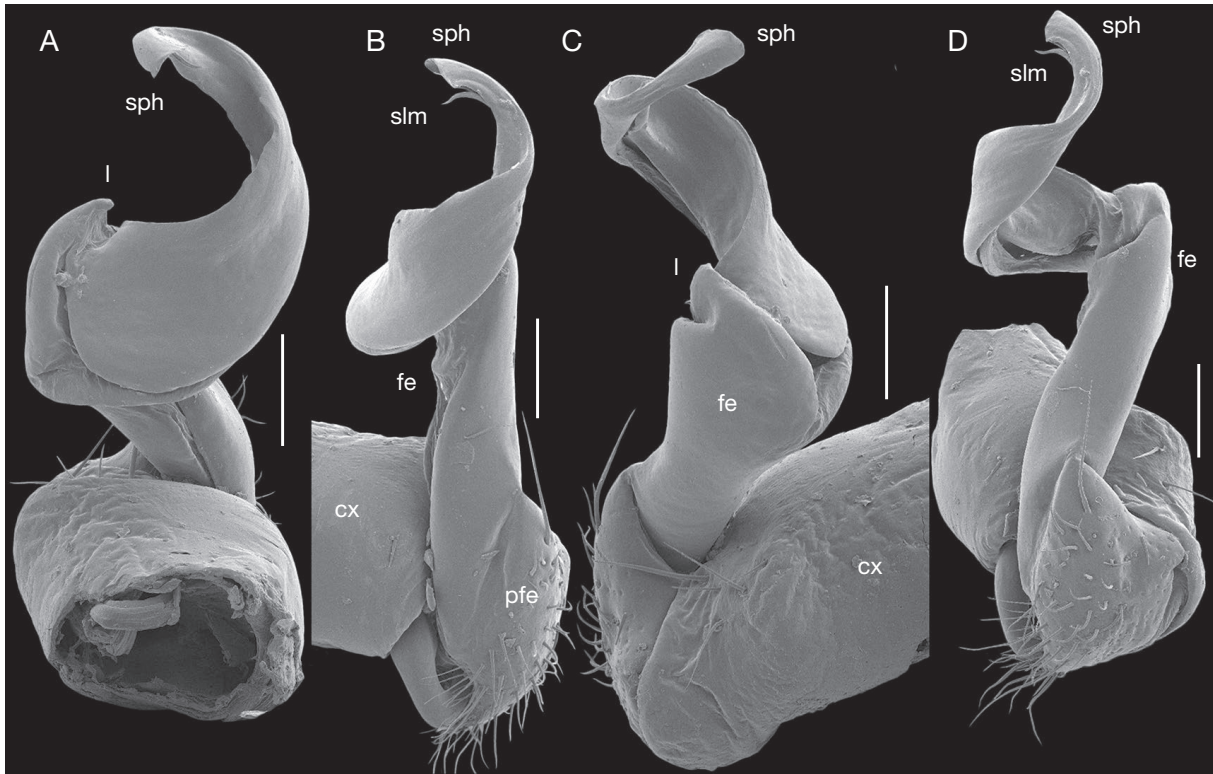


FIG. 8. — *Tylopus khikheb* Likhitrakarn, n. sp., ♂ holotype, left gonopod: **A-D**, subcaudal, submesal, sublateral and suboral views, respectively. Scale bars: 0.2 mm. Abbreviations: **cx**, coxa; **fe**, femur; **l**, lobe I; **pfe**, prefemoral part; **slm**, solenomere; **sph**, solenophore.

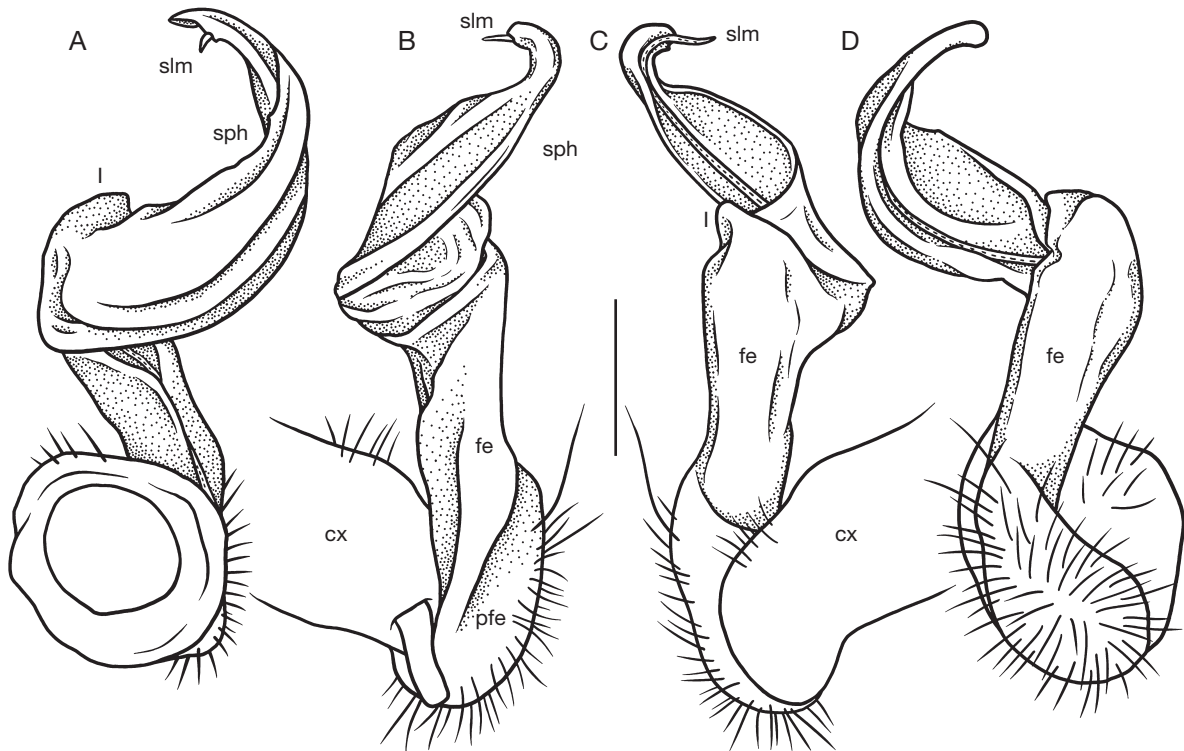


FIG. 9. — *Tylopus khikheb* Likhitrakarn, n. sp., ♂ holotype, left gonopod: **A-D**, subcaudal, mesal, lateral and suboral views, respectively. Scale bar: 0.2 mm. Abbreviations: **cx**, coxa; **fe**, femur; **l**, lobe I; **pfe**, prefemoral part; **slm**, solenomere; **sph**, solenophore.

KEY TO SPECIES OF *TYLOPUS* JEEKEL, 1968  
 KNOWN TO OCCUR IN LAOS (BASED ON MALE CHARACTERS)

1. Body moniliform (Fig. 7A-H). Paraterga present only on rings 2-4, thereafter missing ..... 2  
 — Body not moniliform. Paraterga well-developed on most rings (Fig. 5A-G) ..... 4
2. Both ♂ coxae 3 and 4 with sternal lobes ..... *T. moniliformis* Likhitrakarn, Golovatch & Panha, 2016  
 — A sternal lobe only between ♂ coxae 4 (Fig. 7I, J) ..... 3
3. Body larger: length 16-21 mm. Colour pattern (Fig. 7A) on lighter metaterga. Gonopod process h absent (Figs 8; 9) ..... *T. khikheb* Likhitrakarn, n. sp.  
 — Body smaller: length ca 11 mm. Colour pattern with contrasting lighter paraterga, strictures between pro- and metazona, and insertion spots on metaterga. Gonopod process h present, as high as solenophore .....  
 ..... *T. longisetosus* Golovatch, 2018
4. Collum and following metaterga densely and irregularly hairy. Sternal cones between ♂ coxae 4 isolated .....  
 ..... *T. hirsutus* Golovatch, 2018  
 — Collum and following metaterga not do hairy. Sternal cones between ♂ coxae 4 fused basally into a single lamina ..... 5
5. Metaterga roughly and conspicuously microgranulate ..... 6  
 — Metaterga not microgranulate, dull or smooth ..... 9
6. Adenostyles present (Fig. 6E). Gonopod process x present (Fig. 6A, C, D) ..... 7  
 — Adenostyles absent. Gonopod process x absent ..... 8
7. Coloration blackish, without a cingulate pattern. Tarsal brushes present until ♂ ring 8. Gonopod process z present, process h high, strongly twisted, tip clearly bifid .....  
 ..... *T. thungthaihin* Likhitrakarn, Golovatch & Panha, 2016  
 — Coloration brownish, with a dark cingulate pattern. Tarsal brushes present until ♂ ring 12. Gonopod process z absent, process h short, flattened, tip rounded (Fig. 6A-D) ..... *T. nammonensis* Likhitrakarn, n. sp.
8. Midbody metaterga with two transverse rows of setae, 2+2 and 2+2 in each row, each seta borne on an evident tubercle or knob. Gonopod rather simple: only process h present ..... *T. subtuberculatus* Golovatch, 2018  
 — Midbody metaterga with two transverse rows of setae, 2+2 and 2+2 or 3+3 in each row, mostly traceable due to insertion points. Gonopod rather complex: processes h, z and r present ..... *T. jaegeri* Golovatch, 2018
9. Gonopod process m present ..... 10  
 — Gonopod process m absent ..... 12
10. Colour pattern with contrasting lighter posterior halves of collum and following metaterga and paraterga. Gonopod process m conspicuous, long; process z short without additional tooth, lower than half process h ..... 11  
 — Colour pattern with contrasting lighter paraterga and axial line on each metatergum. Gonopod process m small and short; process z long with a small, ventral, parbasal tooth, higher than process h .....  
 ..... *T. beroni* Golovatch, 2018
11. Gonopod telopodite more slender (slightly longer); process z an inconspicuous, very small lobe. Champasak Province, southwestern Laos ..... *T. panhai* Srisonchai & Likhitrakarn, 2023  
 — Gonopod telopodite stout and thick, expanded distad; process z a conspicuous, rather long and spiniform lobe. Luang Prabang Province, northern Laos ..... *T. nodulipes* (Attems, 1953)
12. Gonopod process z present ..... 13  
 — Gonopod process z inconspicuous or absent ..... *T. retusus* Likhitrakarn, Golovatch & Panha, 2016
13. Tarsal brushes present on legs of rings 2-6. Gonopod process x evident .....  
 ..... *T. dorsalis* Likhitrakarn, Golovatch & Panha, 2016  
 — Tarsal brushes absent or present until ring 18. Gonopod: process x absent ..... 14
14. Tarsal brushes present until ring 18. Gonopod process z evident, rather long and spiniform, longer than half process h ..... *T. altmannae* Golovatch, 2018  
 — Tarsal brushes absent. Gonopod process z very small or absent, shorter than one-third process h .....  
 ..... *T. acuminatus* Likhitrakarn, Golovatch & Panha, 2016



## DISCUSSION

The present study is a contribution to the already remarkable diversity of the genus *Tylopus*, among the largest in the entire family Paradoxosomatidae. With the addition of three new species, it brings it to a total of 83 presently known members. Thailand remains the richest country to support as many as 31 *Tylopus* species (over 34%), followed by Vietnam (24 species), Laos (15 species), southern China (9 species), Myanmar (6 species) and Cambodia (1 species). Further explorations in these regions (Fig. 10) are sure to reveal numerous new records, including a wealth of further congeners.

As previously observed (Likhitrakarn *et al.* 2016; Srisonchai *et al.* 2023), *Tylopus* species tend to demonstrate strong ecological preferences for high-altitude forests, typically dwelling above 500 meters in elevation, especially in northern Laos (Fig. 10). In addition, they tend to largely show very limited geographical distributions, often confined to areas smaller than 4000 square kilometers, earning them the designation of “short-range endemics” (Likhitrakarn *et al.* 2021). This characteristic highlights the high potential for endemism in the still numerous unexplored mountainous regions, particularly in southern China and Laos.

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FIG. 10. — Distribution of newly discovered *Tylopus* species and previously recorded *Tylopus* species in Laos: 1, *T. tropicalis* Likhitrakarn, n. sp.; 2, *T. acuminatus* Likhitrakarn, Golovatch & Panha, 2016; 3, *T. acuminatus* Likhitrakarn, Golovatch & Panha, 2016, *T. dorsalis* Likhitrakarn, Golovatch & Panha, 2016; 4, *T. acuminatus* Likhitrakarn, Golovatch & Panha, 2016, *T. retusus* Likhitrakarn, Golovatch & Panha, 2016; 5, *T. acuminatus* Likhitrakarn, Golovatch & Panha, 2016, *T. jaegeri* Golovatch, 2018; 6, *T. retusus* Likhitrakarn, Golovatch & Panha, 2016; 7, *T. longisetosus* Golovatch, 2018; 8, *T. altmannae* Golovatch, 2018; 9, *T. nodulipes* (Attems, 1953), *T. mutilatus* (Attems, 1953); 10, *T. mutilatus* (Attems, 1953) 11, *T. hirsutus* Golovatch, 2018; 12, *T. thungaihin* Likhitrakarn, Golovatch & Panha, 2016; 13, *T. khikheb* Likhitrakarn, n. sp.; 14, *T. namnonensis* Likhitrakarn, n. sp.; 15, *T. moniliformis* Likhitrakarn, Golovatch & Panha, 2016, *T. subtuberculatus* Golovatch, 2018; 16, *T. panhai* Srisonchai & Likhitrakarn, 2023.

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