

Uncovering Endemism in High Montane Forests: Two New Species of Millipede Genus *Tylopus* Jeekel, 1968 (Diplopoda: Polydesmida: Paradoxosomatidae) from Cambodia and Laos

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ABSTRACT.— Two new species of the predominantly Indochinese to southern Chinese millipedes belonging to the genus *Tylopus* Jeekel, 1968 are described: *Tylopus bokorensis* **sp. nov.** from southern Cambodia, and *T. panhai* **sp. nov.** from southern Laos. These species can be clearly discriminated from congeners by the shape of processes on postfemoral part of the gonopod in combination with some distinct somatic characters. *Tylopus bokorensis* **sp. nov.** is the first in this genus to be found in Cambodia. Both species inhabit montane habitats more than 1,000 m above mean sea level, and we regard them as endemic to these countries. An identification key and distribution map of *Tylopus* occurring in Cambodia and Laos are provided.

KEYWORDS: biodiversity, endemic species, Southeast Asia, Sulciferini

INTRODUCTION

One of the most species-rich millipede genera in the family Paradoxosomatidae is the predominantly Indochinese to southern Chinese genus *Tylopus* Jeekel, 1968. This genus has been reviewed by Jeekel (1965, 1968), Golovatch and Enghoff (1993) and Likhitrakarn et al. (2010, 2016). Previous studies revealed 78 nominal species which are distributed mainly in Southeast Asia (Myanmar, Laos, Thailand and Vietnam), with a few marginal occurrences in southern China (Golovatch, 2013; Liu and Luo, 2013; Golovatch, 2014; Likhitrakarn et al., 2021; Sierwald and Spelda, 2022; Nguyen and Eguchi, 2022).

Most of these species have been found at high elevations (ca. >500 m) dominated by montane forest habitats. Most of them were collected from a single or a few localities, and all were found to exclusively inhabit restricted ranges that are prone to strongly localized endemism. The spectacular phenomenon of endemism that is significantly correlated to the diversity of this genus has been demonstrated by studies in several locations, e.g., the mountains of Doi Inthanon and Doi Suthep in Thailand, with at least 20 species; and northern Laos and Vietnam with six species (Likhitrakarn et al., 2010, 2016; Nguyen and Eguchi, 2022).

In the easternmost part of mainland Southeast Asia, Thailand and Vietnam apparently harbor more species of *Tylopus* than Laos, whereas Cambodia has no records of this genus to date (Likhitrakarn et al., 2015a). Only six species are currently known to occur in Laos, five of which have been encountered in the northern region: *T. acuminatus* Likhitrakarn, Golovatch and Panha, 2016, *T. dorsalis* Likhitrakarn, Golovatch and Panha, 2016, *T. nodulipes* (Attems, 1953), *T. retusus* Likhitrakarn, Golovatch and Panha, 2016, *T. thunghaihin* Likhitrakarn, Golovatch and Panha, 2016. The remaining species, *T. moniliformis* Likhitrakarn, Golovatch and Panha, 2016, is confined to the southern part of Laos (see Table 1).

Revealing the full diversity of *Tylopus* across mainland Southeast Asia still requires further intensive collecting efforts, especially in unexplored places; Cambodia and Laos thus deserve high priority (Clements et al., 2006; Likhitrakarn et al., 2014b; Liu et al., 2017). Recent surveys of millipedes in Cambodia and Laos revealed two undescribed *Tylopus* species. Even without molecular information, they are clearly different from all other species, especially in their gonopod characters. In this work, we describe these two new species of *Tylopus* that were collected in montane forest and are clearly endemic species.

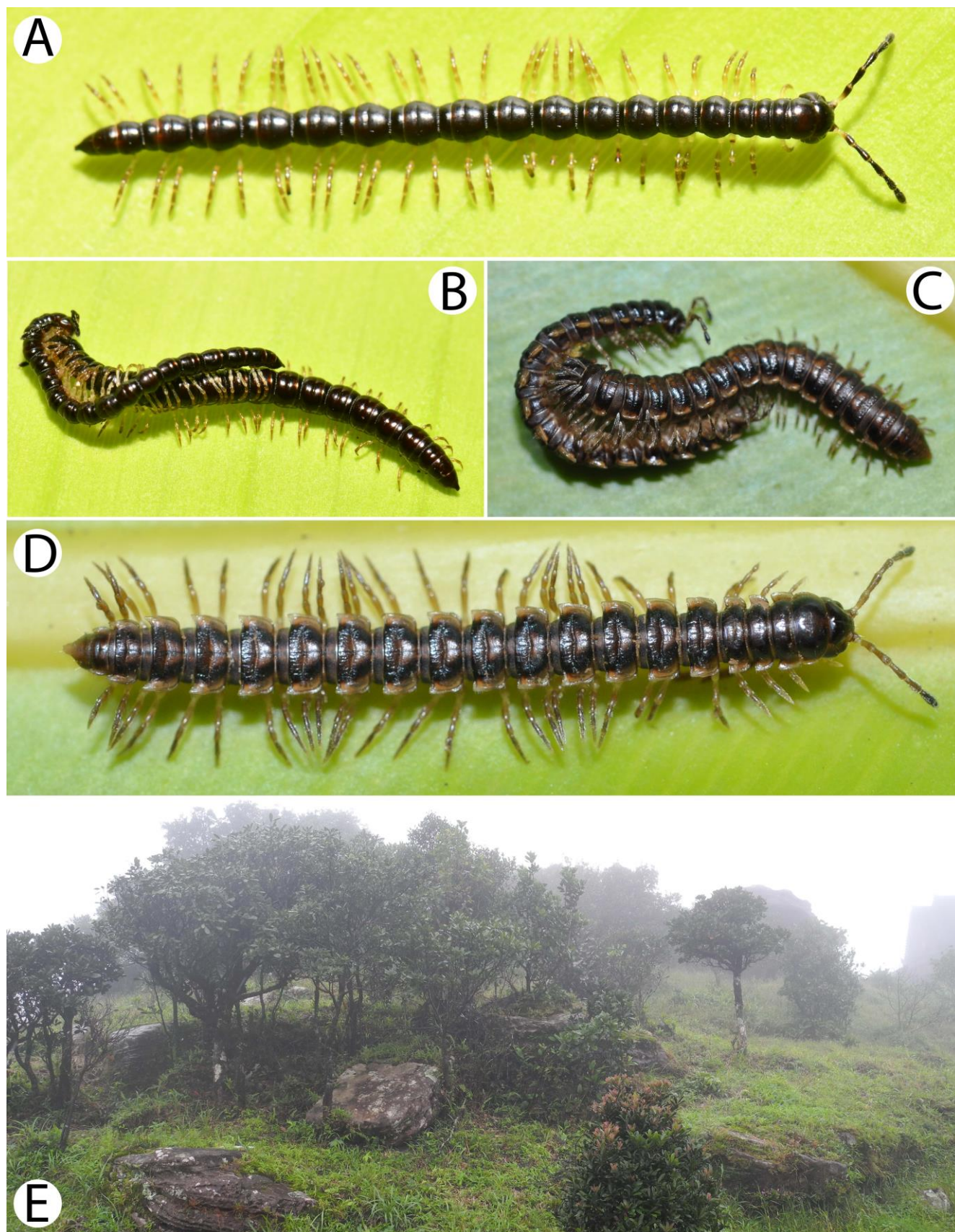


FIGURE 1. Photographs of live specimens and habitat. **A, B.** *Tylopus bokorensis* sp. nov. **C, D.** *Tylopus panhai* sp. nov. **E.** habitat of *Tylopus bokorensis* sp. nov.

MATERIALS AND METHODS

Specimen collection and preservation.— The material was collected during invertebrate biodiversity surveys in Laos (2013–2018) and Cambodia (2017–2019). The collectors were the members of the Department of Biology, Faculty of Science, Chulalongkorn University (ASRU members). A general method for sampling and preserving millipedes was applied based on Means et al. (2015). Specimens were hand-collected and the living ones were photographed. All specimens were euthanized properly based on AVMA guidelines for the euthanasia of animals (American Veterinary Medical Association, 2020), and kept in 70% (v/v) ethanol for morphological study. This work was previously approved by Animal Care and Use committees of Khon Kaen University (IACUC-KKU-136/64) and Chulalongkorn University. Latitude, longitude, and elevation were marked using a Garmin GPSMAP 60 CSx, and all coordinates were verified for accuracy in Google Earth.

The type materials are deposited in Chulalongkorn University Museum of Zoology (CUMZ).

Illustrations.— Living specimens were photographed with a Nikon D700 equipped with a Micro-Nikkor 105 mm lens. Morphological drawings were sketched under stereo microscope and then made by using dot-line skills (stipple). Specimens for scanning electron microscopy (SEM) were dissected under a stereo microscope, mounted on aluminium stubs, coated with gold, and then photographed. Afterwards, the specimens were stored in 70% ethanol. All plates with images were generated and composed in Adobe Photoshop

2021, and the background for the distribution map was downloaded from the Elastic Terrain Map (Willett et al., 2015).

Morphological descriptions.— All specimens kept in alcohol were carefully examined for non-gonopodal and gonopodal characteristics under a stereo microscope. Details of gonopod terms used in the descriptions follow Golovatch and Enghoff (1993) and Likhitrakarn et al. (2010). The number of body segments for the genus *Tylopus* is 20 (collum + 17 podous + one apodous + telson) and the term “ring” is used as short for “body ring” in the descriptions.

Gonopod abbreviations.— ca = cannula, cx = coxa, fe = femur, h = process h, ms = mesal sulcus, l = lobe l, ls = lateral sulcus, m = process m, pfe = prefemoral part, pof = postfemoral part, sg = seminal groove, slm = solenomere, sph = solenophore, z = process z.

Institutional abbreviations

ASRU = Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand

CUMZ = Chulalongkorn University Museum of Zoology, Bangkok, Thailand

IFReDI = Inland Fisheries Research & Development Institute of Cambodia, Phnom Penh, Cambodia

Taxon names.— Descriptions of these two new species are here attributed to the first and last authors, Srisonchai and Likhitrakarn. Therefore, complete citations of the authors are, respectively, Srisonchai and Likhitrakarn in Srisonchai et al.

TABLE 1. Species of *Tylopus* currently known from Cambodia (1) and Laos (7).

Species	Type locality	Distribution	References
<i>T. acuminatus</i> Likhitrakarn, Golovatch and Panha, 2016	LAOS, Phongsaly Province, Boun Neua, Ban Sin Chai	Northern Laos	Likhitrakarn et al. (2016)
<i>T. bokorensis</i> sp. nov.	CAMBODIA, Kampot Province, Preah Monivong Bokor National Park	Southern Cambodia	This study
<i>T. dorsalis</i> Likhitrakarn, Golovatch and Panha, 2016	LAOS, Phongsaly Province, Boun Neua, Phuthalang forest protected area	Northern Laos	Likhitrakarn et al. (2016)
<i>T. moniliformis</i> Likhitrakarn, Golovatch and Panha, 2016	LAOS, Champasak Province, Paksong, Tad Fane Waterfall	Southern Laos	Likhitrakarn et al. (2016)
<i>T. nodulipes</i> (Attems, 1953)	LAOS, Luang Prabang Province (lectotype) VIETNAM, Lao Cai, Fansipan Mountain	Northern Laos, Northern Vietnam	Attems (1953), Enghoff (2004), Likhitrakarn et al. (2014a)
<i>T. panhai</i> sp. nov.	LAOS, Champasak Province, Paksong (Bolaven Plateau), hill with a pine forest patch near Phu Thevada Hotel	Southern Laos	This study
<i>T. retusus</i> Likhitrakarn, Golovatch and Panha, 2016	LAOS, Oudomxay Province, Xay, Muang Xay City	Northern Laos	Likhitrakarn et al. (2016)
<i>T. thungthaihin</i> Likhitrakarn, Golovatch and Panha, 2016	LAOS, Xiangkhouang Province, Plain of Jars	Northern Laos	Likhitrakarn et al. (2016)

RESULTS

Taxonomy

Order Polydesmida Pocock, 1887
Family Paradoxosomatidae Daday, 1889

Genus *Tylopus* Jeekel, 1968

***Tylopus bokorensis* Srisonchai and Likhitrakarn,
 sp. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:AB3D0BAA-0F0A-49D5-95B6-B44E4128DBFB>
 (Figs 1A, B, E; 2; 3; 7)

Material examined.— Holotype: Male (CUMZ-Px0227) CAMBODIA, Kampot Province, Preah Monivong Bokor National Park, 10°37'48" N, 104°01'10"E, ca. 1,150 m a.s.l., coll. R. Srisonchai, C. Sutcharit and IFReDI staff, 17 September 2019. Paratypes: 1 male, 1 female (CUMZ-Px0228), same data as holotype.

Etymology.— The name is an adjective referring to the type locality in southern Cambodia's Kampot Province, Preah Monivong Bokor National Park.

Diagnosis.— Paraterga of midbody ring poorly developed or not evident. It is similar in this respect to *T. hongkhraiensis* Likhitrakarn et al., 2016 and *T. moniliformis* Likhitrakarn et al., 2016. The new species differs from *T. hongkhraiensis* by having a dark body color; postfemoral part of gonopod without processes h and z; and tip of solenophore without small spines. It differs from *T. moniliformis* by having inconspicuous setae on metaterga; axial line absent; lobe 1 of postfemoral part smaller; and solenophore shorter, distally not suberect.

Description

Size (Fig. 1A, B). Length 15–17 mm (male), 17 mm (female); width of midbody metazona ca. 0.7 mm (male), ca. 1.1 mm (female). Width of rings 2 = 3 = 4 < collum < 5–17 < head (male), rings 2 = 3 = 4 = collum < head < 5–17 (female), thereafter body gradually tapering towards telson. Body moniliform.

Color (Fig. 1A, B). Specimens in life black or brownish black; head, antenna (except whitish basal part of antennomere 2 and distal parts of antennomeres 7+8), collum, prozona, metazona, paraterga and telson dark; surface below paraterga brown; sterna and legs pale brown; a few basal podomeres pale brown to whitish brown. Coloration faded to pale brown after two years of storage in alcohol.

Antennae (Figs 1A; 2D, G). Quite long, reaching backward to ring 3–4 in male and 3 in female when stretched dorsally; antennomeres 5–7 with short sensilla near distal part.

Collum (Fig. 2A, D). Quite round, with 5+5 conspicuous setae in anterior row, 1+1 inconspicuous setae in intermediate row. Paraterga poorly developed.

Tegument. Smooth and shining. Collum, metaterga (delicately rugulose near suture on metaterga), paraterga, surface below paraterga and telson smooth; prozona finely shagreened.

Metaterga (Fig. 2A–F). Metaterga 2–4 with 2?+2? inconspicuous setae in anterior row. Metaterga 5–19 without setae. Suture between prozona and metazona deep and wide, conspicuously striolate, ribbed at bottom down to the base of paraterga. Axial line inconspicuous. Suture on metaterga conspicuous on rings 5–18, not reaching to base of paraterga, shallow and wide. Limbus without conspicuous lobe (examined on the dorsal side of midbody rings).

Paraterga (Fig. 2A–F). Conspicuous, round, simple ridges on rings 2–4; following rings presenting inconspicuous small bulges. Ozopore conspicuous, oval in shape, located at about half of midbody height.

Pleurosternal keel (Fig. 2D). Conspicuous, simple ridges on rings 2–4; thereafter missing.

Telson (Fig. 2C, F, K). Preanal ring with a long conical epiproct; lateral setiferous tubercles poorly differentiated, inconspicuous; apical tubercles not prominent; tip subtruncate; spinnerets arranged at the corners of a square, not in a depression. Anal valves (= paraprocts) simple, with margin emerged as narrow lips. Subanal scale (= hypoproct) subtriangular, with inconspicuous setiferous tubercles at distal margin.

Sterna (Fig. 2I). Sparsely setose. Sternal lobes between male coxae 3 and 4 long, rectangular when seen in ventral view.

Legs (Fig. 2J). Relatively long, ca. 2–3 times as long as body diameter, without modification or tubercle; tarsal brushes absent.

Gonopods (Fig. 3). Telopodite slightly curved, simple. Coxa (cx) quite long, as long as femur, laterally without microgranulation. Cannula (ca) long and slender. Prefemoral part (pfe) as long as femur. Femur (fe) quite stout and curved. Mesal sulcus (ms) conspicuous, deep and wide; lateral sulcus (ls) inconspicuous. Seminal groove (sg) running entirely on mesal surface. Postfemoral part (pof) quite short, demarcated by mesal sulcus, without any processes; lobe 1 (l) small, not clearly demarcated from femur, but clearly seen in lateral view. Solenophore (sph) very large, coiled; distal part expanded. Solenomere (slm) sheathed by solenophore and slightly longer than solenophore.

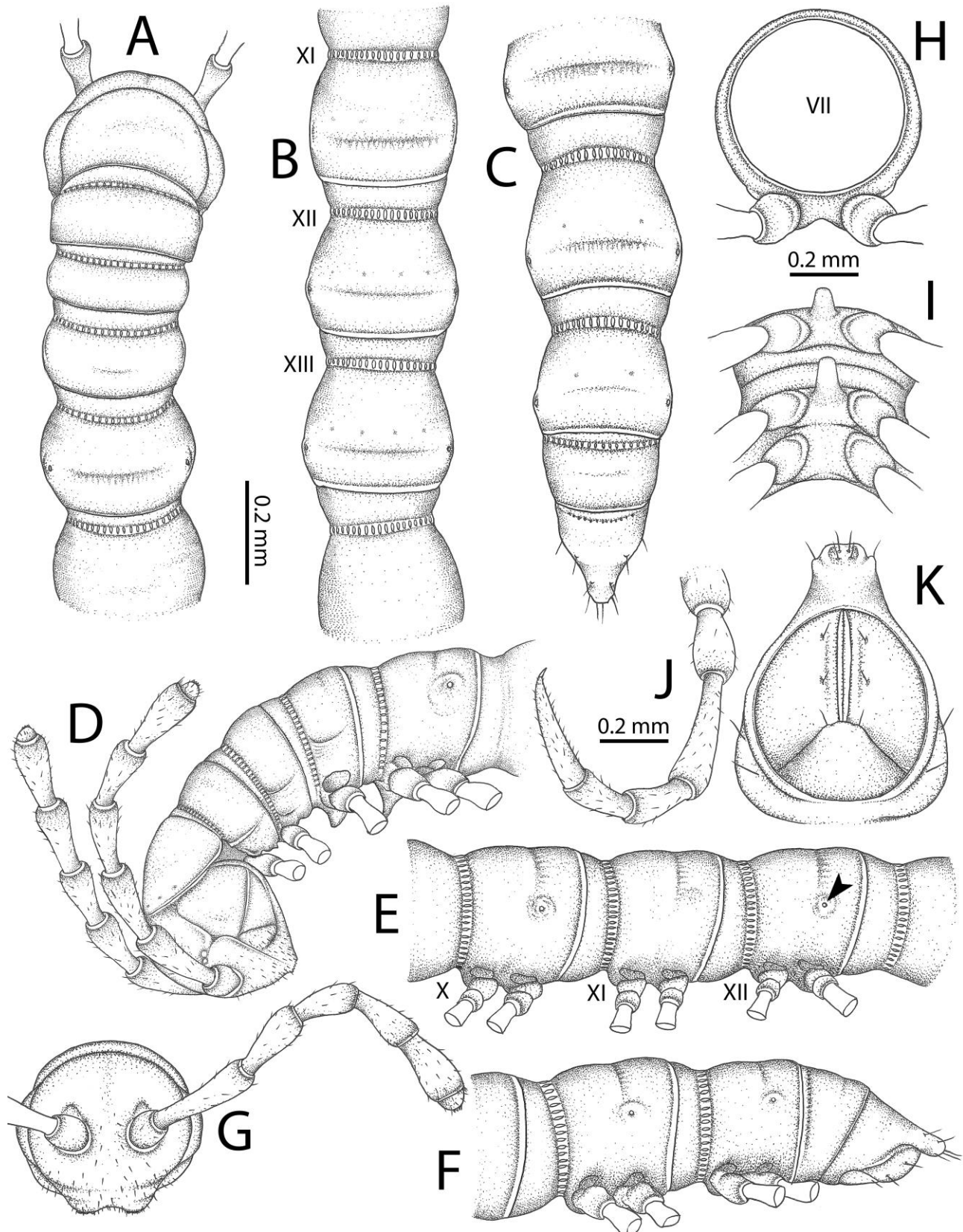


FIGURE 2. *Tylopus bokorensis* sp. nov., male paratype (CUMZ-Px0228). **A–C.** dorsal view. **D–F.** lateral view. **A.** anterior body rings. **B.** body rings 11–13. **C.** posteriormost body rings and telson. **D.** anterior body rings. **E.** body rings 10–12 (arrowhead points to ozopore). **F.** posteriormost body rings and telson. **G.** head and antenna, anterior view. **H.** body ring 7. **I.** sternal lobes between male coxae 3 and 4. **J.** right leg of ring 10. **K.** last ring, ventral view. Scale bar of **A–G** = 0.2 mm, Scale bar of **H, I, K** = 0.2 mm, Scale bar of **J** = 0.2 mm.

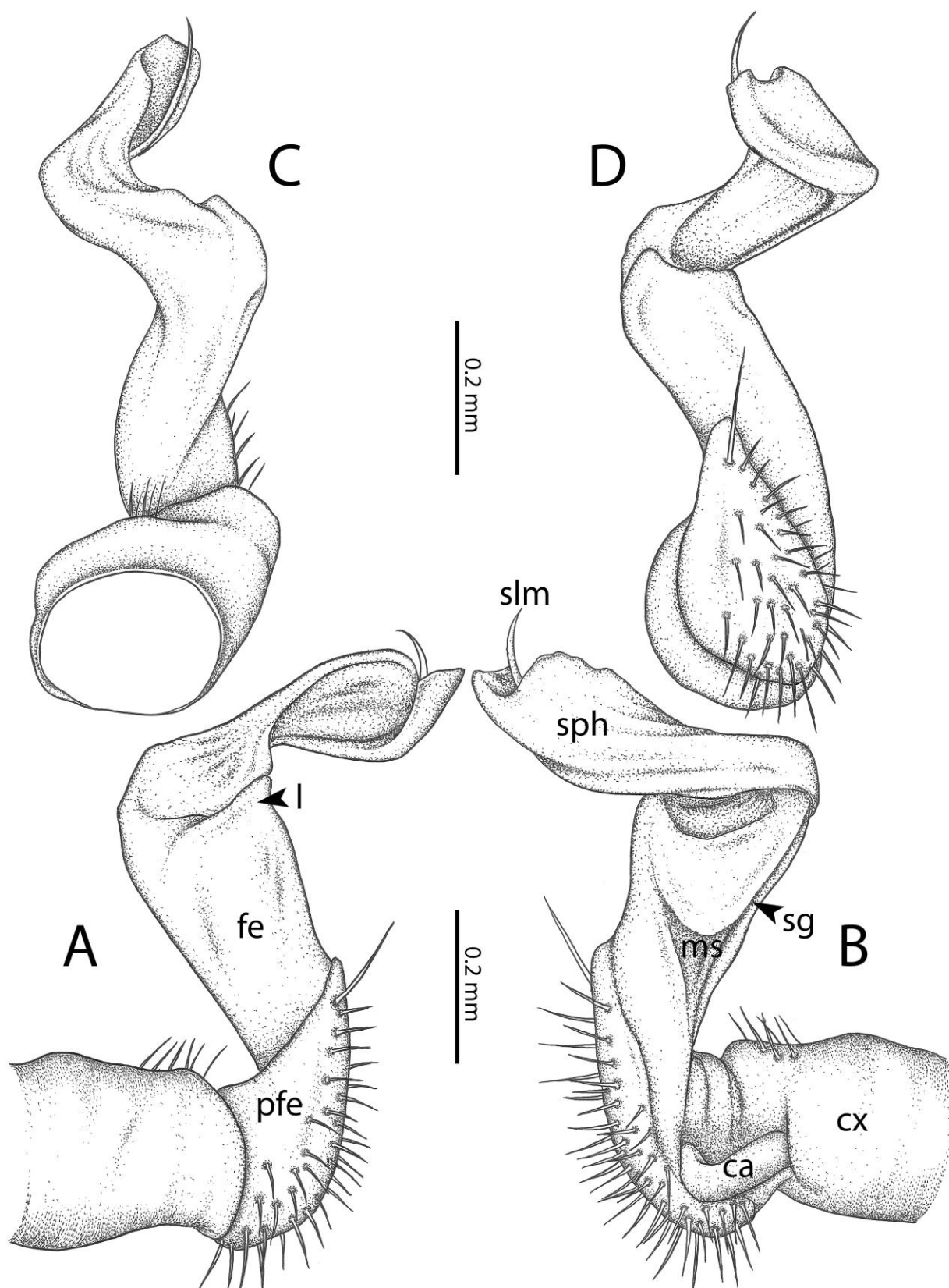


FIGURE 3. *Tylopus bokorensis* sp. nov., right gonopod of male holotype (CUMZ-Px0227). **A.** lateral view. **B.** mesal view. **C.** ventral view. **D.** dorsal view. Abbreviations: cx = coxa, ca = cannula, fe = femur, l = lobe 1, ms = mesal sulcus, pfe = prefemoral part, pof = postfemoral part, sg = seminal groove, slm = solenomere, sph = solenophore.

Distribution and habitat (Figs 1E, 7).— Individuals of *T. bokorensis* sp. nov. were collected from montane evergreen forest habitat predominately composed of Dipterocarpaceae and Fagaceae, and they occurred in syntopy with a member of the micropolydesmoid millipede family Cryptodesmidae, namely *Circulocryptus kompantsevi* Golovatch, 2018. This new species is currently known only from the type locality (Bokor plateau) and we regard *T. bokorensis* sp. nov. as endemic to Cambodia.

Remarks.— Based on somatic characters and external appearance alone, the new species can easily be distinguished from the other 77 congeneric species by its undifferentiated paraterga. Only two species of *Tylopus* have poorly developed paraterga (*T. hongkraiensis* and *T. moniliformis*). In addition, the shape of the postfemoral part of the gonopod is very similar to *T. moniliformis*. No known variation among species has been found.

***Tylopus panhai* Srisonchai and Likhitrakarn,
sp. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:1751CC51-2DD3-43F5-A8E2-4657D407AAEA>
(Figs 1C, D; 4; 5; 6; 7)

Material examined.— Holotype: Male (CUMZ-Px0229), LAOS, Champasak Province, Paksong (Bola-ven Plateau), hill with a patch of pine forest near Phu Thevada Hotel, 15°10'50"N, 106°14'25"E, ca. 1,300 m a.s.l., coll. K. Inkhavilay and ASRU members, 24 February 2017. Paratypes: 7 males, 5 females (CUMZ-Px0230), same data as holotype.

Etymology.— This species is named after Somsak Panha (Chulalongkorn University Museum of Zoology, Thailand), the author of several important papers on myriapods and a long-time mentor to the authors. He has enormously encouraged us and provided his tireless efforts to advance our understanding of myriapod diversity in Thailand and elsewhere in Southeast Asia. The specific name is a genitive noun derived as a patronym.

Diagnosis.— Postfemoral part of gonopod with a very long process (process m). It is similar in this respect to *T. extremus* Likhitrakarn et al., 2010, *T. nodulipes* (Attems, 1953) and *T. perplexus* Golovatch and Eng-hoff, 1993. It differs from these species by a gonopod telopodite that is more slender (slightly longer); process h of postfemoral part coiled, spear-shaped; process z inconspicuous, swollen as a very small lobe; and solenophore more slender.

Description

Size (Fig. 1C, D). Length 24–28 mm (male), 30–33 mm (female); width of midbody metazona ca. 1.3 mm (male), ca. 1.6 mm (female). Width of head < collum < 2 = 3 = 4 < 5–17 (male), head < collum = 2 = 3 = 4 < 5–17 (female), thereafter body gradually tapering towards telson.

Color (Fig. 1C, D). Specimens in life brown or dark brown; head, collum, prozona, surface below paraterga and metazona dark brown (except pale brown middle part of metazona); paraterga brown or yellowish brown; antennae (except whitish distal part of antennomeres 7 and 8), sterna and legs brown; a few basal podomeres pale brown. Coloration faded to pale brown after two years of storage in alcohol.

Antennae (Figs 1D; 5A, B). Quite short, with long setation; reaching backward to ring 3 when stretched dorsally; antennomeres 5–7 with short sensilla near distal part.

Collum (Figs 4A, D; 5A). With 3+3 conspicuous setae in anterior row (inconspicuous in some specimens), 1?+1? inconspicuous setae in intermediate row. Paraterga quite short in both male and female; lateral margin thin, without incision; tip round, directed caudad.

Tegument (Fig. 5E–H). Quite shining. Collum and telson smooth. Prozona finely shagreened. Metaterga smooth and rugulose. Paraterga quite smooth, lateral margin rugulose. Surface below paraterga microgranulate. Limbus (examined on the dorsal side of mid-body rings) without conspicuous lobe, posterior edge tassel-like (with tassel fringe).

Metaterga (Fig. 4A–H). Metaterga 2–19 without setae. Suture between prozona and metazona deep and wide, conspicuously striolate, ribbed at bottom down to the base of paraterga. Axial line visible, conspicuous. Suture on metaterga conspicuous on rings 4–19, reaching to base of paraterga, deep and wide, ribbed.

Paraterga (Fig. 4A–H). Well-developed, especially in male, elevated at ca. 5°–10°; anterior margin round and narrow; lateral margin with two conspicuous incisions on poreless rings, with one incision on pore-bearing rings; posterior margin quite round, directed caudolaterad. Ozopore conspicuous, oval in shape, located at middle part of lateral margin.

Pleurosternal keel (Figs 4D, E; 5C). Conspicuous, well-developed as long ridges on rings 2–6; small ridge on rings 7–11; thereafter simple and not prominent, decreasing in size backward.

Telson (Figs 4C, F, I–K; 5J). Preanal ring with a long triangular epiproct; lateral setiferous tubercles poorly differentiated, inconspicuous; apical tubercles prominent; tip concave; spinnerets arranged at the corners of a square, in a depression, anterior pair close

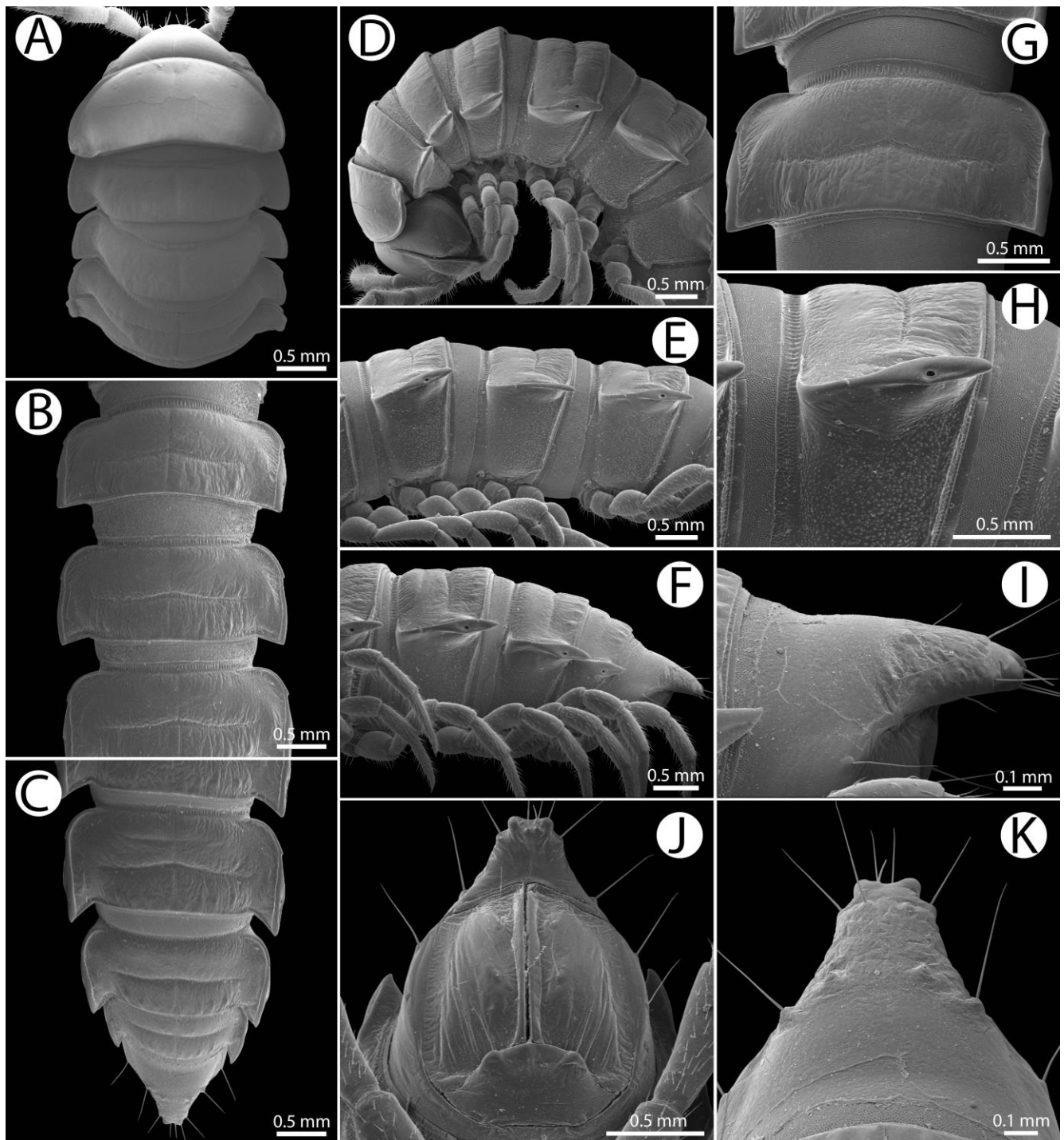


FIGURE 4. *Tylopus panhai* sp. nov., male paratype (CUMZ-Px0230). **A–C.** dorsal view. **D–F.** lateral view. **A, D.** anterior body part. **B, E.** body rings 8–10. **C, F.** posteriormost body rings and telson. **G, H.** body ring 10 in dorsal and lateral views. **I–K.** telson in lateral, ventral and dorsal views, respectively.

to apical tubercles. Anal valves (paraprocts) simple, with margin emerged as narrow lips. Subanal scale (hypoproct) semicircular, with conspicuous setiferous tubercles at distal margin.

Sterna (Fig. 5I). Sparsely setose. Sternal lobe between male coxae 4 large, linguliform, located between anterior legs (pair 4), covered by long setae;

with two small setiferous pits located between posterior legs (pair 5).

Legs (Fig. 5K, L). Relatively long, ca. 2 times as long as body diameter. Male legs in rings 7–18 with a few tubercles (noduli) on ventral side and with dense setae ventrally on tarsus; rings 7 and 8 (legs 7–8) with conspicuous tubercles mostly on tibia and tarsus; rings 9–10 with tubercles mostly on femur, postfemur, tibia

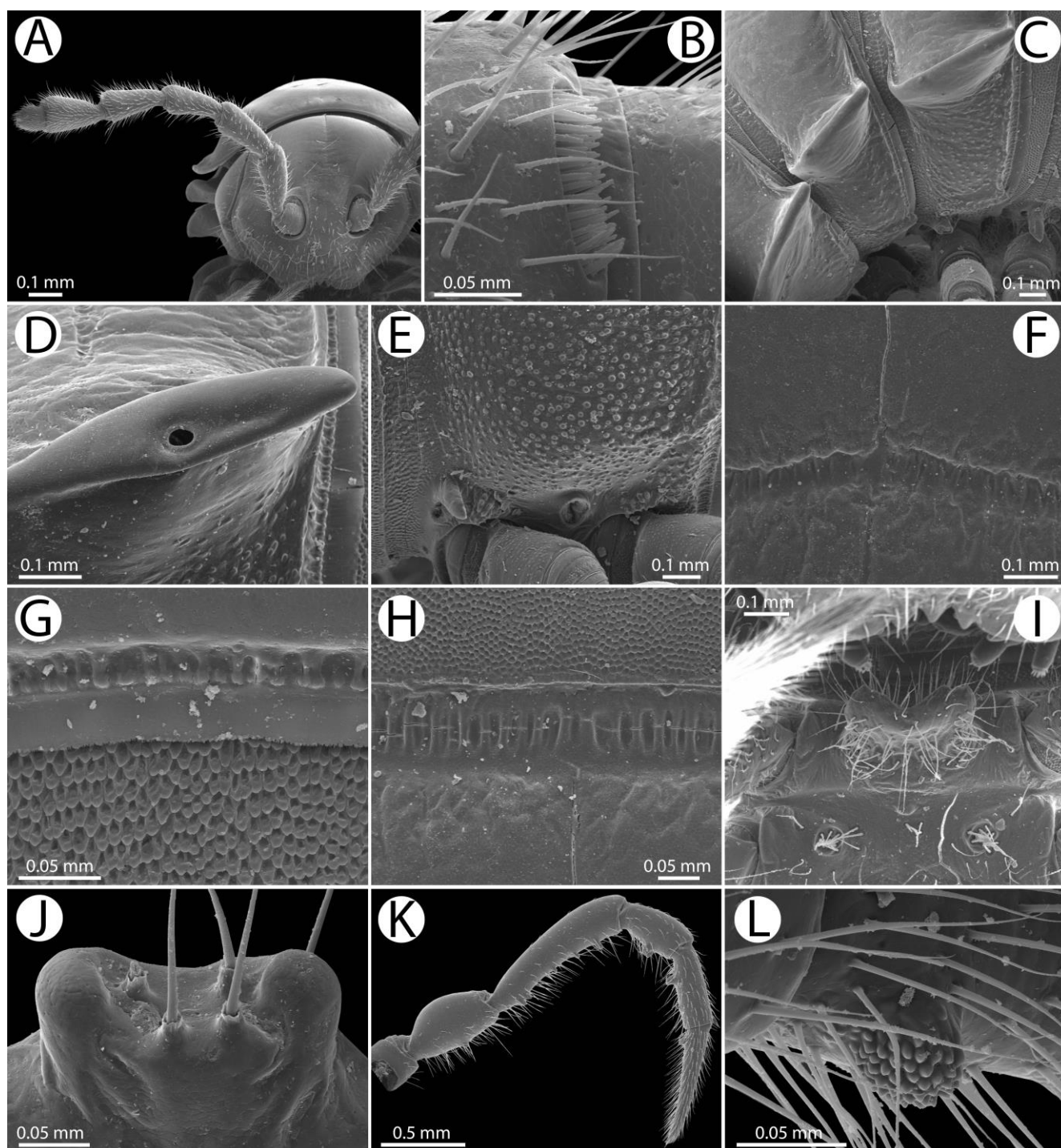


FIGURE 5. *Tylopus panhai* sp. nov., male paratype (CUMZ-Px0230). **A.** head and antenna. **B.** antennal sensilla on antennomere 6. **C.** pleurosternal keels on rings 2–4. **D.** ozopore. **E.** surface below paraterga of midbody ring. **F.** transverse sulcus on midbody ring. **G.** limbus of midbody ring. **H.** suture between prozona and metazona of midbody ring. **I.** sternal lobe on male coxae 4. **J.** tip of epiproct. **K.** male right leg of ring 10. **L.** tubercles on male right leg of ring 10.

and tarsus; rings 11–16 with tubercles mostly on prefemur, femur, postfemur, tibia and tarsus; rings 17–18 with tubercles mostly on femur, postfemur and tibia; absent in ring 19. Tarsal brushes absent.

Gonopods (Fig. 6). Telopodite suberect. Coxa (cx) quite long, longer than femur, laterally microgranulate. Cannula (ca) long and slender. Prefemoral part (pfe) as

long as femur. Femur (fe) straight. Mesal sulcus (ms) deep and wide; lateral sulcus (ls) deep and narrow. Seminal groove (sg) running entirely on mesal surface. Postfemoral part (pof) quite short, demarcated by mesal and lateral sulci; under lobe 1 with long ridge; distal region of postfemoral part with a short process (arrow in Fig. 6F); lobe 1 (l) large and broad,

demarcated from postfemoral ridge, clearly seen in lateral view; process m (m) very long and slender, slightly curved, pointed, tip directed almost ventrad; process h (h) very long, strongly twisted, spear-like, tip directed dorsoanteriad and close to laminate tip of solenophore; process z (z) inconspicuously swollen. Solenophore (sph) very large, strongly coiled, twisted around process h; distal part expanded, flat, laminate-like tip. Solenomere (slm) protected by solenophore and slightly shorter than solenophore.

Distribution and habitat (Fig. 7).— Some individuals of the new species have been collected from leaf litter, while others were found walking on tree branches. Surveys of other sites near the type locality (Bolaven plateau) over a period of approximately two years revealed no further specimens, and *T. panhai* new species is currently known only from the type locality. We therefore consider this species as endemic to the fauna of Laos.

It is important to note that habitat in the type locality is currently being altered or possibly destroyed by local people. Perhaps habitat destruction disproportionately threatens this species, as it has an apparently narrow distribution.

Remarks.— The distinct character used to discriminate this species from the other 76 congeners is the presence of a long process m on the postfemoral part of the gonopod. This process can be clearly seen (in mesal view) in four species, including the new one, *T. extremus*, *T. nodulipes* (in Attems, 1953: 174, fig. 73 = process h) and *T. perplexus*. This process, however, differs in size and direction among these species (see also Attems, 1953: fig. 73; Golovatch and Enghoff, 1993: 106, fig. 70; Likhitrakarn et al., 2014a: 78, fig. 9). Notable variations found in the new species are the number of tubercles in male legs (Fig. 5K, L), e.g., legs of ring 11 in some specimens display 8–10 tubercles, while the others have 5–7 tubercles; and the shape of the apical papillae on the epiproct, which are inconspicuous in some specimens but prominent in the others.

Key to species of *Tylopus* known to occur in Cambodia and Laos (based on males)

1. Body moniliform. Paraterga present only on rings 2–4, thereafter missing 2
- Body not moniliform. Paraterga well-developed on most rings 3
2. Metaterga with conspicuous setae (traceable at least as insertion points). Axial line visible. Gonopod:

- lobe 1 of postfemoral part conspicuous and larger; solenophore longer, distally suberect. Laos
..... *T. moniliformis* Likhitrakarn et al., 2016
- Metaterga with inconspicuous setae. Axial line missing. Gonopod: lobe 1 of postfemoral part smaller; solenophore shorter, distally not suberect (Fig. 3). Cambodia *T. bokorensis* sp. nov.
3. Metaterga roughly microgranulate, conspicuous
..... *T. thungaihin* Likhitrakarn et al., 2016
- Metaterga not microgranulate, dull 4
4. Gonopod: process m conspicuous, long 5
- Gonopod: process m inconspicuous or absent 6
5. Between male coxae 3 and 4 with sternal lobes, linguiform, long and slender (Fig. 5I)
..... *T. panhai* sp. nov.
- Between male coxae 4 with a sternal lobe, linguiform, rectangular shape
..... *T. nodulipes* (Attems, 1953)
6. Gonopod: process z conspicuous, short 7
- Gonopod: process z inconspicuous or absent
..... *T. retusus* Likhitrakarn et al., 2016
7. Tarsal brushes absent in all legs. Gonopod: solenophore without process; process h with a small tooth or denticle
..... *T. acuminatus* Likhitrakarn et al., 2016
- Tarsal brushes present on legs of rings 2–6. Gonopod: solenophore with process (= process x); process h without tooth
..... *T. dorsalis* Likhitrakarn et al., 2016

DISCUSSION

The vast majority of *Tylopus* species are characterized by the presence or absence of processes/lobes on the postfemoral region of the gonopod (Golovatch and Enghoff, 1993; Likhitrakarn et al., 2010). Together with lobe 1, the process h (an outgrowth, located at the base of the solenophore near lobe 1) has long been used to classify almost all members into the genus *Tylopus*. Only three out of 77 constituent species are likely to have lost this process: *T. bokorensis* sp. nov., *T. moniliformis* and *T. stronglylosomoides* Korsós and Golovatch, 1989. Another morphological character, the presence of a remarkable outgrowth (process m), can also be seen in many species, viz., *T. ciriaceus* Golovatch and Enghoff, 1993, *T. extremus*, *T. nodulipes*, *T. panhai* sp. nov., *T. purplexus*, *T. subcoriaceus* Golovatch and Enghoff, 1993 and *T. tamdaoensis* Korsós and Golovatch, 1989. However, the form of

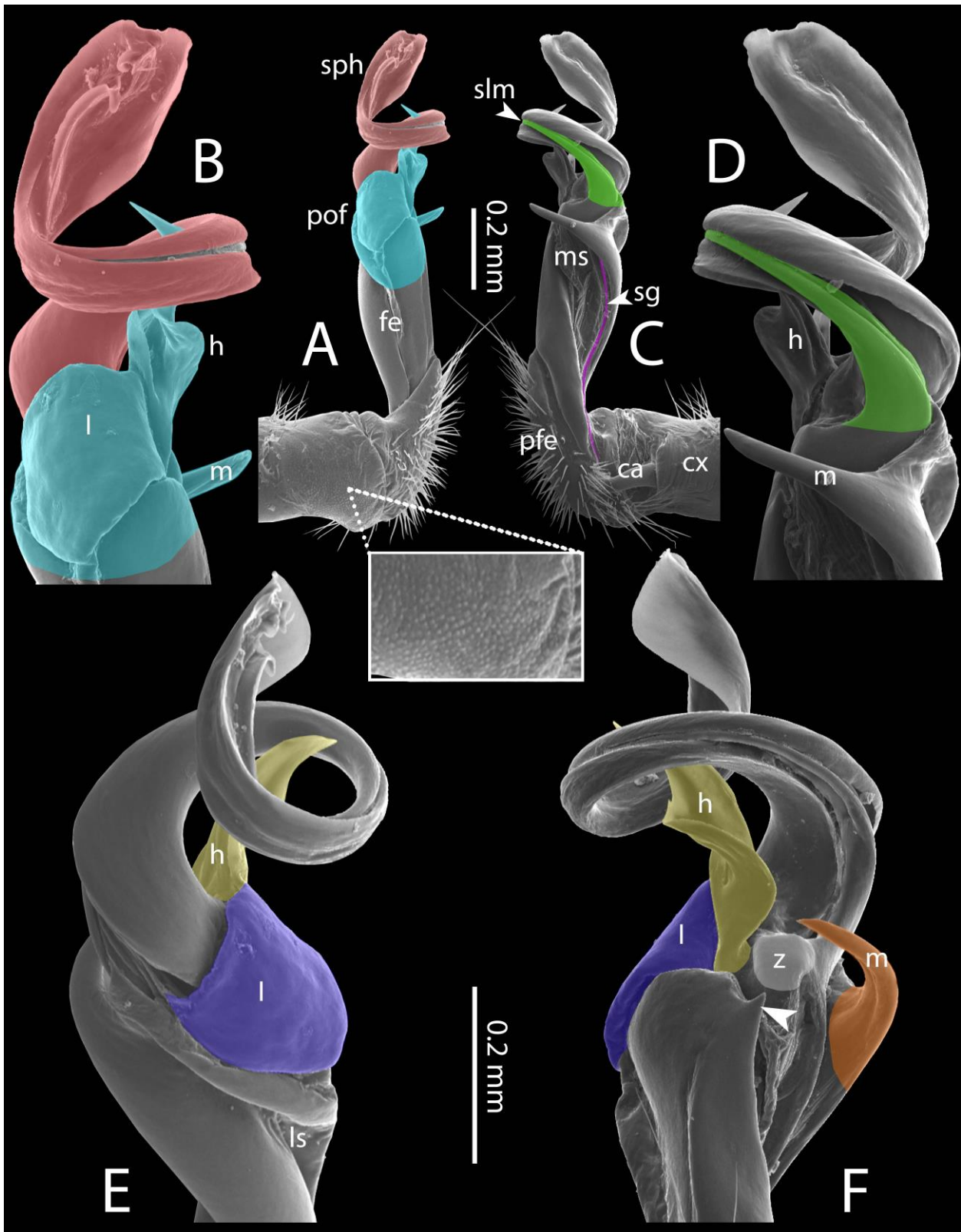


FIGURE 6. *Tylopus panhai* sp. nov., right gonopod of male paratype (CUMZ-Px0230). **A, B.** lateral view (close-up = microgranulation on coxa). **C, D.** mesal view. **E.** dorsal view. **F.** ventral view (arrowhead points to a short process on postfemoral part). Colors: sky blue = postfemoral part (pof), purple = seminal groove (sg), green = solenomere (slm), red = solenophore (sph), lapis blue = lobe I (l), yellow = process h (h), orange = process m (m), white = process z (z). Abbreviations: cx = coxa, ca = cannula, fe = femur, h = process h, l = lobe I, ls = lateral sulcus, m = process m, ms = mesal sulcus, pfe = prefemoral part, pof = postfemoral part, sg = seminal groove, slm = solenomere, sph = solenophore, z = process z. Scale bar **A, C** = 0.2 mm. Scale bar **B, D, E, F** = 0.2 mm.

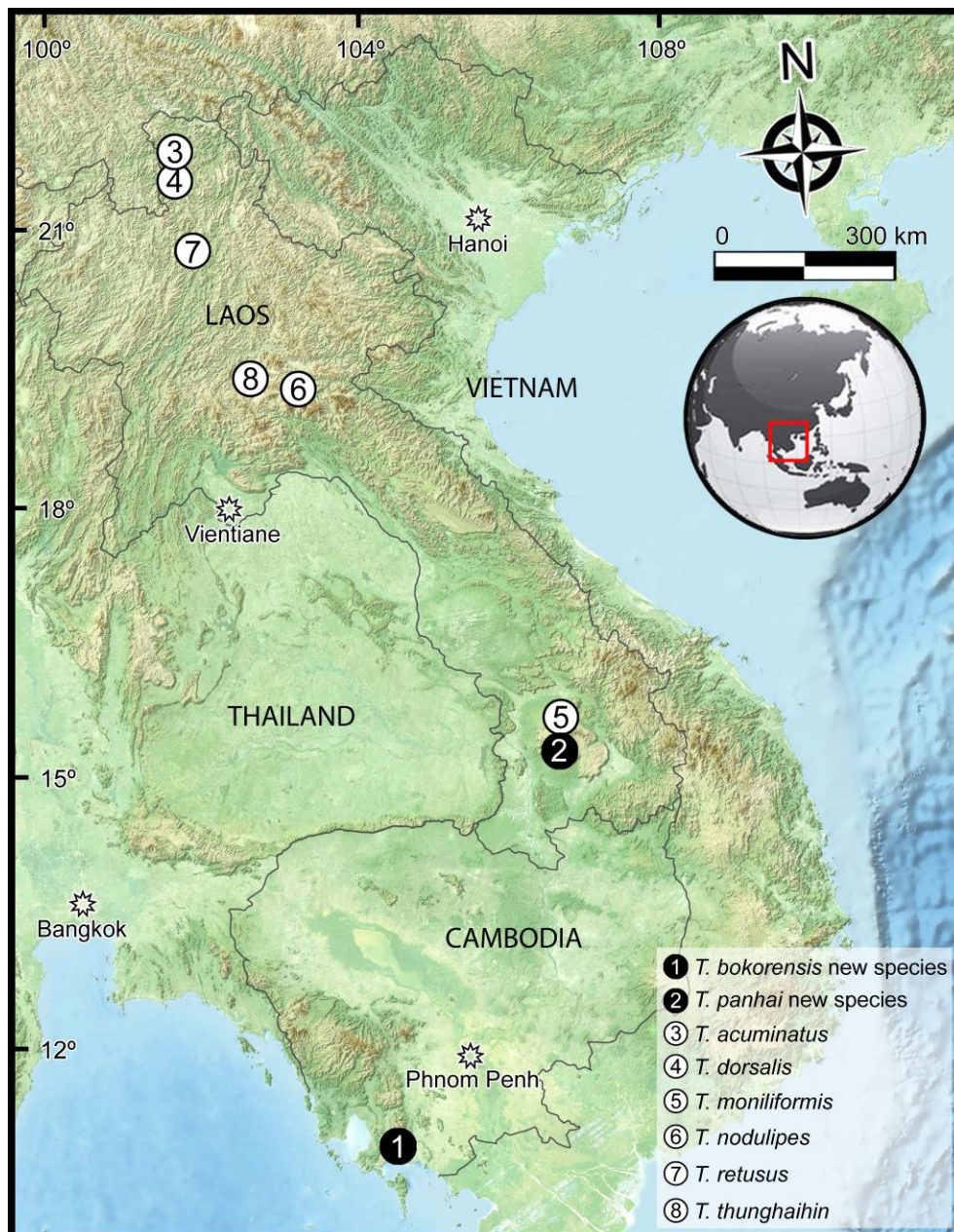


FIGURE 7. Known distributions of *Tylopus* species in Cambodia and Laos (see location detail of the former species in Table and Likhitrakarn et al., 2016). Number represents species: 1 = *T. bokorensis* sp. nov., 2 = *T. panhai* sp. nov., 3 = *T. acuminatus*, 4 = *T. dorsalis*, 5 = *T. moniliformis*, 6 = *T. nodulipes*, 7 = *T. retusus*, 8 = *T. thunghaihin*.

process m may vary in several respects, providing useful taxonomic characters. Further morphological and molecular investigations could reveal the relationships of species with or without processes (possibly monophyletic) and provide more insight into the interrelationships among species of *Tylopus*.

Two new species described herein were collected from montane forest habitats at >1000 m AMSL in the Bolaven and Bokor plateaus. Based on the available knowledge of *Tylopus*, most of its species are quite rare and have been found from a single locality or only a few sites (Golovatch and Enghoff, 1993; Likhitrakarn

et al., 2010, 2014a, 2016). Both new species seem to be restricted to small areas and exclusively confined to montane forests. Due to the very restricted ranges of distribution and low dispersal rates, we here regard the two new species as endemic to Cambodia and Laos, respectively. This pattern of endemism also appears in some paradoxosomatids such as the dragon millipede, *Hylomus rhinoceros* (Likhitrakarn et al., 2015) in Bolaven, Laos and the micropolydesmoid millipede, *Circulocryptus kompantsevi* Golovatch, 2018 in Bokor, Cambodia (Likhitrakarn et al., 2015b; Golovatch, 2018). It is possible that endemism in such high

elevations could be affected by the environmental factors (e.g., temperature; McCain and Grytnes, 2010). Likewise, habitat-specific characteristics (microhabitats) may also play an important role in determining distribution and abundance of *Tylopus* species (Moirm et al., 2009; Bogyó et al., 2015).

The number of described *Tylopus* species occurring mostly or exclusively in high-elevation habitats now reaches 80. Regarding *Tylopus* species in Cambodia, *T. bokorensis* sp. nov. represents the first member of the genus to be recorded in the country. Known diversity of the genus is higher in Laos, where seven species have now been reported, including *T. panhai* sp. nov. described in this study; see also the Table 1 (Attems, 1953; Likhitrakarn et al., 2016). Given the species richness of Thailand, which hosts 31 known species, it is very likely that several additional *Tylopus* species await discovery, especially in Cambodia and Laos. The diverse habitat throughout Cambodia and Laos makes it challenging to do fieldwork, and many of the mountain ranges are incredibly remote or otherwise difficult to access (due to a lack of roads) (ICEM, 2003; Gray et al., 2013). The findings from this study and from other recent paradoxosomatid surveys in the same geographic areas (e.g., *Orthophorha*, *Desmoxytes*) also pointed in the same direction on their diversity and encourage more investigation of millipede diversity in these countries (Likhitrakarn et al., 2011; Srisonchai et al., 2018).

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